SYSTEMATICS AND PHYLOGENY

Phylogenetic lineages and the role of hybridization as driving force of evolution in grass supertribe Poodae

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Abstract To investigate the evolutionary diversification and morphological evolution of grass supertribe Poodae (subfam. Pooideae, Poaceae) we conducted a comprehensive molecular phylogenetic analysis including representatives from most of its accepted genera. We focused on generating a DNA sequence dataset of plastid *matK* gene–3′*trnK* exon and *trnL-trnF* regions and nuclear ribosomal (nr) ITS1–5.8S gene–ITS2 and ETS that was taxonomically overlapping as completely as possible (altogether 257 species). The idea was to infer whether phylogenetic trees or certain clades based on plastid and nrDNA data correspond with each other or discord, revealing signatures of past hybridization. The datasets were analysed separately, in combination, by excluding taxa with discordant placements in the individual gene trees and with duplication of these taxa in a way that each duplicate has only one data partition (plastid or nrDNA). We used maximum likelihood, maximum parsimony and Bayesian approaches. Instances of severe conflicts between the phylogenetic trees derived from both datasets, some of which have been noted earlier, point to hybrid origin of several lineages such as the ABCV clade encompassing several subtribes and subordinate clades, subtribes Airinae, Anthoxanthinae, Antinoriinae, subtr. nov., Aristaveninae, Avenulinae, subtr. nov., Helictochloinae, subtr. nov., Holcinae, Phalaridinae, Scolochloinae, Sesleriinae, Torreyochloinae and genera *Arctopoa*, *Castellia*, *Graphephorum*, *Hyalopodium*, *Lagurus*, *Macrobriza*, *Puccinellia* plus *Sclerochloa*, *Sesleria*, *Tricholemma*, *Tzveleviochloa*, etc. ‘*Calamagrostis*’ *flavens* appears to be an intergeneric hybrid between *Agrostis* and *Calamagrostis*. Analyses excluding all lineages with demonstrably cytonuclear discordance revealed three supported main clades within Poodae that were present in both the plastid and nrDNA trees. They fully corresponded in their delineation but were phylogenetically differently arranged, pointing to hybrid origin of one of them. We propose to consider these main clades in classification as separate tribes Aveneae, Poeae s.str. and Festuceae with a phylogenetic arrangement of Aveneae(Poeae,Festuceae) in plastid versus Festuceae (Aveneae,Poeae) in nrDNA trees. Phylogenetic incongruence of the plastid and nuclear markers extends across all hierarchical taxonomic levels of Poodae, ranging from species (not studied here) to genera, subtribes and tribes, therefore the deepest taxonomic levels, emphasizing the enormous significance of reticulate evolution in this large group of grasses. A partly revised classification is presented, including the introduction of a new tribe Festuceae and a re-instatement of tribe Aveneae. Following a comparatively narrow delineation of preferably monophyletic subtribes, Antinoriinae, Avenulinae, Brizochloinae, Helictochloinae and Hypseochloinae are described as new. New genera are *Arctohyalopoa* and *Hyalopodium*. New combinations are *Anthoxanthum glabrum* subsp. *sibiricum*, *A. nitens* subsp. *kolymense*, *Arctohyalopoa ivanovae*, *A. jurtzevii*, *A. lanatiflora*, *A. momica*, *Colpodium biebersteinianum*, *C. kochii*, *C. pisidicum*, *C. trichopodum*, *C. verticillatum*, *Dupontia fulva*, *Festuca masafuerana*, *F. robinsoniana*, *Graphephorum canescens*, *G. cernuum*, *Hyalopodium araraticum*, *Paracolpodium baltistanicum*, *Parapholis cylindrica*, *P.* ×*pauneroi*. *Festuca dolichathera* and *F. masatierrae* are new names.

Keywords Antinoriinae; *Arctohyalopoa*; Aveneae; Avenulinae; Brizochloinae; classification; cytonuclear discordance; deep incongruence; Festuceae; Helictochloinae; *Hyalopodium*; Hypseochloinae; phylogeny; Poeae; reticulation; taxonomy

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

The grass supertribe Poodae with Poeae sensu lato (s.l.) as the sole tribe (i.e., including Aveneae) encompasses 106–121 genera, depending on the respective width of their delineation, and 2562–2578 species (Kellogg, 2015; Soreng & al., 2017). It is a characteristic group of C_3 grasses proliferating in the northern temperate and boreal regions and represented by

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many annuals especially in the Mediterranean/Near East, a region that was also the cradle of *Avena* L. with cultivated oat(s). Economically enormously significant are also the pasture and forage grasses. Poodae are scarce in the subtropics and tropics but bridge them on the top of high mountains and have a second centre of diversity in the temperate and cool zones of the Southern Hemisphere. Concepts of relationship in this group of grasses based on morphological characters, especially of the highly varied spikelet, floret and flower structures (see Figs. 1–3 for lemma and awn shapes in exemplary species), were summarized in *Genera graminum* (Clayton & Renvoize, 1986), which served as an important basis for later molecular phylogenetic studies. Since then, due to the sheer size of the group, usually representative genera were selected for comparative studies to gain an overview on the whole Poodae and their major groupings using morphological data, plastid DNA restriction site analysis, traditional Sanger and, more recently, plastid genome sequencing (Soreng & Davis, 2000; Davis & Soreng, 2007; Döring & al., 2007; Quintanar & al., 2007; Soreng & al., 2007; Schneider & al., 2009; Saarela & al., 2015, 2018; Pimentel & al., 2017; Orton & al., 2019). Other studies focused on special groups using an in-depth sampling of taxa, for example, within traditional Aveneae (Grebenstein & al., 1998; Döring, 2009; Saarela & al., 2010, 2017; Wölk & Röser, 2014, 2017; Barberá & al., 2019) and Poeae (Schneider & al., 2012; Birch & al., 2014, 2017), in which especially the subtribes Poinae (Hunter & al., 2004; Gillespie & Soreng, 2005; Gillespie & al., 2007, 2008, 2009, 2010, 2018; Refulio-Rodríguez & al., 2012; Hoffmann & al., 2013; Soreng & al., 2010, 2015a; Nosov & al., 2015, 2019), Loliinae (Torrecilla & Catalán, 2002, Catalán & al., 2004, 2007; Torrecilla & al., 2004; Inda & al., 2008; Cheng & al., 2016; Minaya & al., 2017), Sesleriinae (Kuzmanović & al., 2017), Brizinae and Calothecinae (Essi & al., 2008; Persson & Rydin, 2016; Silva & al., 2020) were studied.

Recent classifications of Poodae took up the progress made by molecular phylogenetic studies and numerous changes in classification proposed relative to *Genera graminum*, which was superseded by the comprehensive Poaceae treatment for *The families and genera of vascular plants* (Kellogg, 2015). Most current taxonomic accounts of grasses abandoned the traditional distinction of tribes Aveneae and Poeae (e.g., GPWG, 2001; Kellogg, 2015; Soreng & al., 2015b, 2017), which was suggested already by Tzvelev (1989), who, however, kept Phleeae as tribe separate from Poeae. Merging Poeae and Aveneae was mainly due to the increasing availability of molecular phylogenetic data that did not corroborate their segregation according to previous circumscriptions based on morphology, for example, the presence of a dorsal lemma awn or long glumes in relation to the entire spikelet as presumably typical of Aveneae (Figs. 1–3). Nevertheless, the occurrence of two different plastid DNA sequences ("Aveneae type" and "Poeae type") led to the nomenclaturally informal recognition of two lineages (Soreng & Davis, 2000), each of which was divided into a number of subtribes (Soreng & al., 2007, 2015b, 2017; Kellogg, 2015), as followed also in the molecular phylogenetic account of the Aveneae type lineage of Saarela & al. (2017).

Hybridization between species is a widespread process that acts in almost any group of grasses. It is well-known to be especially frequent in connection with polyploidy and within polyploid complexes, as documented in many grass groups including the economically highly important Triticeae, Andropogoneae and Paniceae (Hunziker & Stebbins, 1987; Kellogg & Watson, 1993; Kellogg, 2015). Hybridization was also considered a potential reason for the discrepancies between traditional morphology- and molecular phylogeny-based classifications for Poodae (Soreng & Davis, 2000).

To address the role of hybridization as suspected factor in the evolution of several of its lineages (Soreng & Davis, 2000; Quintanar & al., 2007; Soreng & al., 2007) and to contribute to an improved classification, we aimed at a comparative sequencing study of representatives of most genera of Poodae, except for some lineages that were already shown to be clearly monophyletic (for example, Calothecinae, Loliinae, Poinae) and in which we sampled only a small selection of taxa. Due to the different inheritance of the plastid and the nuclear genome we tried to generate a taxonomically overlapping dataset for both genomes since incongruent placement of taxa in phylogenetic trees derived from both individual datasets is in most instances a reliable indicator of past hybridization events.

Moreover, we attempted to clarify the phylogenetic position of several genera previously not sampled in molecular phylogenetic investigations, to address questionable data in DNA sequence repositories and to correct a few problematic cases we have created ourselves in previous publications from our lab. Finally, we wanted to compare the molecular phylogenetic information based on extensive sampling of genera with the currently discussed concepts of relationships within Poodae.

■ MATERIALS AND METHODS

Classification employed. — We follow in this study, as far as possible, the classification of the grass subfamily Pooideae displayed by Soreng & al. (2017). This classification utilizes a comparatively narrow delineation of subtribes and the rather infrequently used taxonomic ranks of supersubtribes and supertribes. It is easy to compare with the classification used by Kellogg (2015) for her account on Poaceae in *The families and genera of vascular plants*. We also follow the treatment of genera and synonyms presented by Soreng & al. (2017) unless otherwise stated. Genus names occasionally misapplied in the literature are enclosed in the following by single quotation marks.

Plant material and choice of study taxa. — For the molecular phylogenetic study we tried to sample as comprehensively as possible all currently acknowledged genera and important segregate genera of Poodae except for subtribes

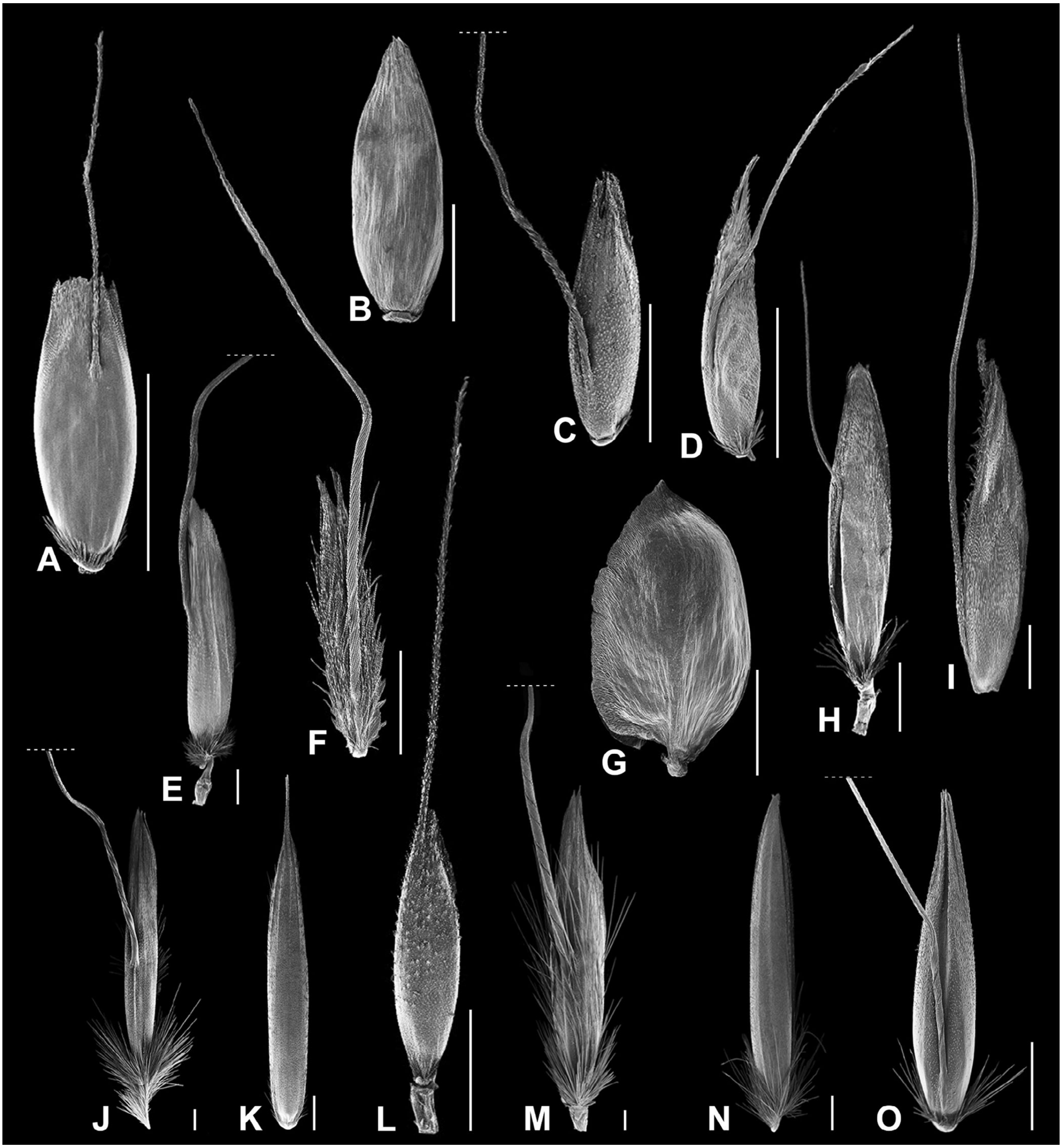

Fig. 1. Morphological diversity of lemmas and awns (partly trimmed) in example species of Poodae; scanning electron microphotographs. All species pictured have been sampled in this study. Collection details, voucher information and subtribe affiliation are given in brackets. **A,** *Agrostis avenacea* (*M. Röser 10762*, HAL; Agrostidinae); **B,** *A. capillaris* (*M. Röser 11296 & N. Tkach*, HAL0140613; Agrostidinae); **C,** *A. rupestris* (*M. Röser 11312 & N. Tkach*, HAL0144916; Agrostidinae); **D,** *Aira praecox* (*M. Röser 11041*, HAL; Airinae); **E,** *Amphibromus nervosus* (*M. Röser 10770*, HAL; Torreyochloinae); **F,** *Anthoxanthum odoratum* (*M. Röser 11006*, HAL; Anthoxanthinae); **G,** *Briza media* (*M. Röser 11072*, HAL; Brizinae); **H,** *Avenella flexuosa* (*M. Röser 11202 & N. Tkach*, HAL0141248; Airinae); **I,** *Alopecurus pratensis* (*M. Röser 11222 & N. Tkach*, HAL0141246; Alopecurinae); **J,** *Avenula pubescens* (*M. Röser 6528*, HAL; Avenulinae); **K,** *Beckmannia eruciformis* (*s.coll. R382*, HAL; Beckmanniinae); **L,** *Apera spica-venti* (*M. Röser 10699*, HAL0140288; Ventenatinae); **M,** *Avena fatua* (*M. Röser 11267 & N. Tkach*, HAL0140638; Aveninae); **N,** *Calamagrostis arenaria* (*M. Röser 11291*, HAL0144749; Agrostidinae); **O,** *Calamagrostis arundinacea* (*M. Röser 11274 & N. Tkach*, HAL0141306; Agrostidinae). — A, B, F, G, J, K, L, M & O, Dorsal view; C, D, E, H, I, N, Lateral view. Scale bars = 1 mm.

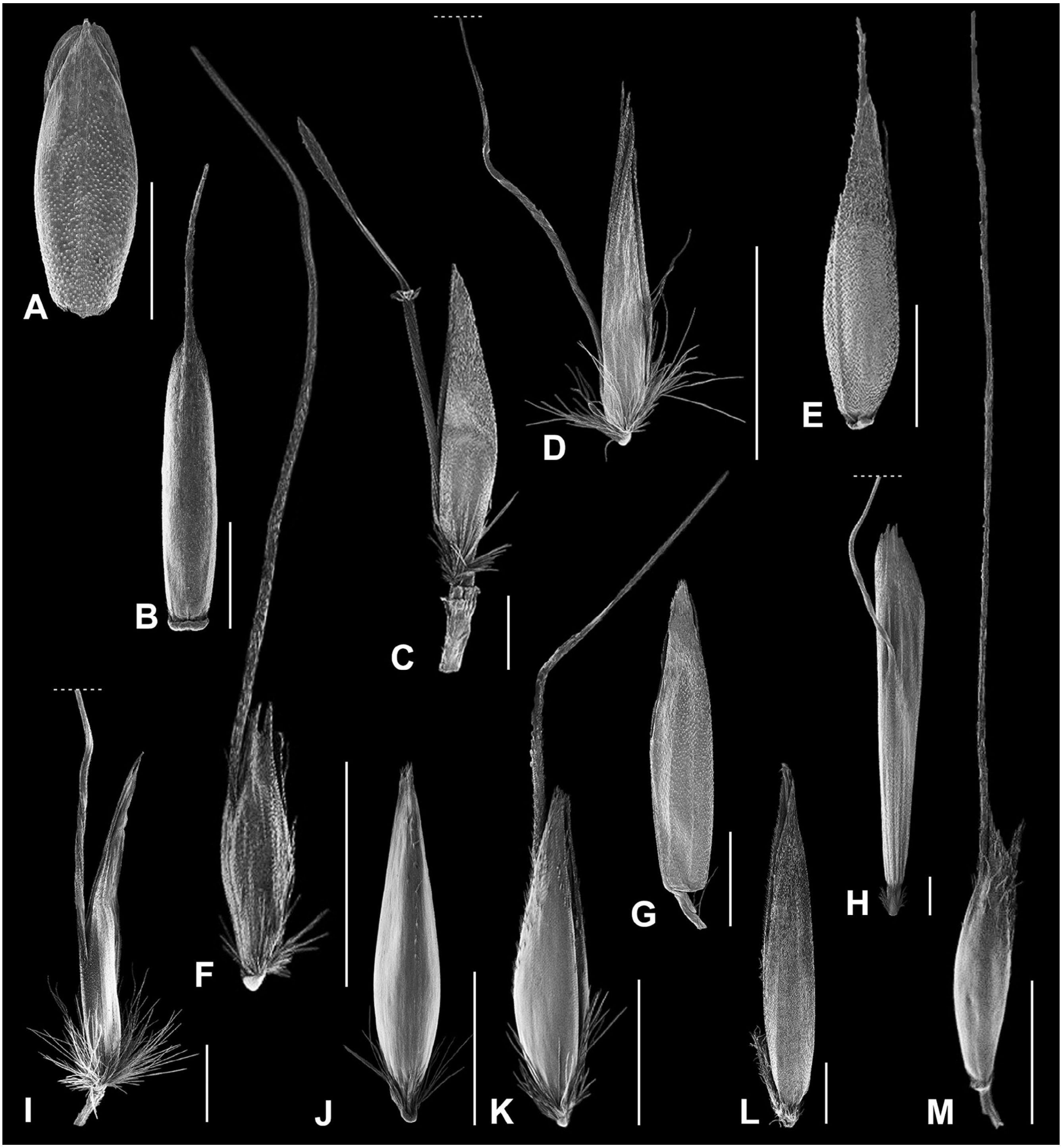

Fig. 2. Morphological diversity of lemmas and awns (partly trimmed) in example species of Poodae; scanning electron microphotographs. All species pictured have been sampled in this study. Collection details, voucher information and subtribe affiliation are given in brackets. **A,** *Catapodium marinum* (*M. Röser 4352*, HAL; Parapholiinae); **B,** *Festuca lachenalii* (*M. Röser 5470*, HAL; Loliinae); **C,** *Corynephorus canescens* (*E. Willing 25.870D*, HAL0108617; Airinae); **D,** '*Calamagrostis*' *flavens* (*I. Hensen*, HAL; Agrostidinae); **E,** *Cynosurus cristatus* (*M. Röser 622*, HAL; Cynosurinae); **F,** *Gastridium nitens* (*G. van Buggenhout 11991*, ROM; Agrostidinae); **G,** *Graphephorum wolfii* (*R.J. Soreng*, NY; Aveninae); **H,** *Helictochloa bromoides* subsp. *bromoides* (*M. Röser 10519*; HAL; Helictochloinae); **I,** *Helictotrichon petzense* subsp. *petzense* (*M. Röser 10646*, HAL; Aveninae); **J & K,** *Holcus mollis* (*M. Röser 10658*, HAL; Holcinae) with lower (**J**) and upper lemma (**K**); **L,** *Hookerochloa eriopoda* (*R. Pullen 4003*, AD96435171; HSAQN clade); **M,** *Lamarckia aurea* (*M. Röser 311*, HAL; Dactylidinae). — A, B, H, J, Dorsal view; C, D, E, F, G, I, K, L, M, Lateral view. Scale bars = 1 mm.

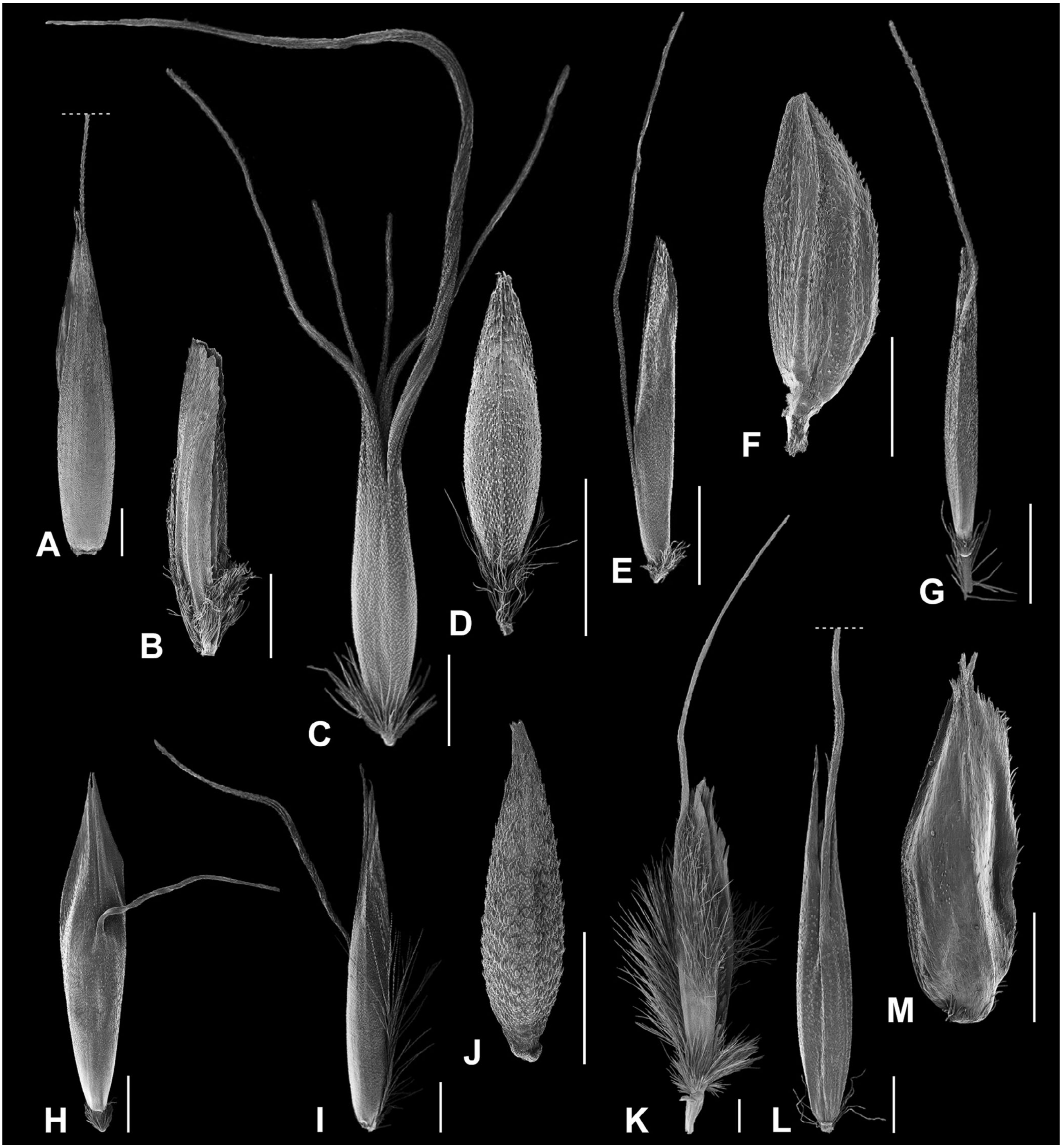

Fig. 3. Morphological diversity of lemmas and awns (partly trimmed) in example species of Poodae; scanning electron microphotographs. All species pictured have been sampled in this study. Collection details, voucher information and subtribe affiliation are given in brackets. **A,** *Lolium giganteum* (*M. Röser 11275 & N. Tkach*, HAL0141305; Loliinae); **B,** *Poa fax* (*D.E. Murfet 1278*, AD99151120; Poinae); **C,** *Pentapogon quadrifidus* (*A. Moscal 11543*, HO 95925; Echinopogoninae); **D,** *Periballia involucrata* (*s.coll. R58/R319*, HAL; Airinae); **E,** *Peyritschia pringlei* (*P. Tenorio 15095*, MEXU542571; Aveninae); **F,** *Phleum crypsoides* (*F. Skovgaard*, C; Phleinae); **G,** *Trisetum flavescens* (*M. Röser 11245 & N. Tkach*, HAL0141270; Aveninae); **H,** *Ventenata macra* (*M. Röser 10688*, HAL; Ventenatinae); **I,** *Tzveleviochloa parviflora* (*S. & G. Miehe & K. Koch 01-073-24*, Institute of Geography, University Marburg, Germany; Aveninae); **J,** *Simplicia buchananii* (*A.P. Druce*, CHR394262; Cinninae); **K,** *Tricholemma jahandiezii* (*M. Röser 10297*, HAL; Aveninae); **L,** *Trisetopsis elongata* (*S. Wagner R118b*, HAL0144713; Aveninae); **M,** *Sesleria caerulea* (*M. Röser 11239 & N. Tkach*, HAL0141254; Sesleriinae). — A, D, G, H, J, L, M, Dorsal view; B, C, E, F, I, K, Lateral view. Scale bars = 1 mm.

Calothecinae, Loliinae and Poinae (see Introduction). The types of the genera were preferably included. For information retrieval on nomenclatural types, we consulted the Index Nominum Genericorum (ING; botany.si.edu/ing/), Tropicos (tropicos.org), Clayton & Renvoize (1986), Clayton & al. (2002 –), the Catalogue of New World Grasses (Soreng & al., 2000 –) and other taxonomic sources (see References). In non-monospecific genera, we tried to investigate two or more species. Sometimes, we used more than one accession for the same taxon. In total, 117 accepted genera and 257 species were treated in this study. No plant material has been obtained in the genera *Agropyropsis* A.Camus, *Agrostopoa* Davidse & al. and *Pseudophleum* Doğan. Taxa selected from the lineages next to Poodae, namely *Hordelymus europaeus* (L.) O.E.Harz, *Hordeum marinum* subsp. *gussoneanum* (Parl.) Thell. and *Secale sylvestre* Host from Triticeae subtribe Hordeinae in the sense of Schneider & al. (2009); *Boissiera squarrosa* (Sol.) Nevski and *Bromus erectus* Huds. from Triticeae subtribe Brominae; *Littledalea racemosa* Keng from Triticeae subtribe Littledaleinae as well as *Brachypodium distachyon* (L.) P.Beauv. from Brachypodieae were selected as suitable outgroup taxa based on previous studies (Davis & Soreng, 1993; Catalán & al., 1997; Hilu & al., 1999; Schneider & al., 2009, 2011; GPWG, 2012; Blaner & al., 2014; Hochbach & al., 2015). The molecular phylogenetic studies were conducted using silica gel-dried leaf material collected in the field from living plants or leaves from specimens of the following herbaria: AD, ALTB, B, BBG, C, CAN, CHR, COL, FI, HAL, HO, ICN, JACA, K, LE, LISU, MEXU, MO, NS, NSK, NSW, NU, NY, PRE, RO, RSA, SGO, TROM, UPS and US. Information on origin, collectors, collection details and ENA/GenBank sequence accession numbers of the analysed taxa is given in Appendices 1 and 2.

Molecular methods and sequence alignment. — FastPrep FP120 cell disrupter (Qbiogene, Heidelberg, Germany) was used to homogenize 20–45 mg leaf tissue per sample. Extraction of total genomic DNA was conducted with the Nucleo Spin Plant Kit in accordance to the manufacturer's protocol (Macherey-Nagel, Düren, Germany). The concentration of the DNA samples was checked with a NanoDrop spectrophotometer (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.). The entire internal transcribed spacer region (ITS) of the nuclear ribosomal (nr) DNA (ITS1–5.8S rRNA gene–ITS2) and the *matK* gene–3′*trnK* exon of the plastid DNA were PCR-amplified following the protocols described by Schneider & al. (2009) and Wölk & Röser (2014). The 3′ end of the external transcribed spacer region (ETS) of the nrDNA was amplified with primers 18S-Rcyper (Starr & al., 2003), RETS4-F (Gillespie & al., 2010) and RETS-B4F (Alonso & al., 2014) under conditions following Tkach & al. (2008). For amplification of the plastid non-coding region of *trnL-trnF*, including the *trnL*(UAA) intron and the adjacent intergenic spacer between the *trnL*(UAA) 3′exon and *trnF* (GAA) gene, were used primers c, d, e and f and the PCR protocol of Taberlet & al. (1991). Additional new primers created for this region (cps ACGGACTTGATTGTATTGAGCC; dps CTCTCTCTTTGTCCTCGTCCG; eps CGGACGAGGACA AAGAGAGAG; fps AACTGAGCATCCTGACCTTTTCT TG) were used in combination with the primers cited. PCR was carried out on a thermocycler manufactured by Eppendorf (Hamburg, Germany). Purification and sequencing of all PCR products were performed in our lab or by StarSEQ (Mainz, Germany), Eurofins MWG Operon (Ebersberg, Germany) and LGC Genomics (Berlin, Germany) with the same primers as used for amplifications. PCR products of the ITS region with ambiguous sequence peaks were cloned. Cloning was performed using the pGEM-T Easy Vector System (Promega Mannheim, Germany). Ligation and transformation of the relevant purified amplicons were carried out according to the technical manual. The plasmid DNA was isolated using the GeneJET Plasmid Miniprep Kit (Fermentas, St. Leon-Rot, Germany) according to the manufacturer's protocol. The PCR products were quantified spectrophotometrically. Highly similar ITS clone sequences in *Pholiurus pannonicus* (Host) Trin. were combined to one consensus sequence (Appendix 1). All sequences were edited by eye in Sequencher v.5.0 (Gene Codes, Ann Arbor, Michigan, U.S.A.). The automatically performed alignments by using ClustalW2 (Larkin & al., 2007) were manually adjusted in Geneious v.9.1.6 (https://www.geneious.com; Kearse & al., 2012).

Phylogenetic analysis. — Sequences generated in this (694 new) or previous studies by our lab encompassed most of our target taxa (Appendix 1). If sequences of different accessions of the same taxon were studied, they were numbered as 1, 2, etc. in Appendix 1 and the dendrograms. For comparison with our own data during the work process and to complete our datasets, we included publicly available sequences listed in Appendix 2 for the taxa and sequence regions in question in the alignments. To avoid redundancy and to improve the clarity of the phylogenetic trees presented in the figures of this study, we finally omitted unnecessary duplicate sequences for the same taxon from the alignments. These final sequence matrices for Poodae and outgroups are provided as fasta files in the supporting information (suppl. Appendices S1–S4).

We assembled the following DNA sequence datasets: Matrix 1 with plastid and Matrix 2 with nrDNA sequences of all taxa; Matrix 3 as concatenated dataset of plastid and nrDNA sequences of Matrices 1 and 2 irrespective of partly discordant (incongruent) placement of some taxa (see Results) in the individual gene trees ("total evidence" approach; Kluge, 1989). Matrix 4 was a concatenated dataset of plastid and nrDNA sequences but with duplication of taxa that were discordantly placed in the individual gene trees (Matrices 1, 2) in a way that one taxon copy had the plastid and the other the nrDNA sequence data and the second partition in each of the taxon copies coded as missing data (resulting in a multilabelled tree; Pirie & al., 2008, 2009). Matrices 5 and 6, referred to as "reduced datasets", were derived from Matrices 1 and 2, respectively, excluding taxa with obviously incongruent placement (Queiroz & al., 1995; Kellogg & al., 1996) in the individual gene trees obtained from these Matrices.

Genera switching their position only within the same subtribe were not duplicated in Matrix 4 to avoid excessively missing data, which lessen node support, and not excluded from Matrices 5 and 6 since they did not impact higher-level nodes or backbone structure of the trees. Matrices 5 and 6 had the same taxon set. They were not concatenated for reasons explained in the Discussion (see Discussion: Deep phylogenetic incongruence …).

All DNA sequence datasets were analysed using the phylogenetic approaches of maximum likelihood (ML), maximum parsimony (MP) and Bayesian inference (BI) following Tkach & al. (2019). The trees were visualized with FigTree v.1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/). Support values are cited in the text in the following sequence: ML bootstrap support/MP bootstrap support/Bayesian posterior probability (PP).

The tree topologies obtained from the individual plastid and nrDNA sequence alignments were examined visually for incongruity. The node bootstrap support of ≥70 in ML analysis was chosen as value for supported incongruence (Wiens, 1998; Schneider & al., 2009; Baker & al., 2011; Pirie, 2015; Tkach & al., 2015, 2019).

Scanning electron microscopes (SEM) observation. — Lemmas and awns of selected representatives of major lineages were investigated using scanning electron microscopy. Up to three samples per species were studied. The lemmas of the samples (legends to Figs. 1–3) were mounted under an incident light microscope on aluminium stubs covered by double stick carbon conductive tabs (Plano, Wetzlar, Germany). Samples were gold-coated using sputter coater MED010 (Balzers Union, Balzers, Liechtenstein). Images were taken on the tabletop scanning electron microscope TM-3030Plus (Hitachi Europe, Maidenhead, U.K.) with 5 kV acceleration voltage and the secondary electron detector.

■ RESULTS

Plastid DNA analysis (Matrix 1). — The plastid *matK* gene–3′*trnK* exon DNA sequence dataset (sequence lengths 768–2190 bp) for 208 taxa included 2512, the *trnL-trnF* DNA dataset (sequence lengths 187–1037 bp) for 199 taxa included 1414 aligned positions, respectively. The combined data matrix of the two plastid DNA markers for 214 taxa included a total of 3926 aligned positions, of which 1472 were variable (*matK* gene–3′*trnK* exon: 984, *trnL-trnF*: 488) and 908 parsimony-informative (*matK* gene–3′*trnK* exon: 622, *trnL-trnF*: 286). In the concatenated plastid DNA dataset, 6 *matK* gene–3′*trnK* exon (2.8%) and 15 *trnL-trnF* DNA sequences (7.0%) were missing.

Poodae formed a monophyletic lineage (100/100/1.00), using our extended set of outgroup taxa. It split into two main clades, which were supported by 100/98/1.00 and 100/99/1.00, respectively (Clades 1 and 2 in Fig. 4).

Clade 1 showed more or less a polytomy of six lineages. Following the recent classification of Soreng & al. (2017) and new names coined in this study (see below: New names and combinations), these lineages corresponded to subtribes Torreyochloinae and Phalaridinae unified in a common clade (93/87/1.00), Aveninae (100/100/1.00), Anthoxanthinae (100/100/1.00), new subtribe Hypseochloinae (only *Hypseochloa* C.E.Hubb.), Brizinae with *Macrobriza* (Tzvelev) Tzvelev (97/98/1.00), Echinopogoninae (100/99/1.00) and a well-supported common clade (90/71/1.00) of Calothecinae and Agrostidinae.

Within Aveninae, *Lagurus ovatus* L., assigned to the monogeneric subtribe Lagurinae by Saarela & al. (2017), and *Tricholemma jahandiezii* (Litard. ex Jahand. & Maire) Röser were opposed to a larger clade (91/95/1.00) formed of supported Aveninae s.str. (98/88/1.00) and a lineage (99/97/1.00) sometimes referred to as separate subtribe Koeleriinae (Quintanar & al., 2007; Saarela & al., 2017; Barberá & al., 2019). *Cinnagrostis rigida* (Kunth) P.M.Peterson & al., traditionally member of Central to South American ‘*Calamagrostis*’ Adans. or ‘*Deyeuxia*’ Clarion ex P.Beauv., was nested among Aveninae and not Agrostidinae as *Calamagrostis* s.str. and *Deyeuxia* s.str. Monospecific *Limnodea* L.H.Dewey (*L. arkansana* (Nutt.) L.H.Dewey), so far considered either Poinae or Agrostidinae (Kellogg, 2015; Soreng & al., 2017), was nested within Aveninae and likewise in its Koeleriinae lineage. Strongly supported Echinopogoninae encompassed among others (*Dichelachne* Endl., *Echinopogon* P.Beauv., *Pentapogon* R.Br., *Relchela* Steud.) also ‘*Deyeuxia*’ *contracta* (F.Muell. ex Hook.f.) Vickery as representative of Australasian ‘*Deyeuxia*’ or ‘*Calamagrostis*’. Altogether, supersubtribe Agrostidodinae (Soreng & al., 2017) encompassing Agrostidinae, Brizinae, Calothecinae, Echinopogoninae and Hypseochloinae received some support (75/–/0.96).

The second main lineage of the plastid DNA tree (Clade 2) had a major basal polytomy consisting of Airinae, which received maximum support (100/100/1.00), a large lineage with 81/61/– support, and the PPAM clade, an acronym derived from the subtribe names Puccinelliinae (= Coleanthinae), Poinae, Alopecurinae and Miliinae (Gillespie & al., 2008, 2010) supported by 71/67/0.99.

The lineage with 81/61/– support encompassed Holcinae (100/100/1.00), Aristaveninae (100/98/1.00), Sesleriinae (81/62/0.99), Loliinae (100/99/1.00), Ammochloinae (only *Ammochloa* Boiss.), Dactylidinae (100/100/1.00), Cynosurinae, Parapholiinae (100/99/1.00) and the new subtribe Helictochloinae (100/100/1.00) with *Helictochloa* Romero Zarco and *Molineriella* Rouy, two genera previously accommodated in Airinae. *Antinoria* Parl. (new monogeneric subtribe Antinoriinae), was closer to *Scolochloa* Link (86/70/0.68). *Dryopoa* Vickery, the second Scolochloinae genus, was placed separate from *Scolochloa* with Sesleriinae but with low support (63/50/0.98). Ammochloinae and Dactylidinae were sister clades (97/95/1.00). Cynosurinae, with *Cynosurus* L. species forming a grade, and Parapholiinae were placed in a common clade (100/100/1.00). Strongly supported Ammochloinae/Dactylidinae and Cynosurinae/Parapholiinae formed a weakly supported clade here termed ADCP clade (57/52/0.70).

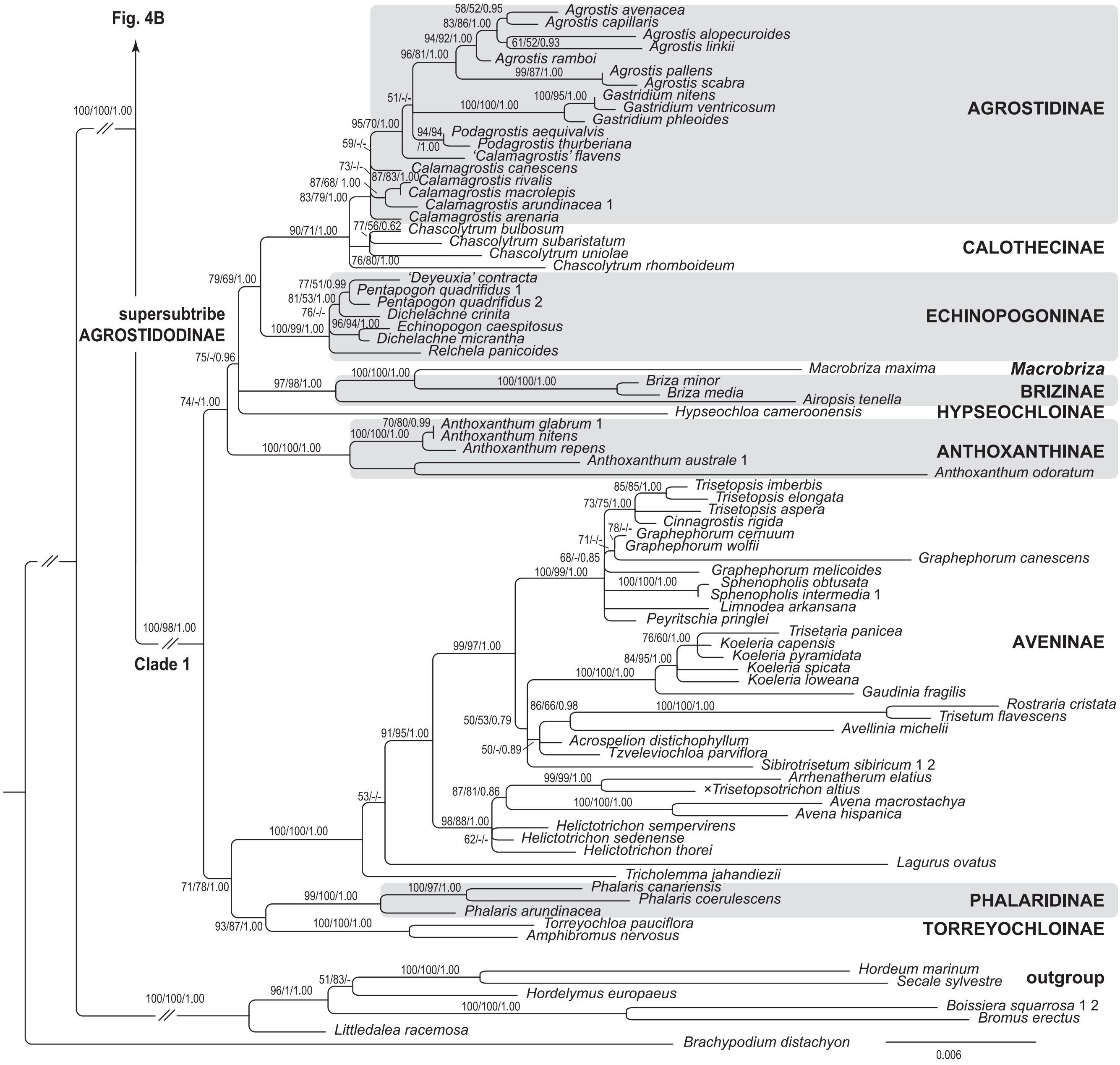

Fig. 4. Maximum likelihood phylogram of Poodae inferred from plastid DNA sequences (*matK* gene–3′*trnK* exon, *trnL-trnF*) with species of Triticodae and Brachypodieae used as outgroup (Matrix 1). Maximum likelihood and maximum parsimony bootstrap support values >50% as well as Bayesian posterior probabilities >0.5 are indicated on the branches. Clades with maximum likelihood support <50% are collapsed. The subtribes mentioned in the text are labelled on the right-hand side.

The PPAM clade split into subtribe Coleanthinae and supersubtribe Poodinae (~PAM clade, an acronym derived from the subtribe names Poinae, Alopecurinae and Miliinae; Gillespie & al., 2008, 2010; Soreng & al., 2015a,b), both of which gained strong support (100/99/1.00 and 100/95/1.00, respectively). It included the subtribes Miliinae (only *Milium* L.), Phleinae (only *Phleum* L.) and Poinae (only *Poa* L.; 86/76/1.00), *Arctopoa* (Griseb.) Prob., monospecific *Avenula* (Dumort.) Dumort. assigned to the monogeneric new subtribe Avenulinae and a considerably supported lineage (84/68/1.00) termed here ABCV clade. It encompassed a large polytomy Alopecurinae, Beckmanniinae, Cinninae, Ventenatinae (85/60/1.00), along with *Brizochloa* V.Jirásek & Chrtek (monogeneric new subtribe Brizochloinae) and a number of genera not classed as to subtribe, including *Arctohyalopoa* Röser & Tkach, a new genus harboring former *Hyalopoa lanatiflora* (Roshev.) Tzvelev and probably three further species (see below Discussion: Poeae). Moreover, Alopecurinae,

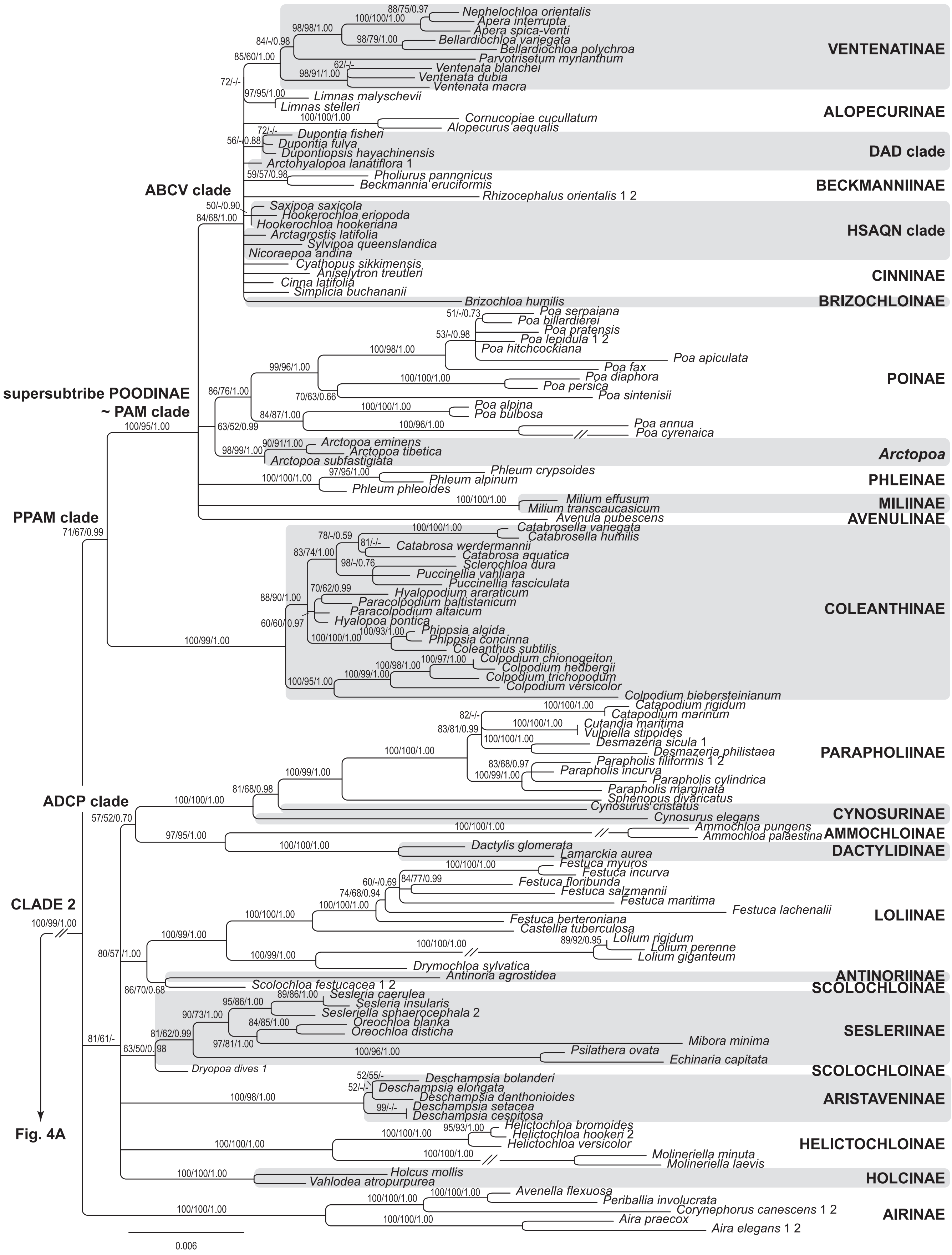

Fig. 4. Continued.

Beckmanniinae and Cinninae did not resolve as monophyletic. Only a sister relation of Alopecurinae genera *Alopecurus* L. and *Cornucopiae* L. was strongly supported (100/100/1.00), whereas *Beckmannia* Host. and *Pholiurus* Trin. (Beckmanniinae) obtained weak support as sister (59/57/0.98). The DAD clade, an acronym originally derived from *Dupontia* R.Br., *Arctophila* (Rupr.) Andersson and *Dupontiopsis* Soreng & al. (Soreng & al., 2015a), in this study encompassing *Dupontia* including *Arctophila*, *Dupontiopsis* and new *Arctohyalopoa*, was obvious within the ABCV clade but with low support, whereas the HSAQN clade (Gillespie & al., 2010; Kellogg, 2015; Soreng & al., 2015a,b) was unresolved.

Nuclear DNA analysis (Matrix 2). — The nr ITS DNA sequence dataset for 215 taxa included 673 (sequence lengths 245–608 bp) and the ETS DNA dataset for 200 taxa (sequence lengths 279–884 bp) included 1135 aligned positions. Both markers yielded no conflicting trees and thus were combined to a single matrix. This Matrix 2, with 218 taxa, included a total of 1808 aligned positions, of which 1093 were variable (ITS: 383, ETS: 710) and 863 parsimony-informative (ITS: 320, ETS: 543). In the concatenated nrDNA dataset, 3 ITS (1.4%) and 18 ETS DNA sequences (8.2%) were missing.

Poodae was supported by the nr ITS and ETS sequence data as monophyletic (100/88/1.00). The tree backbone consisted of a polytomy of six clades (Fig. 5) comprising Antinoriinae, Helictochloinae (100/100/1.00), Aristaveninae (100/96/1.00) and a supported lineage harboring Loliinae (70/–/1.00) and the ADCP clade (69/–/1.00). This well-supported lineage of the latter two elements (100/79/1.00), unresolved in the plastid DNA tree, represented supersubtribe Loliodinae (Soreng & al., 2017). The remaining two clades of the backbone polytomy were the PPAM clade (95/74/1.00) and a large clade with 85/–/1.00 support. The PPAM clade consisted of Miliinae, a common lineage of Phleinae with Poinae (84/–/0.99) that had not been resolved in the plastid DNA tree, Coleanthinae (68/–/0.98), Avenulinae and a lineage termed ABCV+A clade (83/67/1.00), which corresponded to the ABCV clade in the plastid DNA tree except for the placement of *Arctopoa*. Supersubtribe Poodinae (~PAM clade) was not resolved within the PPAM clade. The HSAQN clade was well-defined (97/97/1.00) within the ABCV+A clade. Sister relations of *Alopecurus* and *Cornucopiae* (Alopecurinae) and of *Beckmannia* and *Pholiurus* (Beckmanniinae) were supported (95/97/1.00 and 100/100/1.00, respectively).

The large clade with 85/–/1.00 support of the backbone polytomy showed a partly well-supported internal structure. It encompassed Holcinae (100/100/1.00) and Airinae (100/99/1.00) as sister clades (95/84/1.00), Anthoxanthinae, a lineage (95/–/1.00) of *Macrobriza*, Sesleriinae and Aveninae, which had not been encountered in the plastid DNA tree, and a clade supported by 93/55/1.00. It was formed by Scolochloinae with *Dryopoa* and *Scolochloa* (100/97/1.00), Phalaridinae, Torreyochloinae (100/98/1.00) and supersubtribe Agrostidodinae (81/–/0.99), which contained Hypseochloinae, Brizinae (54/–/0.93), Calothecinae (89/88/1.00) as well as species and small clades of Agrostidinae and Echinopogoninae in a polytomy. *Ancistragrostis* S.T.Blake (available only ITS) was placed with low support along with Echinopogoninae, which encompassed also '*Deyeuxia*' *contracta* (93/91/1.00).

Aveninae segregated into two different lineages similar to the ones encountered in the plastid DNA tree, except for the position of *Tricholemma* (Röser) Röser and *Lagurus* L. One of the lineages, Aveninae s.str. (76/56/1.00), assembled with non-monophyletic Sesleriinae in a common lineage (85/58/1.00), whereas the other corresponded to the Koeleriinae lineage (96/53/1.00). It had *Lagurus* (Lagurinae) as early-branching genus and encompassed *Cinnagrostis rigida*.

Combined plastid and nuclear DNA dataset including all taxa (Matrix 3). — Following the rationale outlined in Material and Methods, we analyzed a concatenated dataset of plastid and nrDNA sequence data to evaluate which of the clades retrieved by the individual analyses kept stable or eventually became even better supported and which clades became less supported or collapsed.

The combined data matrix of all plastid and nrDNA sequences for 218 taxa included a total of 5734 aligned positions (sequence lengths 245–4397 bp) of which 2562 were variable and 1770 parsimony-informative. In the concatenated plastid and nrDNA dataset, four plastid (1.8%) sequences and no nrDNA sequence were missing.

The backbone of the Poodae tree showed a deep dichotomy as the plastid DNA tree, whereas further tree resolution was overall low (suppl. Fig. S1). Within one of the main clades (100/67/1.00), a series of lineages arranged in a polytomy was found. Anthoxanthinae (100/100/1.00), Aveninae (100/92/1.00), Torreyochloinae (100/100/1.00) and Phalaridinae (100/99/1.00) were well-supported, to a lesser extent Brizinae excluding *Macrobriza* (75/–/1.00) and Calothecinae (85/90/1.00). Agrostidinae and Echinopogoninae did not resolve as monophyletic, respectively, but were part of a polytomy. Supersubtribe Agrostidodinae under exclusion of *Macrobriza* was slightly supported (62/–/1.00). Aveninae showed an internal structure of two main clades (Aveninae s.str., Koeleriinae), with *Tricholemma* sister to the former (93/90/1.00) and *Lagurus* to the latter (69/61/1.00; not shown).

Within the second main clade (98/64/1.00), several highly supported lineages were resolved but were part of a polytomy: Scolochloinae, Aristaveninae, Helictochloinae (100/100/1.00 each), Sesleriinae (100/99/1.00), Holcinae (100/100/1.00) unified with Airinae (100/100/1.00) in a common clade (88/88/1.00), a low-support clade of Antinoriinae with supersubtribe Loliodinae (100/68/1.00) containing Loliinae (99/67/1.00) and the ADCP clade (80/56/1.00) and, finally, the PPAM clade (100/96/1.00). The latter encompassed Coleanthinae (100/99/1.00) and supersubtribe Poodinae (~PAM clade; 100/82/1.00), in which also Avenulinae was placed. Within Poodinae, the ABCV+A (97/92/1.00), the HSAQN (99/96/1.00) and the DAD clade (96/91/1.00) were supported.

Combined dataset with duplicated conflicting taxa (Matrix 4). — By comparison of the individual plastid and nrDNA trees (Matrices 1 and 2; Figs. 4, 5), several lineages

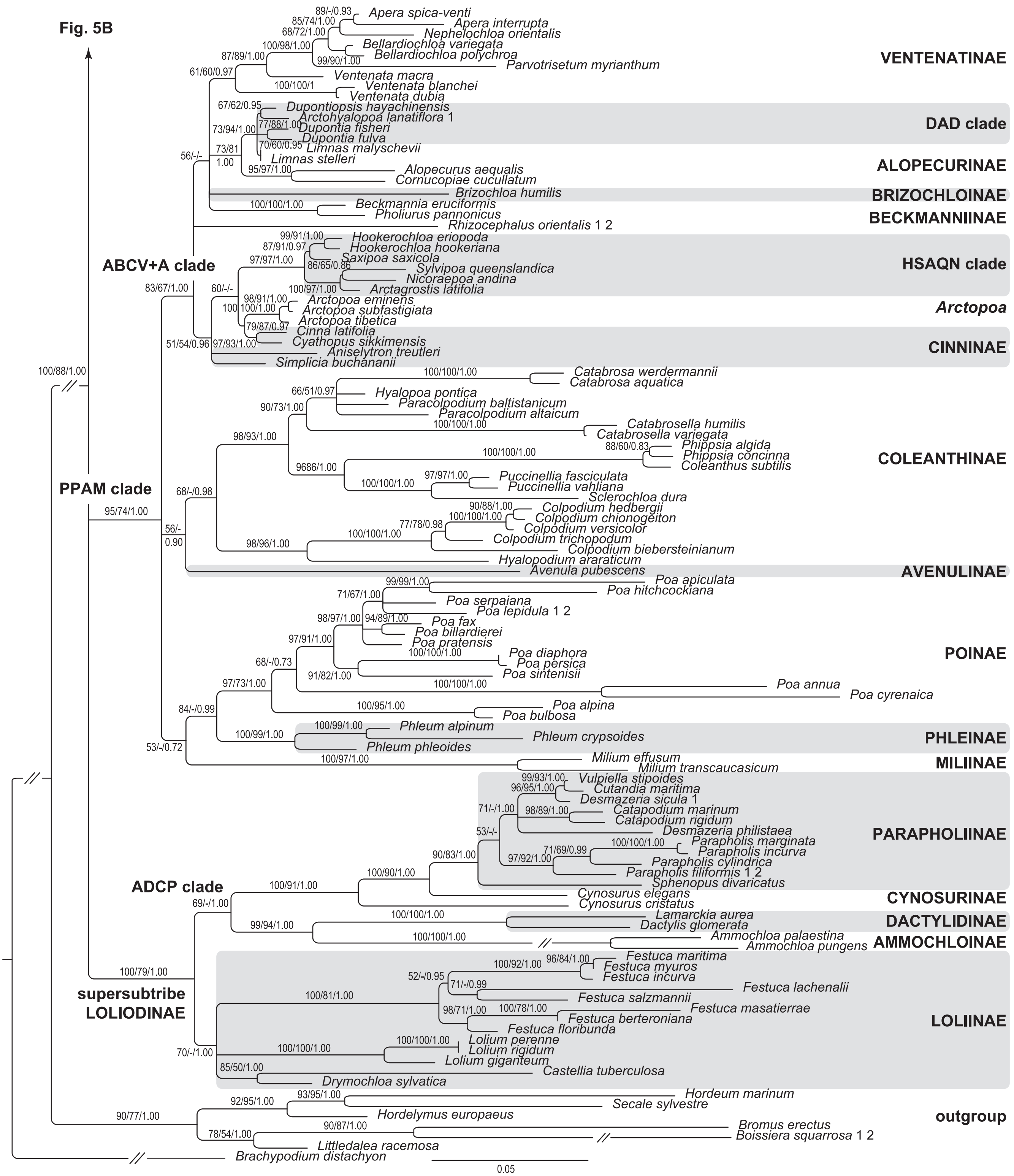

Fig. 5. Maximum likelihood phylogram of Poodae inferred from nrDNA sequences (ITS, ETS) with species of Triticodae and Brachypodieae as outgroup (Matrix 2). Maximum likelihood and maximum parsimony bootstrap support values >50% as well as Bayesian posterior probabilities >0.5 are indicated on the branches. Clades with maximum likelihood support <50% are collapsed. The subtribes mentioned in the text are labelled on the right-hand side.

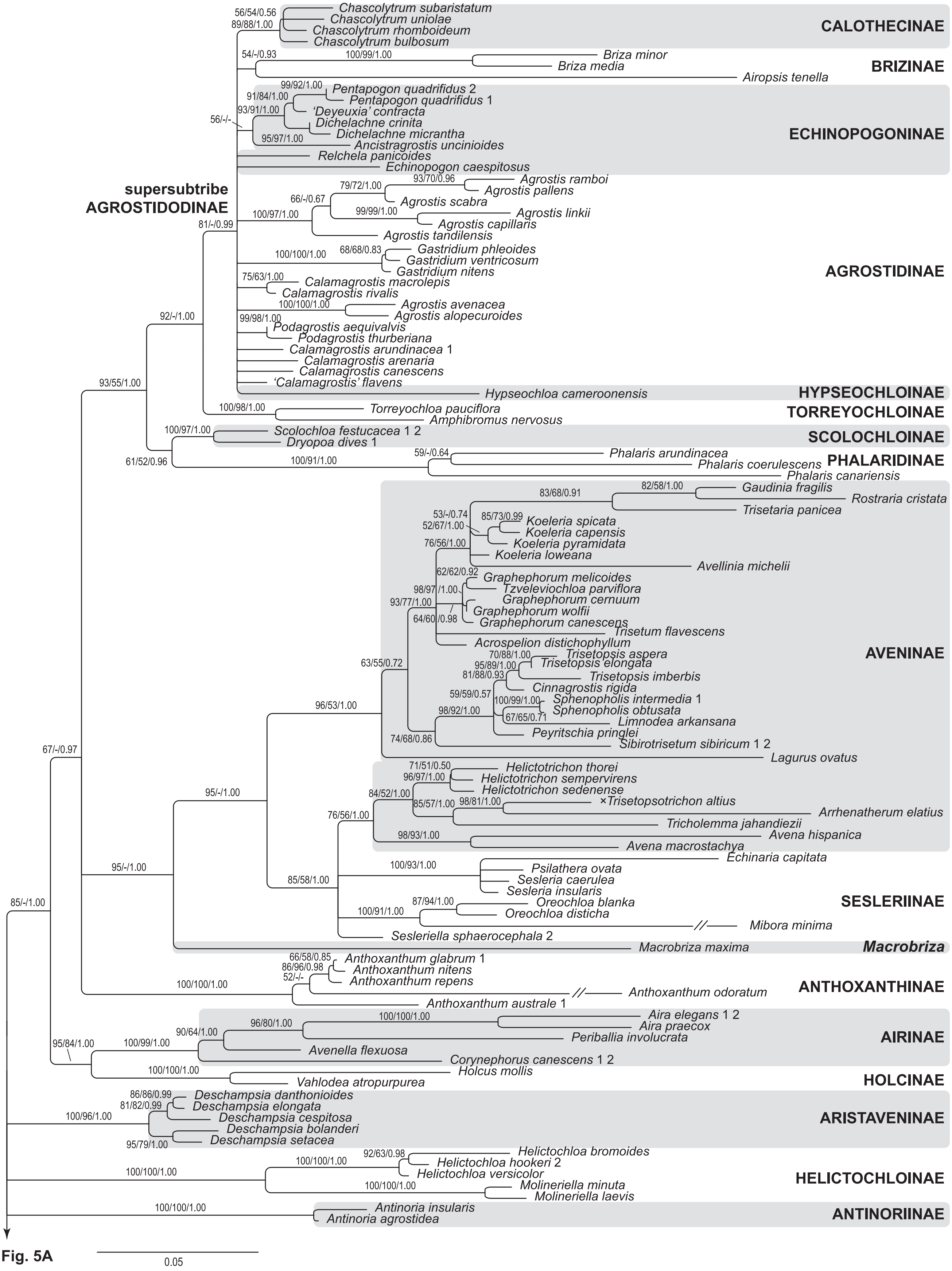

Fig. 5A

Fig. 5. Continued.

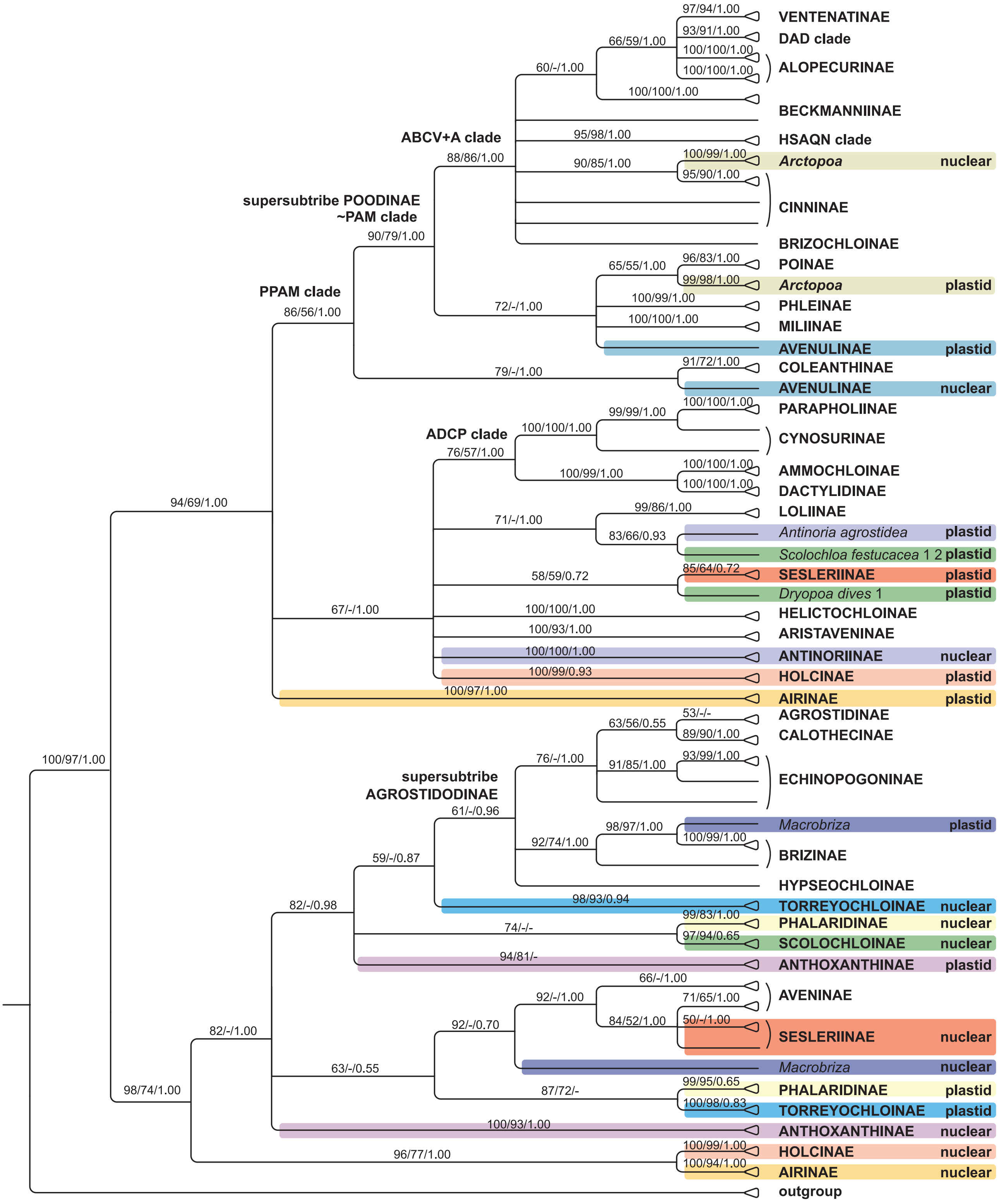

Fig. 6. Simplified maximum likelihood cladogram inferred from Matrix 4. Concatenated plastid and nrDNA sequences together with plastid and nrDNA partitions used for taxa with conflicting placement in the individual plastid and nuclear DNA analyses. The duplicated taxa are marked in color. The partitions are designated as “plastid” and “nuclear” after the taxon name. Maximum likelihood and maximum parsimony bootstrap support values >50% as well as Bayesian posterior probabilities >0.5 are indicated on the branches. Clades with maximum likelihood support <50% are collapsed. Note: genera having conflicting positions within the same subtribe are represented by their concatenated plastid and nrDNA sequences and not as separate plastid and nrDNA partitions (see Material and Methods).

or taxa with unambiguously incongruent placement were identified (see bootstrap support criterion in Material and Methods). Additional tests with duplicated taxa were made for several further subtribes placed in polytomies of both individual trees, for example, Aristaveninae, Helictochloinae and Phleinae. We did not consider in these analyses taxa (mostly genera) that showed discordant placements within but not between major lineages such as prevailingly represented by subtribes (see Discussion: Reticulations within major lineages). Matrix 4 contained 181 taxa with concatenated plastid and nrDNA data partitions. Of the duplicated taxa, 33 were represented by their plastid and nrDNA partitions. Four taxa had the nuclear partition only.

The phylogenetic tree (Fig. 6) split into two main clades, one of which had nuclear Airinae and nuclear Holcinae sister to a clade with Agrostidinae, Anthoxanthinae, Aveninae, Brizinae, Calothecinae, Echinopogoninae, Hypseochloinae, Phalaridinae, nuclear Scolochloinae, nuclear Sesleriinae, Torreyochloinae and *Macrobriza*. Plastid and nrDNA sequences of Anthoxanthinae, Phalaridinae, Torreyochloinae and *Macrobriza* were widely separated from each other, respectively.

The second main clade showed a polytomy of three lineages, (1) the clade of plastid Airinae; (2) a weakly supported clade of nuclear Antinoriinae, Aristaveninae, Helictochloinae, plastid Holcinae, plastid Scolochloinae with *Dryopoa* and *Scolochloa* not as sister since the latter was sister to plastid Antinoriinae, plastid Sesleriinae, the taxa of supersubtribe Loliodinae; (3) the taxa of the PPAM clade with plastid and nrDNA sequences of Avenulinae and *Arctopoa* separated from each other, respectively.

If Aristaveninae and Helictochloinae were treated using separate plastid and nrDNA partitions, the plastid DNA sequences were placed in the clade of Loliinae, plastid Sesleriinae, etc., whereas nrDNA sequences resolved in a basal polytomy of the entire tree (not shown). If Aristaveninae were represented by concatenated plastid and nrDNA sequences, plastid and nrDNA partitions of duplicated Helictochloinae both stood in the polytomy of Loliinae, plastid Sesleriinae and Aristaveninae, etc. as in Fig. 6 (not shown). If Phleinae were treated using separate plastid and nrDNA partitions, their plastid sequences stood in a basal polytomy of the PPAM clade, whereas nrDNA sequences were placed near Poinae and plastid *Arctopoa* (not shown).

Reduced plastid and nuclear DNA datasets (Matrices 5 and 6). — The reduced plastid and nrDNA datasets (Matrices 5 and 6) contained an identical set of 168 taxa. As specified in Material and Methods, we excluded all lineages with signs of cytonuclear discordance retrieved from the analyses of individual plastid and nrDNA sequence partitions (Matrices 1 and 2; Figs. 4, 5) and of the concatenated plastid and nrDNA sequences (for taxa with congruent tree positions) analysed along with separate plastid and nrDNA data partitions for duplicated taxa with conflicting tree positions (Matrix 4; Fig. 6). Thus, we excluded subtribes Airinae, Anthoxanthinae, Antinoriinae, Aristaveninae, Avenulinae, Helictochloinae, Holcinae, Phalaridinae, Phleinae, Scolochloinae, Sesleriinae, Torreyochloinae as well as *Arctopoa* and *Macrobriza*.

The combined data matrix (Matrix 5) of the two plastid DNA markers (*matK* gene–3′*trnK* exon and *trnL-trnF*) included a total of 3756 aligned positions (sequence lengths 824–3148 bp), of which 1254 were variable and 750 parsimony-informative. The ingroup Poodae split into two strongly supported main clades (Clades 1 and 2; suppl. Fig. S2). Clade 1 (100/99/1.00) consisted of Aveninae (100/100/1.00) opposed to a weakly supported lineage of Agrostidinae, Brizinae, Calothecinae, Echinopogoninae and Hypseochloinae. Clade 2 (100/100/1.00) split into two lineages, one of which (Clade 3; 86/83/0.99) consisted of Coleanthinae as sister to a lineage (100/99/1.00) with Miliinae and Poinae (87/72/0.99) opposed to the ABCV clade (88/68/1.00), the other (Clade 4; 94/81/1.00) of Ammochloinae, Cynosurinae, Dactylidinae, Loliinae and Parapholiinae.

The combined data matrix (Matrix 6) of the two nrDNA markers ITS and ETS included a total of 1765 aligned positions (sequence lengths 471–1477 bp), of which 950 were variable and 724 parsimony-informative. Poodae split into two main clades (suppl. Fig. S3), one of which represented Clade 4 as just circumscribed (100/97/1.00), which was sister to the weaker supported Clade 5 (74/72/1.00). This clade split into Clades 1 (99/92/1.00) and 3 (100/96/1.00), both delineated as just mentioned for the reduced plastid DNA tree. Within Clade 3, Miliinae and Poinae were sister to a moderately supported lineage of Coleanthinae and the ABCV clade.

■ DISCUSSION

Molecular phylogenetics

Comparison of the plastid and nuclear DNA trees. — Both phylogenetic trees agreed widely in the resolution of minor clades, whose support values were frequently comparatively high (Figs. 4, 5, 7). The larger clades, by contrast, corresponded only partly and disagreed strikingly in some instances.

Concordant groupings were (1) supersubtribe Agrostidodinae, which was resolved in both individual analyses although excluding *Macrobriza* in the nuclear tree, in which it was sister to a clade of Aveninae and Sesleriinae; (2) the PPAM clade; (3) the ADCP clade. There were (4) many congruent clades that corresponded to subtribes, for example, Ammochloinae, Anthoxanthinae, Aristaveninae, Coleanthinae, Dactylidinae, Holcinae, Loliinae, Miliinae, Parapholiinae, Phalaridinae, Phleinae, Poinae, Torreyochloinae, and Ventenatinae. (5) Former subtribe Airinae (Airinae s.l.) was non-monophyletic in both analyses, but its subgroups were resolved and congruent (Airinae, Antinoriinae, Helictochloinae).

Several clades emerged in only one of the individual plastid and nrDNA analyses, whereas they were unresolved in the other, appearing as a polytomy or a grade. We consider this not as severe conflict. Supersubtribe Loliodinae was clearly

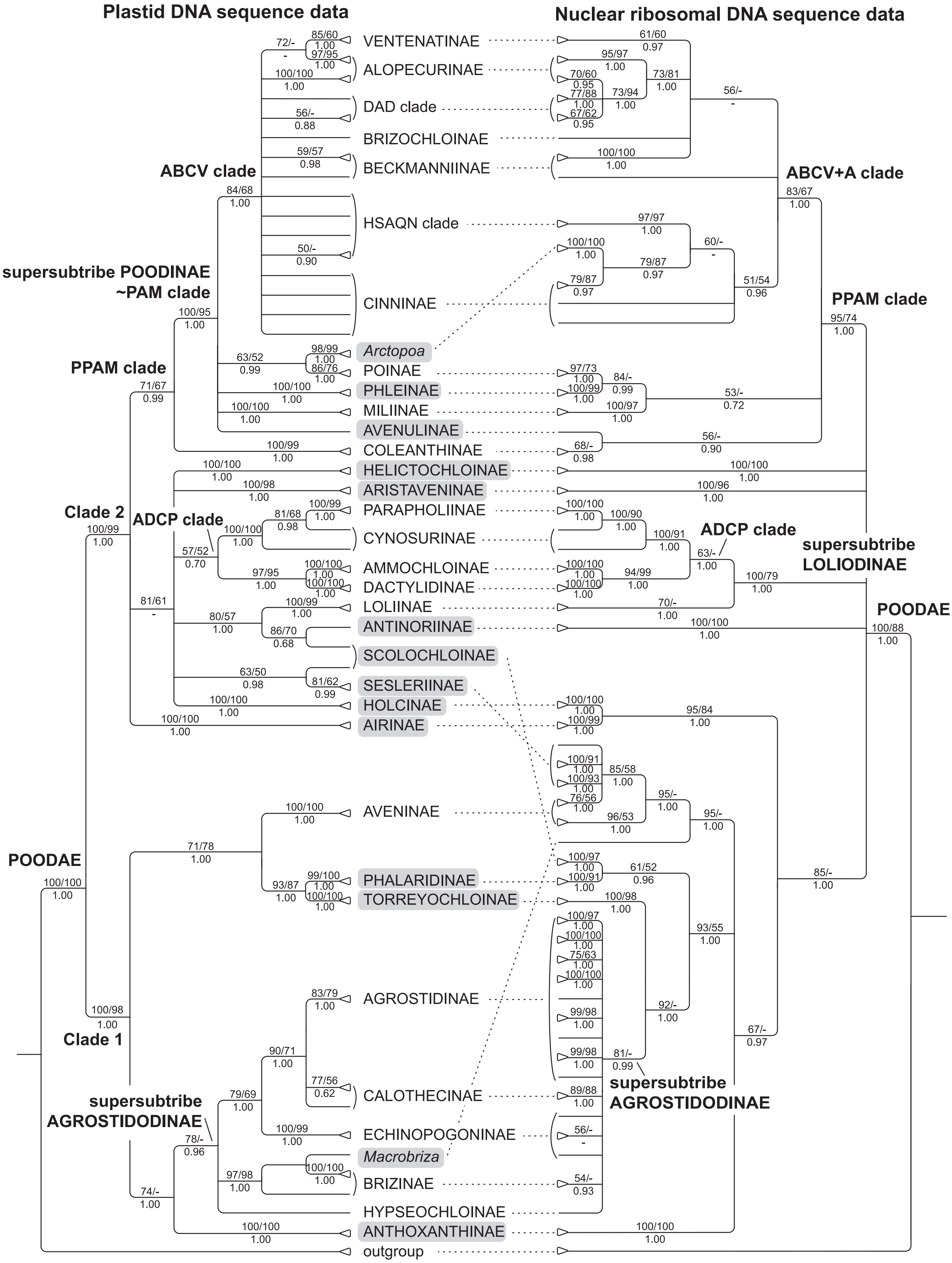

Fig. 7. Comparison of simplified maximum likelihood cladograms of Poodae inferred from plastid (*matK* gene–3′*trnK* exon, *trnL-trnF*) and nrDNA sequences (ITS, ETS) with species of Triticodae and Brachypodieae as outgroup (Matrices 1 and 2). Maximum likelihood and maximum parsimony bootstrap support values >50% as well as Bayesian posterior probabilities >0.5 are indicated on the branches. Clades with maximum likelihood support <50% are collapsed. The expanded trees are displayed in Figs. 4 and 5, respectively. Areas shaded in grey designate taxa with conflicting phylogenetic placements in the individual plastid and nuclear DNA analyses (see Figs. 4–6 and text for further explanation).

monophyletic in the nrDNA tree but formed a polytomy with several other lineages in the plastid DNA tree. Calothecinae, Scolochloinae and the DAD clade were likewise monophyletic in the nr but non-monophyletic in the plastid DNA tree. Conversely, supersubtribe Poodinae (~PAM clade) including Avenulinae as well as subtribes Agrostidinae, Echinopogoninae and Sesleriinae were monophyletic in the plastid DNA tree but formed polytomies with other lineages in the nrDNA tree.

Discordant groupings started with the backbone of the trees since the dichotomy of the plastid DNA tree into Clades 1 and 2 was not reflected in the nrDNA tree, which showed a polytomy. A number of subtribes had different affiliations depending on the individual tree (grey-shaded in Fig. 7). Sesleriinae from Clade 2 of the plastid DNA tree were placed along with Aveninae in the nrDNA tree (Quintanar & al., 2007; Saarela & al., 2017). Subtribes Airinae and Holcinae as part of Clade 2 in the plastid DNA tree were placed in the nrDNA tree close to subtribes Aveninae, Agrostidinae, etc. The same pattern was encountered in Scolochloinae as belonging to Clade 1 (plastid) but nested (nuclear) in a common clade with subtribes Agrostidinae, Echinopogoninae, Phalaridinae, Torreyochloinae, etc. Phalaridinae and Torreyochloinae were sister in the plastid but not in the nrDNA analyses (Saarela & al., 2017). Subtribe Aveninae was monophyletic in the plastid DNA tree but disintegrated in the nrDNA tree into two lineages, one of which (Aveninae s.str. with *Tricholemma*) aggregated with the taxa of Sesleriinae, whereas the other (Koeleriinae with *Lagurus*) was separate.

Macrobriza as member of monophyletic Brizinae in the plastid DNA tree was nested along with Sesleriinae and Aveninae in the nrDNA tree. Furthermore, *Arctopoa* was placed in a clade along with Poinae in the plastid but within the ABCV +A clade in the nrDNA tree (Gillespie & al., 2008, 2010; Nosov & al., 2015, 2019). Many further genera showed switching positions within their respective subtribes, for example, within Aveninae, Coleanthinae, Loliinae and Sesleriinae (see below: Reticulations within major lineages).

Tree of the combined DNA dataset including all markers and taxa. — Lineages retrieved in both individual analyses (plastid and nrDNA; Figs. 4, 5) were present also in the combined tree, for example, the PPAM clade, supersubtribe Agrostidodinae (except for *Macrobriza*) and the ADCP clade (suppl. Fig. S1). Also, many subtribes were recovered in the combined analyses such as Ammochloinae, Anthoxanthinae, Aristaveninae, Coleanthinae, Dactylidinae, Holcinae, Loliinae, Miliinae, Parapholiinae, Phalaridinae, Phleinae, Poinae, Torreyochloinae, Ventenatinae and the monophyletic subdivisions of former Airinae s.l., namely Airinae s.str., Antinoriinae and Helictochloinae. Occasionally, the clade support values of concordant lineages were higher in the analysis of the combined dataset than in the individual analyses, for example, for the PPAM clade (combined 100/96/1.00, plastid 71/67/0.99, nuclear 95/74/1.00), the ABCV(+A) clade (combined 97/92/1.00, plastid 84/68/1.00, nuclear 83/67/1.00) or the ADCP clade (combined 80/56/1.00, plastid 57/52/0.70, nuclear 69/–/1.00).

The combined tree contained most well-resolved groups from the individual trees, even if they were supported only in one of them. It followed this way the main dichotomy of Clades 1 and 2 observed in the plastid DNA tree and resolved supersubtribe Poodinae and subtribe Agrostidinae, which were likewise supported only in the plastid DNA tree. Conversely, supersubtribe Loliodinae, the ABCV+A and the HSAQN clade, subtribes Calothecinae, Scolochloinae and the Koeleriinae lineage combined with *Lagurus* found within Aveninae were present in the combined tree although they were supported only in the nr but not the plastid DNA tree.

Lineages with a discordant grouping in the individual analyses followed one of these placements in the combined tree. The particular placement was determined by either the (1) plastid or the (2) nuclear phylogenetic signal. Pattern 1 was encountered in Sesleriinae that were nested within the same main clade as in the plastid DNA tree but not together with Aveninae as in the nrDNA tree. Subtribe Aveninae resolved as monophyletic as in the plastid DNA tree; however, the placement of *Lagurus* and *Tricholemma* was different (see below). Subtribe Scolochloinae grouped as in the plastid DNA tree, whereas it was affiliated in the nrDNA tree with supersubtribe Agrostidodinae, namely subtribes Torreyochloinae and Phalaridinae. Pattern 2 occurred in Torreyochloinae and Phalaridinae, which built a clade sister to supersubtribe Agrostidodinae as similarly encountered in the nrDNA tree, whereas they were sister to Aveninae in the plastid DNA tree. *Lagurus* was sister to the Koeleriinae lineage as in the nrDNA tree. *Tricholemma* belonged to the Aveninae s.str., although its position was new relative to the nrDNA tree. Finally, *Macrobriza* was sister to the lineage of Aveninae and Sesleriinae in the nr but was placed within Brizinae in the plastid DNA tree.

Hybrid origin of major lineages, or subtribes and genera derived from hybridization between them. — Some lineages and genera have seemingly reticulate origin documented by the incongruent placement in the plastid and nrDNA trees and the different placement of their plastid and nuclear sequence partitions treated as duplicated taxa in Matrix 4 (Fig. 6; grey shading in Fig. 7). The examples of discordant grouping are best explained by ancient processes of hybridization or introgression resulting in "chloroplast capture", which means establishment of a new combination of nuclear and plastid genomes encountered in many groups of angio- and gymnosperms (Rieseberg & Soltis, 1991; Seehausen, 2004; Folk & al., 2017; Kawabe & al., 2018). It was recently discussed also as significant process in the origin of major phylogenetic lineages (Sun & al., 2015; García & al., 2017). Incomplete lineage sorting or other causes of incongruence appear to be less likely although we have not explicitly investigated this (see, for example, Lee-Yaw & al., 2019).

Due to the usually uniparental and maternal inheritance of organelles in angiosperms, the ancestors contributing the plastids were supposedly the maternal parent although low levels of paternal leakage, possibly widespread in angiosperms (Azhagiri & Maliga, 2007), backcrossing and lineage sorting in hybrid populations could also allow for fixation of parental plastid genomes and, therefore, alternative organellar relationships.

Both parental nrDNAs seemingly are no longer present in our hybrid origin lineages/taxa or at least were not detected by our approach using direct sequencing of PCR products. This can be due to (1) repeated backcrosses of hybrid generations with the paternal parent species as pollen donor in agreement with the chloroplast capture scenario or (2) due to sequence homogenization in favor of one parental copy type, a well-documented process of unidirectional loss of this repetitive DNA after hybridization (Alvarez & Wendel, 2003; Winterfeld & al., 2009, 2012; Kotseruba & al., 2010; Wölk & al., 2015; Tkach & al., 2019).

To account for the contrasting phylogenetic signals of the plastid and nrDNA sequence markers, they were included as separate partitions in Matrix 4 for taxa with incongruent placement in the individual gene trees. Several subtribes had plastid and nrDNA sequences (1) widely separated from each other in the tree, respectively (Airinae, Holcinae, Scolochloinae, Sesleriinae; Fig. 6). Likewise distinctively, though (2) less widely separated from each other were the plastid and nrDNA sequences of Anthoxanthinae, Antinoriinae, Avenulinae, Phalaridinae and Torreyochloinae as well as of *Arctopoa* and *Macrobriza*, respectively. The tree positions (3) of Aristaveninae and Helictochloinae were inconclusive because of the unsupported position of their nrDNA in the Matrix 4 analyses (see above Results: Combined dataset with duplicated…).

(1) Subtribes Airinae, Holcinae, Scolochloinae and Sesleriinae had one ancestor with Clade 2 plastid DNA, most likely from outside the PPAM clade (Figs. 4, 6, 7). In Scolochloinae, the genera *Dryopoa* (Australia) and *Scolochloa* (Holarctic) apparently had different plastid origins from relatives of Sesleriinae or Loliinae, respectively, but support for this is weak (Figs. 4, 6, 7). Plastid *Scolochloa* were closest to plastid Antinoriinae (Mediterranean; see below: Circumscription of lineages or genera). The likely paternal ancestor in Sesleriinae inherited the Aveninae-like nrDNA (Figs. 5–7) and, specifically, it was an Aveninae s.str.- and not Koeleriinae-like parent (Fig. 8 and above, Results: Plastid DNA analysis …). In Scolochloinae, the paternal ancestor for both of its genera as indicated by the nrDNA was close to supersubtribe Agrostidodinae such as seen in Phalaridinae and Torreyochloinae. The paternal ancestors of Scolochloinae and Sesleriinae, therefore, were distant to each other, in contrast to the plastid donor. An example showing the opposite are Airinae and Holcinae, which likely had the same paternal ancestor (nrDNA). This clade was sister to a lineage with Agrostidinae, Aveninae, etc. (Figs. 5–7).

(2) Anthoxanthinae, Phalaridinae, Torreyochloinae and *Macrobriza* had a maternal ancestor contributing as donor of plastid DNA of Clade 1 type (Figs. 4, 6, 7). Phalaridinae and Torreyochloinae both had the supposedly same ancestor with Aveninae-like plastid DNA as indicated by Figs. 4, 6. They had different ancestors as nrDNA donors that were close to supersubtribe Agrostidodinae. The Torreyochloinae ancestor was sister to supersubtribe Agrostidodinae, whereas Phalaridinae had seemingly the same paternal ancestor as Sclolochloinae. Anthoxanthinae displayed a different pattern because its maternal ancestor was close to supersubtribe Agrostidodinae, whereas its nrDNA donor belonged neither to Agrostidodinae nor to Aveninae but was close to both (Figs. 4–7). Monospecific *Macrobriza* had a maternal ancestor with Brizinae plastid DNA and an Aveninae-/Sesleriinae-like nuclear DNA donor. Antinoriinae, Avenulinae and *Arctopoa* had an ancestor contributing as donor of Clade 2 type plastid DNA. Antinoriinae hade possibly the same plastid donor ancestor as *Scolochloa* (Scolochloinae). The precise paternal ancestor of Antinoriinae was unclear because of the unresolved position of nuclear Antinoriinae within the clade of Loliinae, Parapholiinae, plastid Sesleriinae, etc. The maternal ancestor of Avenulinae belonged to supersubtribe Poodinae (~PAM clade), whereas the other parent inheriting its nrDNA was close to Coleanthinae. Both ancestors of *Arctopoa* belonged to supersubtribe Poodinae. The plastid donor of *Arctopoa* was related with, or belonged to, Poinae, whereas its paternal ancestor belonged to the ABCV clade in accordance with Gillespie & al. (2008, 2010).

An origin from hybridization across major lineages was discussed also in the instance of *Aniselytron* Merr. In *A. treutleri* (Kuntze) Soják, a strongly divergent, *Poa*-like ITS copy was found in previous studies in addition to the regular type belonging to the ABCV clade, pointing to either hybrid origin of *Aniselytron* or recent hybridization with *Poa* (Soreng & Davis, 2000; Gillespie & al., 2008, 2010; Soreng & al., 2017). Our results, however, indicated a concordant placement of *Aniselytron* sequences in the plastid and nuclear DNA trees within the ABCV clade, supporting recent hybridization or introgression of *Poa* in *Aniselytron* rather than hybrid origin of *Aniselytron* to explain the "alien" nrDNA copies.

Further instances of hybrid origin of lineages were revealed by the analyses of Matrices 5 and 6, with the reduced taxon sets (see below: Deep phylogenetic incongruence …).

Reticulations within major lineages. — (1) Within Aveninae, *Tricholemma* and *Lagurus* have a plastid DNA seemingly characteristic of early-branching Aveninae as a whole (Figs. 4, 8) (Wölk & Röser, 2017) and nrDNA sequences with characteristics of either Aveninae s.str. or the lineage of Koeleriinae, respectively. In the nrDNA tree, *Lagurus* was sister to the remaining genera of the latter and represents an early-branching offspring (Figs. 5, 8). *Tricholemma* was nested amidst the taxa of Aveninae s.str. Within the Koeleriinae lineage, there were several further instances of non-concordant placements of taxa, the most remarkable being that of *Graphephorum* Desv. (Wölk & Röser, 2017; see below: Aveneae).

(2) *Sesleria* Scop. (Sesleriinae) was sister to *Sesleriella* Deyl according to the plastid DNA data (Figs. 4, 9), whereas the nrDNA of *Sesleria* pointed to a close relation with *Psilathera* Link and *Echinaria* Desf. (Figs. 5, 9; see below: Unplaced lineages). As suggested by Kuzmanović & al. (2017), *Sesleria* originated most likely from hybridization

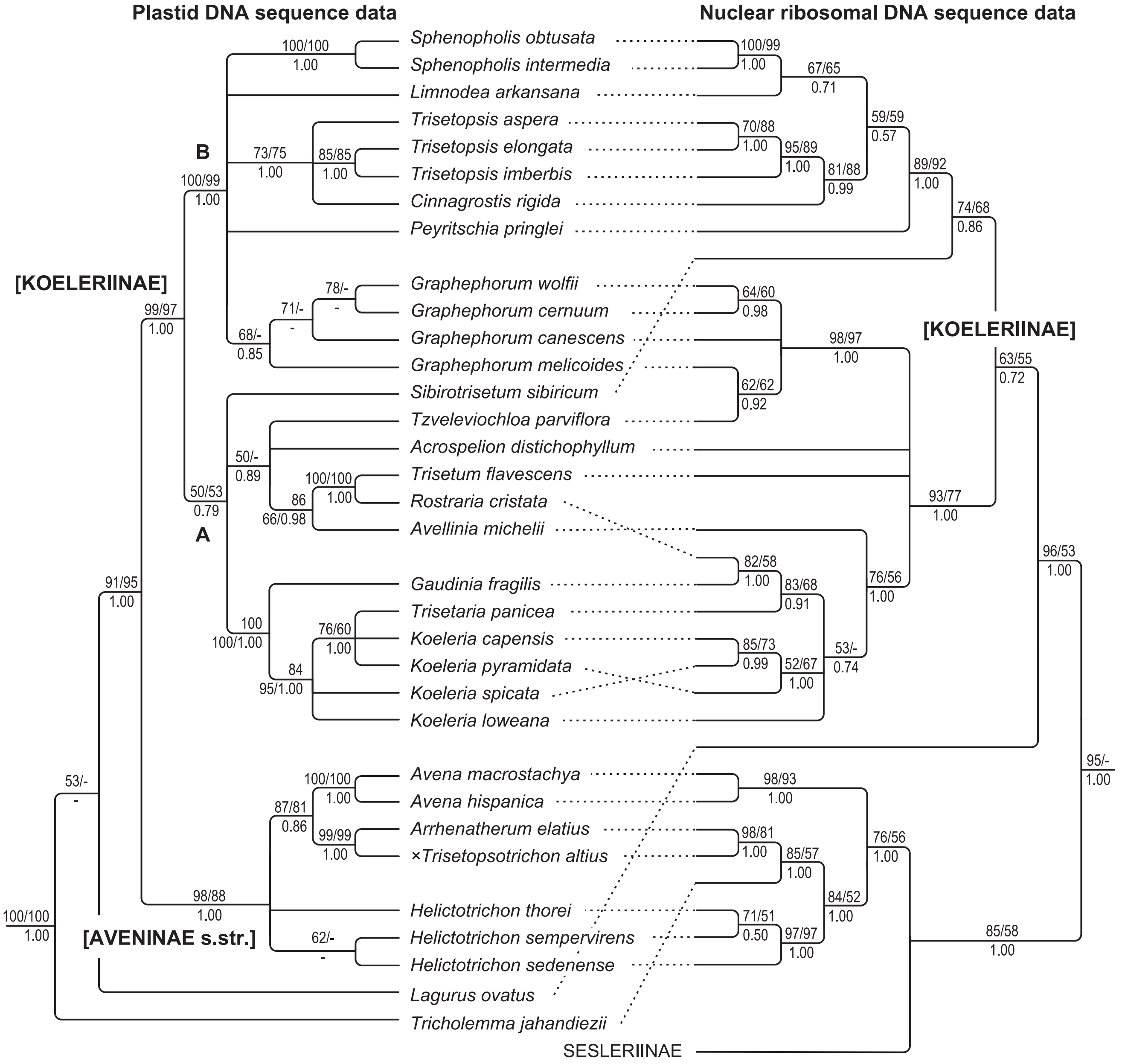

Fig. 8. Comparison of maximum likelihood cladograms for the genera of subtribe Aveninae inferred from plastid (*matK* gene–3′*trnK* exon, *trnL-trnF*) and nrDNA sequences (ITS, ETS). Maximum likelihood and maximum parsimony bootstrap support values >50% as well as Bayesian posterior probabilities >0.5 are indicated on the branches. Clades with maximum likelihood support <50% are collapsed. Aveninae is sometimes split into Koeleriinae, clades A and B, and Aveninae s.str. (square brackets).

between a maternal *Sesleriella*- and a paternal *Psilathera*-like ancestor. The monospecific genus *Echinaria* is unlikely to be involved in the origin of *Sesleria* because it is a short-lived annual of the Mediterranean lowlands in contrast to the other genera in question, which are characteristic perennials of mountainous habitats such as *Sesleria*.

(3) The new Coleanthinae genus *Hyalopodium*, gen. nov., comprises only *H. araraticum*, comb. nov. (≡ *Colpodium araraticum* (Lipsky) Woronow ex Grossh.). With respect to the nrDNA, *Hyalopodium* largely agreed with *Colpodium* Trin. (Figs. 4, 10) (Rodionov & al., 2008; Kim & al., 2009), whereas it shared plastid DNA characteristics with *Hyalopoa* (Tzvelev) Tzvelev (*H. pontica* (Balansa) Tzvelev) and *Paracolpodium* (Tzvelev) Tzvelev (*P. altaicum* (Trin.) Tzvelev, *P. baltistanicum* Dickoré; Figs. 5, 10), indicative of hybrid background.

The incongruent tree position of the sister genera *Puccinellia* Parl. and *Sclerochloa* P.Beauv. also points to hybrid origin because they clustered with *Catabrosa* P.Beauv. and *Catabrosella* (Tzvelev) Tzvelev in the plastid but with *Coleanthus* Seidel ex Roem. & Schult. and *Phippsia* (Trin.) R.Br. in the nrDNA tree (Figs. 4, 5, 10) (Schneider & al., 2009).

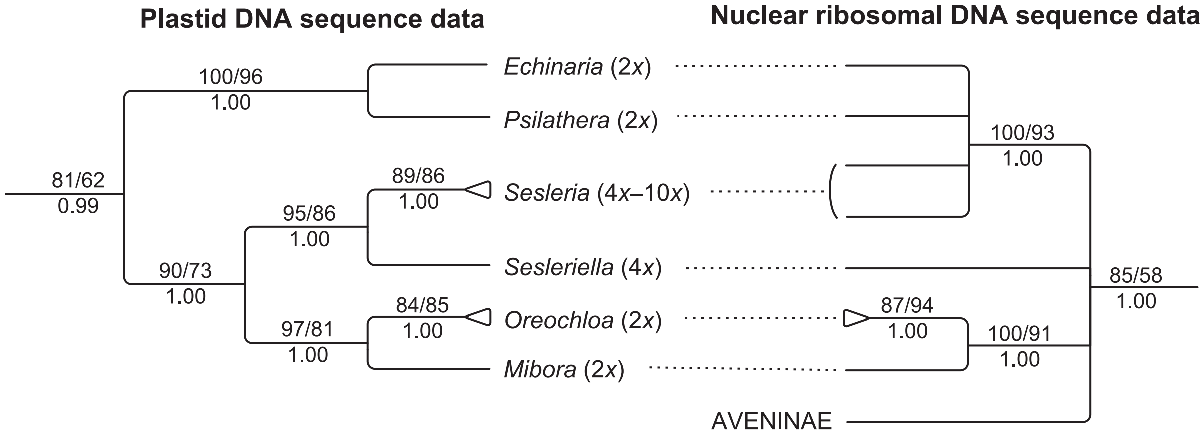

Fig. 9. Comparison of maximum likelihood cladograms for the genera of subtribe Sesleriinae inferred from plastid (*matK* gene–3′*trnK* exon, *trnL-trnF*) and nrDNA sequences (ITS, ETS). Maximum likelihood and maximum parsimony bootstrap support values >50% as well as Bayesian posterior probabilities >0.5 are indicated on the branches. Clades with maximum likelihood support <50% are collapsed.

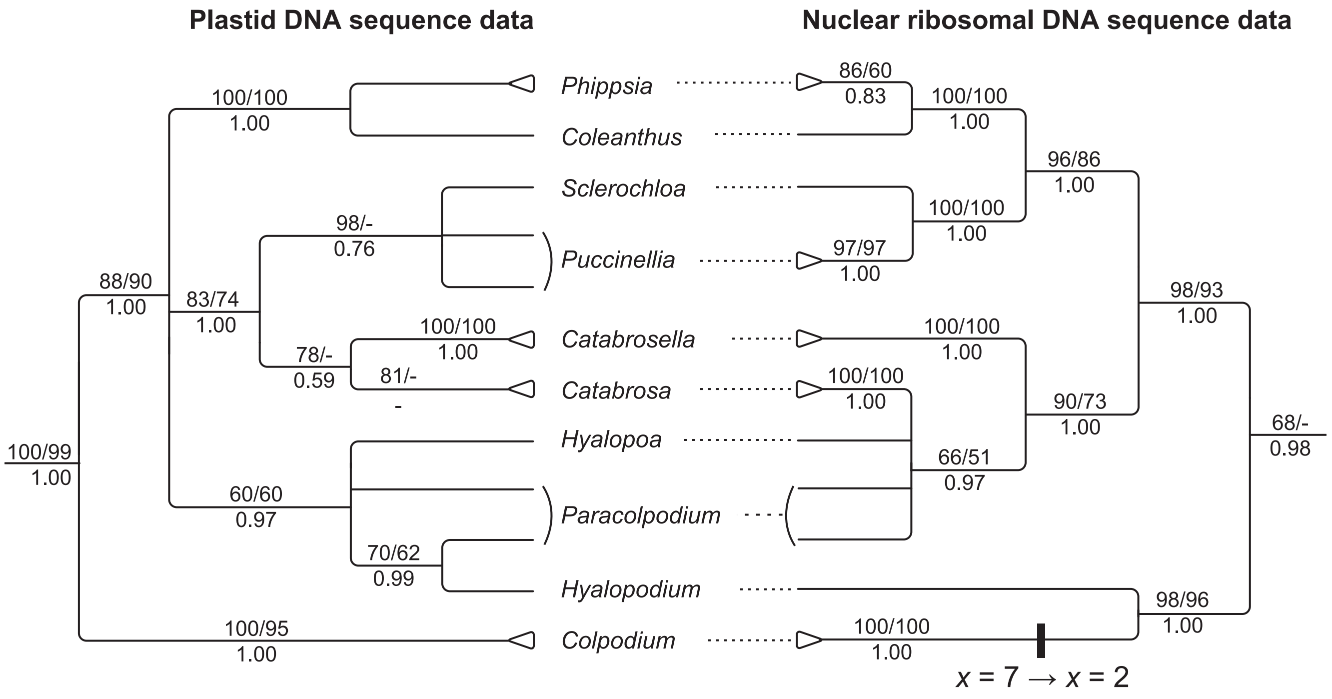

Fig. 10. Comparison of maximum likelihood cladograms for the genera of subtribe Coleanthinae inferred from plastid (*matK* gene–3′*trnK* exon, *trnL-trnF*) and nrDNA sequences (ITS, ETS). Maximum likelihood and maximum parsimony bootstrap support values >50% as well as Bayesian posterior probabilities >0.5 are indicated on the branches. Clades with maximum likelihood support <50% are collapsed.

(4) The monospecific genus *Castellia* Tineo (*C. tuberculosa* (Moris) Bor) of subtribe Loliinae presumably originated from a *Festuca* Tourn. ex L.-like maternal ancestor providing the plastid and a paternal ancestor related to *Drymochloa* Holub but a more extended sampling of broad- and narrow-leaved fescues would be worthwhile to verify this conclusion (Figs. 4, 5; see below: Festuceae).

Deep phylogenetic incongruence in Poodae. — Excluding taxa with discordant placements in the individual plastid and nrDNA analyses (not considering taxa, usually genera, with hybrid origin from within the same phylogenetic lineage or subtribe) revealed a deep phylogenetic incongruence in Poodae (suppl. Figs. S2, S3). The phylograms derived from Matrices 5 and 6 with the reduced datasets showed a similar number of major clades, but the sequence of their divergence and sister-group relations was different between the plastid and nrDNA trees (Fig. 11). In the plastid DNA phylogram (Figs. 11, 12; suppl. Fig. S2), the basal dichotomy was between Clades 1 and 2, which disintegrated into Clades 3 and 4 as encountered in principle also in Fig. 4. In the nrDNA phylogram (Figs. 11, 12; suppl. Fig. S3), the basal bifurcation was between Clades 4 and 5, which encompasses

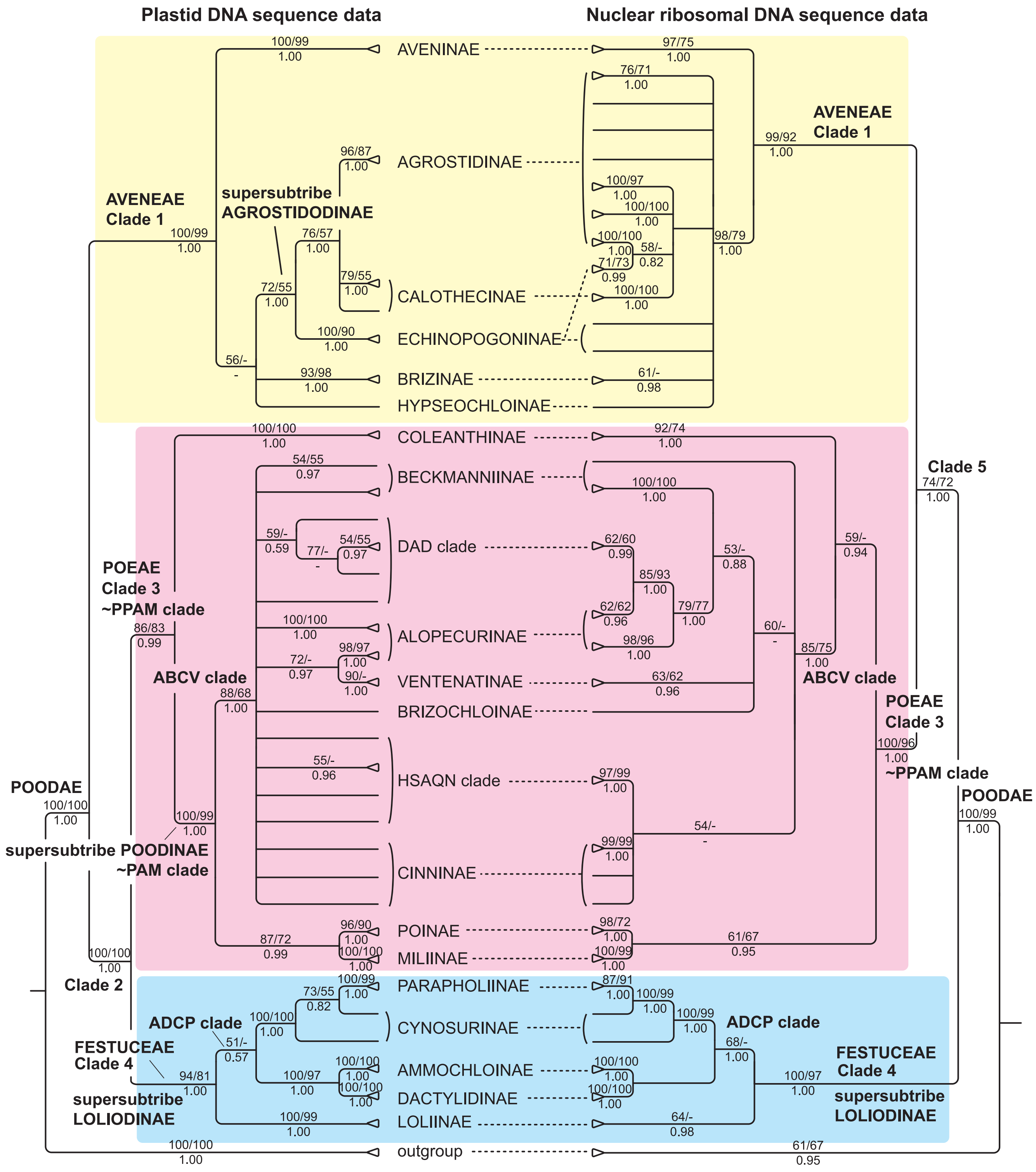

Fig. 11. Comparison of simplified maximum likelihood cladograms of Poodae inferred from Matrices 5 and 6 (reduced plastid and nrDNA sequence datasets excluding the taxa marked in Fig. 7). Maximum likelihood and maximum parsimony bootstrap support values >50% as well as Bayesian posterior probabilities >0.5 are indicated on the branches. Clades with maximum likelihood support <50% are collapsed. The expanded trees are displayed in supplementary Figs. S2 and S3, respectively.

Clades 1 and 3, a clade structure obscured in Fig. 5 by a basal polytomy. The taxonomic delineations of Clades 1, 3 and 4 were identical in both analyses, respectively. We interpret these results of deep incongruence as indicative of hybridization events involved in the early evolution of supertribe Poodae (Fig. 12). In other words, Clade 4 shares a plastid DNA

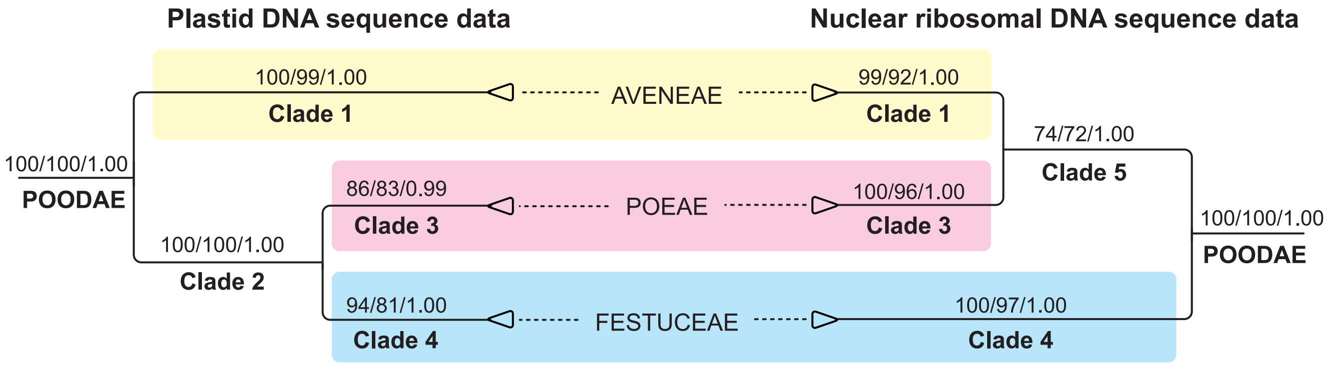

Fig. 12. Phylogenetic relationship of the major clades (Clades 1–5) of Poodae and proposed classification of tribes. Simplified maximum likelihood cladograms inferred from Matrices 5 and 6 (see Fig. 11). Maximum likelihood and maximum parsimony bootstrap support values >50% as well as Bayesian posterior probabilities >0.5 are indicated on the branches.

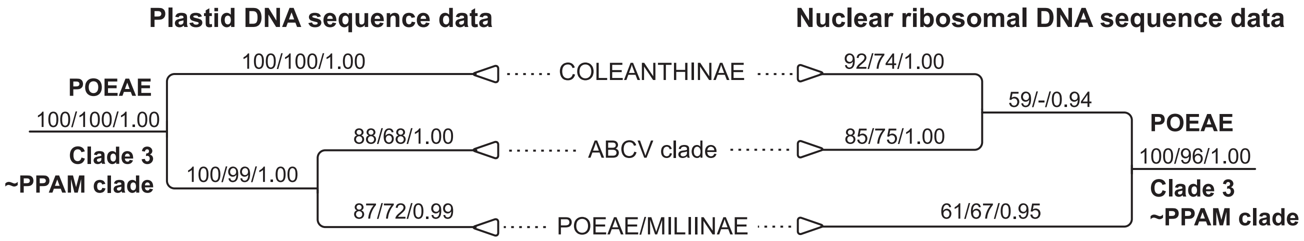

Fig. 13. Phylogenetic relationships of main clades within Poeae. Simplified maximum likelihood cladograms inferred from Matrices 5 and 6 (see Fig. 11). Maximum likelihood and maximum parsimony bootstrap support values >50% as well as Bayesian posterior probabilities >0.5 are indicated on the branches.

type with Clade 3 but not with Clade 1, whereas Clade 1 shares a nrDNA type with Clade 3 but not with Clade 4. Clade 3 had the same maternal ancestor as Clade 4 and the same paternal ancestor as Clade 1, indicating hybrid origin of the whole Clade 3 and making it an interesting example for the reticulate origin of a major lineage in grasses. Comparable instances of deep reticulation were recently documented also in other angiosperm families and orders (García & al., 2014, 2017; Sun & al., 2015; Bruun-Lund & al., 2017; Folk & al., 2017; Knowles & al., 2018; Herrando-Moraira & al., 2019).

Within Clade 3, the sister relations of the whole ABCV clade were different in the plastid DNA and the nuclear DNA analyses of the reduced datasets (Figs. 11, 13). According to the plastid DNA data, the ABCV clade was sister to Poinae/Miliinae, and their common lineage was sister to Coleanthinae. The nrDNA data, conversely, placed the ABCV clade as sister to Coleanthinae and their common lineage as sister to Poinae/Miliinae, although with lower support. This reveals the comparatively large ABCV clade as hybrid offspring (within hybrid Clade 3) with a Coleanthinae-like ancestor contributing as plastid and a Poinae/Miliinae-like ancestor as nuclear DNA donor, respectively.

Due to the fundamental cytonuclear discordance of the whole Clade 3, representing one of the three main lineages in Poodae, and of the ABCV clade within Clade 3 we did not combine Matrices 5 and 6 in a concatenated dataset to infer an "overall phylogeny" based on plastid and nrDNA sequence markers. In other words, after having excluded all taxa with obvious discordant placements (grey shading in Fig. 7) in the individual plastid and nuclear DNA sequence analyses (Figs. 4, 5), the data Matrices 5 and 6 still comprise large groups of taxa with allegedly but not actual congruent phylogenetic placements in the plastid and nrDNA analyses (Fig. 11). These deep levels of discordance (Figs. 12, 13) prevent the phylogenetic relationships of main lineages of Poodae to be displayed by a simple dichotomously branching tree.

Revised classification of Poodae

Three main clades with different sister relations in the plastid and nrDNA trees give evidence on a deep level of phylogenetic reticulation in Poodae, which is difficult to adequately deal with by formal taxonomic classification. Currently, an enlarged tribe Poeae (Poeae s.l.) is acknowledged in most recent classifications (Kellogg, 2015; Soreng & al., 2015b, 2017; Saarela & al., 2017), frequently making use of an informal arrangement of the subtribes in two groups (Clades 1 and 2 in this study) according to the plastid DNA types (Soreng & Davis, 2000; Davis & Soreng, 2007; Döring & al., 2007; Quintanar & al., 2007; Soreng & al., 2003, 2007; Döring, 2009; Schneider & al., 2009, 2012; Saarela & al., 2010, 2017, 2018; Kellogg, 2015; Pimentel & al., 2017; Orton

& al., 2019). To regard the two main clades (Clades 3 and 4) found in one of these groups (Clade 2) in the plastid DNA analyses and a similar phylogenetic structure in nrDNA (Clade 4 vs. Clade 5 with Clades 1 and 3 as its subclades) though with different sister relationships, we suggest recognition of three tribes, i.e., Aveneae (Clade 1), Poeae (Clade 3), with probably hybrid origin (see above), and Festuceae (Clade 4). Alternatively, maintenance of a sole tribe Poeae (s.l.) with recognition of supersubtribes Agrostidodinae (name applicable for Clade 1), Poodinae (Clade 3) and Loliodinae (Clade 4) could be envisaged. Our preferred solution, however, is more straightforward in our opinion because it, firstly, agrees with Art. 4.1 of the *International Code of Nomenclature for algae, fungi, and plants* (Turland & al., 2018), which recommends tribe (tribus) as secondary rank of taxa between family and genus, and, secondly, makes the use of an additional intercalated rank (Art. 4.3) such as supersubtribe dispensable. Following our suggestion and using narrowly delineated and preferably monophyletic subtribes as applied in most recent treatments of the study group (for example, Soreng & al., 2007, 2015b, 2017; Kellogg, 2015; Saarela & al., 2017), tribes and subtribes could be arranged as such:

Supertribe Poodae L.Liu: (1) tribe Aveneae Dumort.: subtribes Agrostidinae Fr., Anthoxanthinae A.Gray, Aveninae J.Presl, Brizinae Tzvelev, Calothecinae Soreng, Echinopogoninae Soreng, Hypseochloinae Röser & Tkach, Phalaridinae Fr., Torreyochloinae Soreng & J.I.Davis; (2) tribe Poeae R.Br.: subtribes Alopecurinae Dumort., Avenulinae Röser & Tkach, Beckmanniinae Nevski, Brizochloinae Röser & Tkach, Cinninae Caruel, Coleanthinae Rouy, Miliinae Dumort., Phleinae Dumort., Poinae Dumort., Ventenatinae Holub ex L.J.Gillespie & al.; (3) tribe Festuceae Dumort.: subtribes Ammochloinae Tzvelev, Cynosurinae Fr., Dactylidinae Stapf, Loliinae Dumort., Parapholiinae Caro. (4) Unplaced (incertae sedis) and presumably of hybrid origin between tribes Aveneae and Festuceae are subtribes Airinae Fr., Antinoriinae Röser & Tkach, Aristaveninae F.Albers & Butzin, Helictochloinae Röser & Tkach, Holcinae Dumort., Scolochloinae Tzvelev and Sesleriinae Parl.

Avenulinae has hybrid origin between ancestors both belonging to Poeae. Anthoxanthinae, Phalaridinae and Torreyochloinae have hybrid origin between ancestors both belonging to Aveneae. These subtribes can be accommodated under the respective tribes.

Circumscription of lineages or genera

Our molecular phylogenetic data support the circumscription of many lineages that have already been recognized previously. However, due to the inclusion of several taxa that have not been sampled before and the sampling strategy including a comparatively broad representative set of taxa used for both plastid and nrDNA sequence data, some re-arrangements and emendations are required.

Aveneae. — *(1) Aveninae*. – This large lineage encompasses two main subgroups, namely Aveninae s.str. and the Koeleriinae lineage. Additionally, there are two somewhat isolated genera with hybrid background (see above: Reticulations within major lineages), namely monospecific *Lagurus* (type *L. ovatus*) and *Tricholemma* (two species; type *T. jahandiezii*; Röser, 1989, 1996; Röser & al., 2009; Gabriel & al., 2020) (Fig. 3K), making a separation of Aveninae s.str. and Koeleriinae as distinct subtribes not straightforward (Figs. 4, 5, 8), even if *Lagurus* is accommodated under a monogeneric subtribe Lagurinae (Saarela & al., 2017). For this reason, it might be better to summarize all of them under a broader subtribe, i.e., Aveninae.

The taxa of Aveninae have several flowers per spikelet, but there are exceptions with only a single flower such as *Lagurus*, *Limnodea* or Mexican to South American members of ‘*Calamagrostis*’/‘*Deyeuxia*’ recently transferred to *Cinnagrostis* Griseb. (Peterson & al., 2019). The phylogenetic trees of the Aveninae s.str. showed a rather narrowly delineated genus *Helictotrichon* Besser after exclusion of *Tricholemma*, Subsaharo-African to Southeast Asian *Trisetopsis* Röser & A.Wölk (type *T. elongata* (Hochst. ex A.Rich.) Röser & A.Wölk; Fig. 3L) and East Asian *Tzveleviochloa* Röser & A.Wölk (type *T. parviflora* (Hook.f.) Röser & A.Wölk; Fig. 3I), which are members of the Aveninae but belong to the Koeleriinae lineage. Excluded from *Helictotrichon* were also *Helictochloa* and *Avenula*, which were placed even more distantly in the molecular phylogenetic analyses (Figs. 4, 5). Further excluded was the nothogenus ×*Trisetopsotrichon* Röser & A.Wölk. The redefined genus *Helictotrichon* (type *H. sempervirens* (Vill.) Pilg.; studied also by Wölk & Röser, 2014, 2017; Wölk & al., 2015) (Fig. 2I) encompasses the former genus *Pseudarrhenatherum* Rouy (type *H. thorei* Röser = *P. longifolium* (Thore) Rouy) and was corroborated in this circumscription as monophyletic (data not shown; Appendix 1) (Schneider & al., 2009). *Avena* (Fig. 1M), a genus with consistently annual species except for the perennial *A. macrostachya* Balansa ex Coss. & Durieu, was close to *Arrhenatherum* P.Beauv. (type *A. elatius* (L.) P.Beauv. ex J.Presl & C.Presl) according to the plastid DNA but not the nrDNA trees, in which *Arrhenatherum* clustered with *Tricholemma* and *Helictotrichon* (Figs. 4, 5, 8).

The delineation of genera within the Koeleriinae lineage still is an insufficiently solved problem as there are seemingly intermediates between traditionally acknowledged genera and a considerable degree of hybrid speciation and allopolyploid evolution (Quintanar & al., 2010; Saarela & al., 2010, 2017; Wölk & Röser, 2014, 2017; Wölk & al., 2015; Soreng & al., 2017; Barberá & al., 2019). As a possible consequence, all genera of Koeleriinae widely accepted at the present time were unified by Kellogg (2015) under a single genus, *Trisetaria* Forssk. More detailed investigations using a broad phylogenetic sampling of taxa are evidently necessary to delineate well-defined genera within Koeleriinae or, alternatively, infrageneric entities in broadly delineated *Trisetaria*.

The backbone of the plastid DNA tree showed largely a polytomy for Koeleriinae (excluding *Lagurus*) if not considering the unsupported placement of *Sibirotrisetum* Barberá & al.

(Figs. 4, 8). A maximally supported clade (100/99/1.00) contained the sampled species of *Graphephorum* (type *G. melicoides* (Michx.) Desv.; Fig. 2G), *Limnodea* (type *L. arkansana*), *Peyritschia* E.Fourn. (type *P. koelerioides* (Peyr.) E.Fourn., used together with *P. pringlei* (Scribn.) S.D. Koch [Fig. 3E] in this study and *P. deyeuxioides* (Kunth) Finot studied by Wölk & Röser, 2017 showing their monophyly), *Sphenopholis* Scribn. (type *S. obtusata* (Michx.) Scribn.), *Trisetopsis* and *Cinnagrostis rigida* in agreement with our previous findings (Wölk & Röser, 2014). This clade agreed largely with Koeleriinae clade B of Saarela & al. (2017) and Barberá & al. (2019). It was present in principle also in the nrDNA analyses (98/92/1.00; Figs. 5, 8) but without *Graphephorum* species. They assembled in a strongly supported clade (98/97/1.00) with *Avellinia* Parl. (type *A. michelii* (Savi) Parl.), *Gaudinia* J.Gay (type *G. fragilis* (L.) P.Beauv.), *Rostraria* Trin. (type *R. pubescens* Trin. = *R. cristata* (L.) Tzvelev), *Trisetaria*, *Koeleria* Pers. (type *K. pyramidata* (Lam.) P.Beauv.) including the former genus *Parafestuca* E.B.Alexeev (type *P. albida* (Lowe) E.B.Alexeev ≡ *K. loweana* Quintanar & al.), *Trisetum* Pers. (type *T. flavescens* (L.) P.Beauv.; Fig. 3G), *Acrospelion* Besser (type *A. distichophyllum* (Vill.) Barberá) and *Tzveleviochloa*. This clade agreed with Koeleriinae clade A (Saarela & al., 2017; Barberá & al., 2019) despite different sampling. The changing position of American *Graphephorum* (Figs. 4, 5, 8) (Wölk & Röser, 2014, 2017; Saarela & al., 2017) points to its likely hybrid origin.

The American *Trisetum* species *T. canescens* Buckley and *T. cernuum* Trin. were unified in all analyses in a common lineage with *Graphephorum* supporting their inclusion in this genus (see below: New names and combinations). South East Asian *Tzveleviochloa parviflora* and *T. potaninii* (Tzvelev) Röser & A.Wölk (the latter not shown) were allied with *Graphephorum* in the nrDNA data analyses but assembled with Koeleriinae clade A species in the plastid DNA tree, suggesting reticulate origin.

Sibirotrisetum sibiricum (Rupr.) Barberá, type of *Sibirotrisetum*, segregated from the species currently ascribed to genera *Trisetum* and *Acrospelion* in both the plastid and the nrDNA analysis. It was part of the backbone polytomy or placed in an unsupported clade with clade A genera (Figs. 4, 8) in the former analysis and sister to the Koeleriinae clade B (74/68/0.86) in the latter (Figs. 5, 8). Most likely due to the different taxon sampling, *S. sibiricum* stood in the study of Barberá & al. (2019) in a polytomy with, or was unsupported sister to, clades A and B according to the nrDNA, whereas it was sister to clade B according to their plastid DNA data.

(2) Agrostidinae and Hypseochloinae; Calamagrostis and Deyeuxia. – Subtribe Agrostidinae, characterized by single-flowered spikelets, is well-supported as monophyletic by the plastid DNA (83/79/1.00) but not the nrDNA data analyses, due to the polytomy mentioned. African *Hypseochloa* deviated from Agrostidinae but belonged to supersubtribe Agrostidodinae in the plastid DNA analyses (Figs. 4, 5, 7). It may be best to assign it to a new monogeneric subtribe, Hypseochloinae, which is morphologically supported by peculiar lemma characters not found elsewhere in Agrostidodinae (Hubbard, 1936, 1981; Clayton & Renvoize, 1986; Kellogg, 2015; see below: New names and combinations).

Agrostidinae comprised three well-supported lineages in the plastid DNA tree, which were arranged largely in a polytomy with the remainder of this subtribe and, in the nrDNA tree, in an even more extensive polytomy with taxa of Brizinae, Calothecinae and Echinopogoninae.

One of these well-supported Agrostidinae lineages in both analyses (plastid and nrDNA; 100/100/1.00 and 100/100/1.00, respectively) was composed of *Gastridium phleoides* (Nees & Meyen) C.E.Hubb., *G. ventricosum* (Gouan) Schinz & Thell. (type of *Gastridium* P.Beauv.) and *G. nitens* (Guss.) Coss. & Durieu (type of *Triplachne* Link; Fig. 2F) as similarly found in several previous studies (Davis & Soreng, 2007; Quintanar & al., 2007; Soreng & al., 2007; Döring, 2009; Saarela & al., 2010, 2017; Orton & al., 2019). Species of *Gastridium* and former *Triplachne* were even intermingled in the plastid DNA tree. This supports their assignment to a single genus, which is emphasized also by their strong morphological similarity (Clayton & Renvoize, 1986).

The second supported lineage in the plastid DNA tree (96/81/1.00; Fig. 4) comprised *Agrostis alopecuroides* Lam. (= *Polypogon monspeliensis* (L.) Desf., type of *Polypogon* Desf.), *A. avenacea* J.F.Gmel. (= *Lachnagrostis filiformis* (G.Forst.) Trin., type of *Lachnagrostis* Trin.; Fig. 1A), *A. capillaris* L. (Fig. 1B), *A. linkii* Banfi & al. (= *Chaetopogon fasciculatus* (Link) Hayek, type of *Chaetopogon* Janch.), *A. pallens* Trin., *A. ramboi* Parodi (≡ *Bromidium ramboi* (Parodi) Rúgolo) and *A. scabra* Willd. In the nrDNA tree (Fig. 5), this lineage disintegrated into a polytomy with strongly supported *A. avenacea* and *A. alopecuroides* as sister (100/100/1.00) and a monophyletic lineage of the remaining species (100/97/1.00), which was complemented by a further species of the former genus *Bromidium* Nees & Meyen (*A. tandilensis* (Kuntze) Parodi; only ITS). *Agrostis linkii* was sister to *A. capillaris*, and former *Bromidium* was non-monophyletic. This makes it reasonable to include all taxa in a broadly circumscribed genus *Agrostis* L. as suggested already for *Chaetopogon* (Kellogg, 2015; Soreng & al., 2017; Banfi & al., 2018). Former *Chaetopogon* was also nested within *Agrostis* considering the ITS data investigated by Quintanar & al. (2007) and Saarela & al. (2010, 2017). The same applies to former *Polypogon*, which shares spikelets falling entire and other characters with former *Chaetopogon*. Barely separable are also *Lachnagrostis*, a richly evolved group in temperate Australasia encompassing ~38 species (Jacobs & Brown, 2009), and *Bromidium*, which encompasses five species in South America (Rúgolo de Agrasar, 1982).

The third well-supported lineage of Agrostidinae (plastid 94/94/1.00, nuclear 99/98/1.00) was represented by two species sampled of *Podagrostis* (Griseb.) Scribn. & Merr., *P. aequivalvis* (Trin.) Scribn. & Merr. (type of *Podagrostis*) and *P. thurberiana* (Hitchc.) Hultén. It was separate from *Agrostis* in both analyses, which supports maintenance of *Podagrostis* as a distinct genus (Figs. 4, 5).

The (1) holarctic, temperate species of *Calamagrostis* sampled in this study (Old and New World; Appendix 1) belonged to Agrostidinae, whereas (2) the Mexican to South American, now transferred to *Cinnagrostis* (Peterson & al., 2019), and (3) Australasian taxa sampled, were nested in the lineages of Aveninae and Echinopogoninae, respectively (Figs. 4, 5) (Saarela & al., 2010, 2017; Wölk & Röser, 2014, 2017). The latter (2, 3) were usually treated under either *Calamagrostis* or, more frequently, *Deyeuxia* (for example, Bor, 1960; Rúgolo de Agrasar, 1978, 2006; Nicora & Rúgolo de Agrasar, 1987; Edgar, 1995; Villavicencio, 1995; Renvoize, 1998; Edgar & Connor, 2000; Sharp & Simon, 2002; Weiller & al., 2009; Rúgolo, 2012a). Neither genus name can be used for them because the type of *Calamagrostis* is *Arundo calamagrostis* L., a synonym of *C. canescens* (Weber) Roth, which was nested within Agrostidinae (Figs. 4, 5). The type of *Deyeuxia* is *D. montana* (Gaud.) P.Beauv., a synonym of *C. arundinacea* (L.) Roth based on *Agrostis arundinacea* L., not *Arundo calamagrostis* L., which likewise belongs to Agrostidinae. Moreover, *Deyeuxia* is synonymous with *Calamagrostis* (Wölk & Röser, 2014; Saarela & al., 2017; Soreng & al., 2017), if *C. canescens* and *C. arundinacea* belong to a single genus, which is more than likely considering the plastid and nrDNA analyses, in which both species were placed with all other species of *Calamagrostis* sampled from Eurasia and North America in a polytomy (Figs. 4, 5).

An exception was the Tibetan '*Calamagrostis*' *flavens* (Keng) S.L.Lu & Z.L.Wu (Fig. 2D). This species clustered in the plastid DNA tree together with *Podagrostis*, *Gastridium* and *Agrostis* in a considerably supported clade (95/70/1.00), whereas it was part of the polytomy of Agrostidinae/Brizinae/Calothecinae/Echinopogoninae in the nrDNA tree (Figs. 4, 5). Morphologically, this species has an unusual combination of characters otherwise found in *Agrostis* and *Calamagrostis* as noted by Lu & al. (2006), which seems to fit its ambiguous placement in the trees and points to a possible intergeneric hybrid origin.

Calamagrostis arenaria (L.) Roth (Fig. 1N), type of the former genus *Ammophila* Host, fell within *Calamagrostis* in the nrDNA data tree (Fig. 5) in agreement with Saarela & al. (2017). Our plastid DNA tree (Fig. 4) was not decisive, whereas that of Saarela & al. (2017) clearly showed *C. arenaria* nested within traditional *Calamagrostis* species (Fig. 1O). Inclusion of this awnless or short-awned species in *Calamagrostis* agrees also with morphological data, although previous literature mostly kept this ecologically notable species of coastal dune sands separate (Tutin, 1980; Conert, 1979, 1998, 2000). Species of the former genus *Ammophila*, viz. *C. arenaria* in Europe and *C. breviligulata* (Fernald) Saarela in North America, are known to hybridize with *C. epigejos* and *C. canadensis* (Michx.) P.Beauv., respectively. Hybrids between the former species were named *C.* ×*baltica* (Flüggé ex Schrad.) Trin. (≡ ×*Calammophila baltica* (Flüggé ex Schrad.) Brand ≡ ×*Ammocalamagrostis baltica* (Flüggé ex Schrad.) P.Fourn. = *Calamagrostis* ×*calammophila* Saarela). They form amazingly extensive stands along the coasts of the North and the Baltic Sea (Conert, 1979, 1998; Tutin, 1980), where they are locally more abundant than the parental species.

(3) Echinopogoninae and Calothecinae. – These are subtribes of the Southern Hemisphere. Australasian Echinopogoninae were strongly supported (100/99/1.00) as monophyletic by the plastid DNA data (not available for New Guinea to Queensland *Ancistragrostis*; Fig. 4) but formed to a large extent a polytomy with other subtribes of supersubtribe Agrostidodinae in the nrDNA data (Fig. 5). Echinopogoninae were represented in this study by monospecific *Ancistragrostis*, two species of *Dichelachne*, *Echinopogon*, *Relchela* (monospecific), two accessions of *Pentapogon* (monospecific; Fig. 3C) and '*Deyeuxia*' *contracta*. A placement within Echinopogoninae was reported also for the species of '*Deyeuxia*' from Australia and New Zealand studied by Saarela & al. (2017). They belong to the ~40 species of this region unified under the genus name '*Deyeuxia*' (Vickery, 1940; Edgar & Connor, 2000; Weiller & al., 2009) as a presumed segregate of *Calamagrostis*. '*Deyeuxia*' *contracta* was closer to *Pentapogon* than to *Dichelachne* according to the plastid and nrDNA data (Figs. 4, 5). Merging *Dichelachne* with '*Deyeuxia*' (Kellogg, 2015), therefore, was not supported, unless *Pentapogon* would likewise be abandoned as a genus. For nomenclature reasons, the genus name '*Deyeuxia*' is not applicable anyway (see above).

Calothecinae (Mexico to South America) encompass only *Chascolytrum* Desv. (type *C. subaristatum* (Lam.) Desv.) after inclusion of several segregate genera such as *Erianthecium* Parodi (type *E. bulbosum* Parodi), *Rhombolytrum* Link (type *R. rhomboideum* Link), *Poidium* Nees (*P. uniolae* (Nees) Matthei sampled) and others (Essi & al., 2017; Silva & al., 2020). *Chascolytrum* proved monophyletic in this study according to the nrDNA data (89/88/1.00; Fig. 5) such as found by Persson & Rydin (2016) for their set of taxa, whereas *Briza media* L. was nested among the New World *Chascolytrum* taxa in the ITS/GBSSI tree of Essi & al. (2008: fig. 2) although without support. As addressed above, this was possibly due to insufficient taxon sampling.

(4) Brizinae and Macrobriza. – Monospecific *Airopsis* Desv. (*A. tenella* Coss. & Durieu) was a supported member of subtribe Brizinae. It segregated from the representatives of the genus *Briza* L. (type *B. minor* L.) in the molecular phylogenetic trees and is also morphologically distinct enough to be acknowledged as separate genus (Figs. 4, 5). *Briza media* (Fig. 1G), *B. minor* and *Macrobriza maxima* (L.) Tzvelev were placed in a common lineage according to the plastid DNA data, whereas *Macrobriza* deviated clearly in the nrDNA tree (see above: Hybrid origin of major lineages …). This discordant placement is implicitly obvious also in the study of Persson & Rydin (2016), which showed *M. maxima* placed together with *B. marcowiczii* Woronow, *B. media* and *B. minor* in a common clade according to the plastid DNA data, whereas *M. maxima* clustered with taxa of Aveninae according to the nuclear ITS/GBSSI data. The sample studied by Essi & al. (2008) encompassed *Briza*, *Macrobriza* and

species nowadays assigned to *Chascolytrum* but no taxa of Aveninae. *Macrobriza* clustered with *B. minor* in the ITS/GBSSI tree of their fig. 5, whereas *B. media* clustered with taxa of *Chascolytrum*, which may be due to insufficient taxon sampling as noted by Saarela & al. (2017).

Considering morphology, monospecific *Macrobriza* by and large resembles *Briza* but differs by its overall tall size, comparatively few-flowered spikelets and a linear instead of elliptic hilum of the caryopsis, which induced Tzvelev to treat it firstly as *Briza* subsect. *Macrobriza* Tzvelev and later as a genus (Tzvelev, 1970, 1993). Its hybrid origin between ancestors from Brizinae contributing as plastid DNA donor and Aveninae/Sesleriinae as nrDNA donor as discussed above suggests its exclusion from Brizinae. Alternatively, the odd placement of *Macrobriza* according to its nrDNA sequences could be due to an artefactual placement in a way that long branches are erroneously grouped together in tree estimations (long-branch attraction; Felsenstein, 1978; Sanderson & al., 2000; Parks & Goldman, 2014; Qu & al., 2017; Mai & Mirarab, 2018) caused by mutation-saturated DNA sequences in presumably rapidly evolving taxa such as annuals and giving a spurious phylogenetic signal. Annual *Macrobriza* shares a considerable branch length with other annuals investigated in this study, for example, *Airopsis* (Brizinae), *Ammochloa* (Ammochloinae), *Brizochloa* (Brizochloinae), *Echinaria* (Sesleriinae), *Lagurus* (Aveninae), *Mibora* Adans. (Sesleriinae), *Molineriella* (Helictochloinae), *Rhizocephalus* Boiss. (Beckmanniinae), annual species of *Poa* (*P. annua* L., *P. cyrenaica* E.A.Durand & Barratte; Poinae) and *Phalaris* L. (*P. canariensis* L.; Phalaridinae; Figs. 4, 5) but also some perennials, for example, *Anthoxanthum odoratum* L. (Anthoxanthinae) or *Arrhenatherum elatius* (Aveninae). In all of these instances, their phylogenetic placement does not appear to be spurious considering the comparatively straightforward alignment of their sequences (see alignments; suppl. Appendices S1–S4).

(5) Anthoxanthinae. – Cumarin-scented Anthoxanthinae were corroborated as clearly monophyletic and distinct from scentless Phalaridinae as suggested by several previous molecular phylogenetic studies (Figs. 4, 5, 7) (Döring & al., 2007; Quintanar & al., 2007; Döring, 2009; Saarela & al., 2015, 2017; Rodionov & al., 2017; Orton & al., 2019). Anthoxanthinae had a reticulate origin with ancestors from different lineages within Aveneae, which applies also to Torreyochloinae and Phalaridinae (see above). Species traditionally assigned to *Hierochloe* R.Br. (including the type, *H. odorata* (L.) P.Beauv. = *Anthoxanthum nitens* (Weber) Y.Schouten & Veldkamp), namely *H. australis* (Schrad.) Roem. & Schult. (≡ *A. australe* (Schrad.) Veldkamp), *H. glabra* Trin. (≡ *A. glabrum* (Trin.) Veldkamp), *H. pauciflora* R.Br. (= *A. arcticum* Veldkamp), *H. redolens* (Vahl) Roem. & Schult. (≡ *A. redolens* (Vahl) P.Royen) and *H. repens* (≡ *A. repens* (Host) Veldkamp; not all shown in Figs. 4, 5), were not consistently separated from *Anthoxanthum* L. since *A. odoratum* (type of *Anthoxanthum*; Fig. 1F) was sister to traditional *H. australis* (plastid DNA tree) or was placed between species of traditional *Hierochloe* (nrDNA tree). The peculiar tree position of *H. australe*, a species not sampled by Pimentel & al. (2013), agreed with that obtained by Rodionov & al. (2017) on ITS. All in all, the findings support the inclusion of *Hierochloe* in *Anthoxanthum* (Schouten & Veldkamp, 1985) as suggested also by Pimentel & al. (2013: 1025) in view of the intermediate floral characters of *A.* sect. *Ataxia* (R.Br.) Stapf between typical *Anthoxanthum* and *Hierochloe* (Connor, 2012).

(6) Torreyochloinae and Phalaridinae. – Subtribe Torreyochloinae consists of South Hemispheric *Amphibromus* Nees (Fig. 1E) and North American/East Asian *Torreyochloa* Church. Torreyochloinae shared a plastid DNA type with *Phalaris* (Döring, 2009; Saarela & al., 2015; Orton & al., 2019), the only genus of holarctic Phalaridinae, but were more distant to each other in nr ITS since Torreyochloinae were supported sister to supersubtribe Agrostidodinae, whereas Phalaridinae were closer to Scolochloinae (Figs. 4, 5, 7). Interestingly, the three subtribes share eco-morphological characteristics since *Amphibromus*, *Torreyochloa*, *Phalaris*, *Scolochloa* and *Dryopoa* have rather tall, sometimes reed-like perennial species, which prefer aquatic habitats or wet mountain forests (*Dryopoa*), except for the annuals of *Phalaris*, some of which are adapted to seasonally dry Mediterranean-type climate but preferring ephemeral wetlands (Baldini, 1995).

Poeae. — The tribe Poeae in sense of this study corresponds to the PPAM clade. It was resolved in all of our phylogenetic analyses. Poeae were more strongly supported in the nr than the plastid DNA analyses (Figs. 4, 5; suppl. Figs. S2, S3).

(1) Coleanthinae. – Within the monophyletic subtribe Coleanthinae (= Puccinelliinae), several species were repeatedly transferred from one genus to another, and genus limits are still in dispute. Our results support recognition of ten genera, which partly have a new delineation. A close relationship of perennial *Colpodium* and annual species that usually were treated under *Zingeria* P.A.Smirn. was suggested by all our trees and has already been noted by Tzvelev & Bolkhovskikh (1965) and Soreng & al. (2017). The tree from the plastid DNA data showed the sampled representatives of *Colpodium* and former *Zingeria* intermingled (Fig. 4; see below: New names and combinations), namely *C. versicolor* (Steven) Schmalh. (type of *Colpodium*), *Z. biebersteiniana* (Claus) P.A.Smirn. (type of *Zingeria*), *Z. trichopoda* (Boiss.) P.A. Smirn, *C. hedbergii* (Melderis) Tzvelev and *C. chionogeiton* (Pilg.) Tzvelev. Both these latter species occur in Africa and had sometimes been accommodated under *Keniochloa* Melderis (type *K. chionogeiton* (Pilg.) Melderis). The nrDNA tree showed the former *Zingeria* species in a grade with the other *Colpodium* species sampled (Fig. 5) as similarly encountered by Kim & al. (2009). If their different life form is left aside, there are no striking differences between *Colpodium* and former *Zingeria*, both of which have small spikelets with a single bisexual flower, and we suggest unifying them under a single genus. *Colpodium* is the genus with the lowest monoploid chromosome number known in grasses of $x = 2$. There are known diploids with $2n = 4$, namely (*C. biebersteinianum*, comb. nov., and *C. versicolor*) and several polyploids, namely

C. trichopodum, comb. nov., and *C. pisidicum*, comb. nov., with 2*n* = 8, and *C. kochii*, comb. nov., with 2*n* = 12. *Colpodium versicolor* (2*x*) was shown to be the donor of one genome in allohexaploid *C. kochii* (Kotseruba & al., 2010), whereas it is not represented in allotetraploid *C. trichopodum* (Kotseruba & al., 2005).

The nrDNA tree revealed *Hyalopodium* (*H. araraticum*) as sister to the clade with the species of *Colpodium*, which was similarly encountered in the ITS studies of Rodionov & al. (2008) and Kim & al. (2008, 2009). However, the plastid DNA tree supported a deviant relationship of *Hyalopodium* (Figs. 4, 5, 10; suppl. Figs. S2, S3), namely to *Paracolpodium* and *Hyalopoa* (*H. pontica*). These differences between the plastid and nrDNA analyses suggest an origin of *Hyalopodium* as a hybrid between two different lineages of Coleanthinae (Fig. 10). *Hyalopodium araraticum* has formerly been treated under *Catabrosa*, *Colpodium* or *Catabrosella*. It is long-known as remarkable species because of its odd combination of morphological characters and had been placed in a monospecific section of *Catabrosella*, namely *C.* sect. *Nevskia* (Tzvelev) Tzvelev (Tzvelev, 1976), which seemingly had never been validly raised to genus rank although that was stated by Kim & al. (2008). *Hyalopodium araraticum* has spikelets with several flowers such as found in *Catabrosella* and *Hyalopoa* s.str., has creeping underground shoots like *Paracolpodium* and *Hyalopoa*, whereas *Catabrosella* and *Colpodium* are not creeping (Tzvelev, 1964a). A conspicuous character of *Hyalopodium* among Coleanthinae are its aerial shoots with reticulate-fibrous sheaths of dead leaves at the base, which, however, resemble the filamentously, though not reticulately decaying basal leaf sheaths of *Hyalopoa pontica* (pers. obs.; Mill, 1985). Chromosomally, it has a monoploid number of *x* = 7 like *Paracolpodium* and *Hyalopoa* (CCDB, 2019), not *x* = 2 as in *Colpodium*. This makes it likely that the paternal parent of *Hyalopodium* did not come from present-day *Colpodium*, but was an ancestor still having the plesiomorphic monoploid chromosome number of *x* = 7 (Fig. 10).

Paracolpodium altaicum (type of *Paracolpodium*) and *P. baltistanicum* clustered together with *Hyalopoa pontica* (type of *Hyalopoa*) in all analyses of this study although with weak support (Figs. 4, 5, 10; suppl. Figs. S2, S3). Both genera consistently encompass species with creeping underground shoots in contrast to tufted *Colpodium* and *Catabrosella*. *Paracolpodium* and *Hyalopoa* also share further morphological characters such as comparatively long glumes, large lodicules, a caryopsis with a rostrate tip and a long hilum and the margins of leaf sheaths fused for more than 1/3 from the base (Tzvelev, 1976: Cope, 1982). The main differences are the number of florets in the spikelets, which usually have a single but sometimes an additional sterile floret in *Paracolpodium*, or the spikelet is two-flowered with the lower floret sterile (*P. baltistanicum*; Dickoré, 1995), whereas *Hyalopoa* has 3–4-flowered spikelets.

Catabrosa (type *C. aquatica* (L.) P.Beauv.) and *Catabrosella* (type *C. humilis* (M.Bieb.) Tzvelev) were well-supported separate genera (see Appendices 1 and 2 for further species molecularly studied). In the plastid DNA analyses, both genera formed a sister clade to *Puccinellia*/*Sclerochloa*. In the nrDNA tree, they were together with *Hyalopoa*/*Paracolpodium* sister to a clade of *Puccinellia*/*Sclerochloa* and *Coleanthus*/*Phippsia* as similarly found in other studies (Fig. 10) (Rodionov & al., 2008; Schneider & al., 2009; Soreng & al., 2015a; Nosov & al., 2019). This suggests a reticulation process within Coleanthinae in way that the *Puccinellia*/*Sclerochloa* lineage has a hybrid background, namely *Coleanthus*/*Phippsia*-like nrDNA from its paternal ancestor while its maternal nrDNA from *Catabrosa*/*Catabrosella* was lost.

Monospecific holarctic annual *Coleanthus* (*C. subtilis* (Tratt.) Seidel ex Roem. & Schult.) was clear sister to the perennial Arctic (two species) and high Andean (one species) *Phippsia* (type *P. algida* (Sol.) R.Br.). Both genera share conspicuous morphological characters such as missing or obsolescent small glumes and a caryopsis protruding from the floret at maturity (Nicora & Rúgolo de Agrasar, 1981; Clayton & Renvoize, 1986; Rúgolo, 2012b).

The sister relation of the small genus *Sclerochloa* (2–3 species; type *S. dura* (L.) P.Beauv.) and the large genus *Puccinellia* (110 species) was likewise firmly supported (Figs. 4, 5, 10), even after inclusion of more species of the latter genus (data not shown; Appendix 2) (Hoffmann & al., 2013; Soreng & al., 2015b).

(2) Avenulinae, Miliinae and Phleinae. – The small subtribes Miliinae (*Milium*) and Phleinae (*Phleum*) formed together with Poinae and the elements of the ABCV(+A) clade the supersubtribe Poodinae (~PAM clade), which was resolved in the plastid DNA data analysis and encompassed also Avenulinae (Fig. 4). The PAM clade was unresolved in the nrDNA tree since its subtribes did not join together in a separate clade but stood in a polytomy with Coleanthinae (Figs. 5, 7).

In the plastid and nrDNA analyses, monogeneric Miliinae and Avenulinae were more or less in a polytomy with the remainder of the PAM clade. Considering the plastid DNA tree (Fig. 4), this applies also to monogeneric Phleinae, in which three species of *Phleum* including *P. crypsoides* (d'Urv.) Hack. (Fig. 3F), the type of *Maillea* Parl., were sampled. Phleinae, however, were sister to Poinae with considerable support according to the nrDNA analysis (Figs. 5, 7). For Avenulinae (monospecific *Avenula* with *A. pubescens* (Huds.) Dumort.; Fig. 1J), there was no strongly supported incongruence between the placements in the plastid and nrDNA trees since *Avenula* was unsupported sister to Coleanthinae in the nrDNA tree (Figs. 5, 7), whereas it was part of the PAM clade resolved only in the plastid DNA tree (Figs. 4, 7). The analysis using separate partitions, however, strengthens recognition of *Avenula* as a hybrid taxon between the letter clades (Fig. 6). An origin as intergeneric hybrid between *Helictotrichon* (Aveninae) and *Helictochloa* (Helictochloinae) as previously discussed (Soreng & Davis, 2000) seems unlikely, a conclusion supported also by morphological characteristics (Gabriel & al., 2020).

(3) Poinae. – The monogeneric subtribe Poinae was sampled in this study using a small selection of species of traditional *Poa* s.str., namely *P. annua*., *P. bulbosa* L. and the type of the genus, *P. pratensis* L. This set of taxa was complemented by several species of previous segregate genera that meanwhile were shown to belong to an enlarged but subsequently monophyletic genus *Poa* (see Introduction for references). Our results corroborate monophyly of *Poa* encompassing *P. apiculata* Refulio (type of *Tovarochloa* T.D.Macfarl. & P.But), *P. labillardierei* Steud. (type of *Austrofestuca* (Tzvelev) E.B.Alexeev), *P. cyrenaica* (type of *Libyella* Pamp.), *P. fax* J.H.Willis & Court (type of *Neuropoa* Clayton), *P. hitchcockiana* Soreng & P.M.Peterson (type of *Aphanelytrum* Hack.), *P. lepidula* (Nees & Meyen) Soreng & L.J.Gillespie (type of *Anthochloa* Nees & Meyen), *P. persica* Trin. (type of *Eremopoa* Roshev.), *P. serpaiana* Refulio (type of *Dissanthelium* Trin.), *P. sintenisii* H.Lindb. (type of *Lindbergella* Bor) and *P. diaphora* Trin., a second species of former *Eremopoa*.

The plastid and nrDNA trees were widely congruent and showed sister relations of *P. alpina* and *P. bulbosa*, of *P. annua* and *P. cyrenaica*, of *P. diaphora* and *P. persica*, respectively, and the latter two species together with *P. sintenisii* (corresponding to *Poa* clade E in Gillespie & al., 2018) as sister to the remaining species of *Poa* included in our study (Figs. 4, 5). Nevertheless, there were some differences between the plastid and nrDNA analyses. The nrDNA tree (Fig. 5), for example, revealed a supported sister relation between *P. labillardierei* and *P. fax* or between *P. apiculata* and *P. hitchcockiana*, respectively, whereas the plastid DNA tree placed them, along with others, in a polytomy (Fig. 4).

(4) ABCV(+A) clade. – This morphologically varied clade with hybrid origin (see above: Deep phylogenetic incongruence …) contains many monospecific or species-poor genera, *Alopecurus* with ~40 species being the largest genus (Fig. 1I). *Arctopoa* joined this clade only in the nrDNA analyses, whereas it was placed outside of it in the plastid DNA tree and close to subtribe Poinae (see above: Comparison of the plastid and nuclear DNA trees).

Relationships within the ABCV(+A) clade were overall weakly resolved, except for the well-supported monophyletic subtribe Ventenatinae, which was retrieved in all analyses. Our results support the abandonment of *Gaudinopsis* (Boiss.) Eig as monospecific genus (*G. macra* (Steven ex M.Bieb.) Eig) distinct from *Ventenata* Koeler (type *V. dubia* (Leers) Coss. & Durieu; Fig. 3H). Monospecific *Parvotrisetum* Chrtek (*P. myrianthum* (Bertol.) Chrtek) was clearly excluded from *Trisetaria*, a member of the distantly related subtribe Aveninae, supporting their recognition as separate genera. The monospecific genus *Nephelochloa* Boiss. (*N. orientalis* Boiss.) was sister to *Apera* Adans. (type *A. spica-venti* (L.) P.Beauv.; Fig. 1L) in the nrDNA analyses (Fig. 5) (Hoffmann & al., 2013). With regards to the plastid DNA tree (Fig. 4), *N. orientalis* was even nested within the two species sampled of *Apera* (altogether ca. 5 species). Also morphologically, both genera share certain characters (usually richly branched inflorescences with numerous primary branches in whorls, similar shape of glumes and lemmas). The main difference is the number of flowers in the spikelets, one in *Apera* and three to six in *Nephelochloa*, which supports their maintenance as separate genera.

The HSAQN clade was well-supported only in the trees of the nrDNA data, such as the DAD clade (Fig. 5). The former is biogeographically characterized by bipolar distribution. *Arctagrostis* Griseb. (two species; type *A. latifolia* (R.Br.) Griseb.) is distributed in the boreal and arctic regions of the Northern Hemisphere, whereas the remaining taxa of the HSAQN clade (e.g., *Hookerochloa* E.B.Alexeev; Fig. 2L) occur in Australasia and southern South America.

The taxa of the DAD clade, a lineage with a well-documented hybrid origin (Soreng & al., 2015a), also occur in the boreal and the arctic regions of the Northern Hemisphere. The new genus *Arctohyalopoa* (type *A. lanatiflora*, comb. nov.; see below: New names and combinations) was placed in the nrDNA analyses within this clade (Fig. 5), whereas the plastid DNA tree placed it along with many other taxa in the large polytomy of the ABCV clade (Fig. 4). *Arctohyalopoa* comprises altogether ca. four species (see below: New names and combinations), which previously have been accommodated in the genus *Hyalopoa* together with *H. pontica*, the type of this genus, and few other species. The studied *A. lanatiflora* was not nested in the clade of Coleanthinae but in the ABCV or ABCV+A clade, respectively, in which it was part of a polytomy with many other taxa according to the plastid DNA data. It belongs to the DAD clade according to the nrDNA data along with *Dupontia* (type *D. fisheri* R.Br.), which includes *Arctophila* (type *A. fulva* (Trin.) Andersson; see below: New names and combinations), and monospecific *Dupontiopsis* (*D. hayachinensis* (Koidz.) Soreng, L.J.Gillespie & Koba; Figs. 5, 6). This placement of *Arctohyalopoa lanatiflora* distant to Coleanthinae was verified in this study also by analyzing a second accession (data not shown; Appendix 1). In should be noted that our previously published sequence of *H. lanatiflora* (Döring & al., 2007; Döring, 2009) is wrong, such as seemingly a sequence of Rodionov & al. (2008), which was also used by Hoffmann & al. (2013; see Appendix 3).

The molecular phylogenetic results on *Arctohyalopoa* were supported also by morphological data because, as pointed out by Tzvelev (1964a: 8, 1964b: 14–15), *A. lanatiflora* (≡ *Colpodium lanatiflorum* (Roshev.) Tzvelev) differs from both the other species of *Colpodium* subg. *Hyalopoa* Tzvelev (≡ *Hyalopoa*) and *Poa* by "lemmas … on basal half especially on nerves with rather copious and long pubescence, with distal part of callus (including that adjoining internerves) also copiously covered with rather long crinkly hairs, … paleas bare and smooth on keels …" (cited from Tzvelev, 1995a: 94–95). The epithet *lanatiflora* refers to the conspicuous indumentum of the lemmas. Tzvelev (1964c, 1995b) also addressed that *A. lanatiflora* otherwise strikingly resembles *Dupontia fulva* (Trin.) Röser & Tkach (≡ *Arctophila fulva*). As an endemic of northern East Siberia, *Arctohyalopoa* is geographically separated from the species of *Hyalopoa*, which are Caucasian to South Siberian (ca. six species) and West Himalayan (only *H. nutans* (Stapf) E.B.Alexeev ex T.A. Cope) in distribution. It seems to be also ecologically different due to its preference of non-carbonatic bedrock (Tzvelev, 1964c, 1995b).

Merging the small genera *Dupontia* und *Arctophila* as already suggested by Kellogg (2015) was supported also by Hoffmann & al. (2013), who showed that the nr ITS sequences of both were intermingled in the molecular phylogenetic tree. It further agrees with their overall morphological similarity except for rather small differences in the shape of their lemmas (Clayton & Renvoize, 1986; Cayouette & Darbyshire, 2007a, b; see also Brysting & al., 2004; Soreng & al., 2015a) and the occurrence of hybrids between *D. fisheri* and *D. fulva*, comb. nov., that were formerly regarded as intergeneric hybrids and treated under the nothogenus ×*Arctodupontia* Tzvelev (Tzvelev, 1973; Brysting & al., 2003; Darbyshire & Cayouette, 2007).

Tribes Alopecurinae, Beckmanniinae and Cinninae in each case did not resolve as monophyletic but mostly stood in a larger polytomy encompassing further taxa and the hybrid DAD clade. The sampled species of *Limnas* Trin. (type *L. stelleri* Trin. and *L. malyschevii* O.D.Nikif.) resolved in none of the analyses in a clade with the other species of Alopecurinae (*Alopecurus aequalis* Sobol., *Cornucopiae cucullatum* L., type of *Cornucopiae*), which were close to the DAD clade in the nrDNA tree. *Alopecurus* and *Cornucopiae* were always sister, which agrees with their common spikelet structure.

Beckmannia (type *B. eruciformis* (L.) Host; Fig. 1K) and monospecific *Pholiurus* (*P. pannonicus*) were well-supported sister in the nrDNA tree in agreement with Hoffmann & al. (2013) but less supported in the plastid DNA tree (Figs. 4, 5). *Rhizocephalus orientalis* Boiss., type of the monospecific genus *Rhizocephalus* Boiss., the third genus of tribe Beckmanniinae as delineated by Soreng & al. (2017), was placed in all analyses remotely from *Beckmannia* and *Pholiurus* in the main polytomy of the ABCV(+A) clade. Spikelets in *Alopecurus*, *Cornucopiae*, *Limnas* and *Rhizocephalus* are single-flowered, in *Beckmannia* (the upper staminate) and *Pholiurus* two-flowered (Schneider & al., 2012).

Also the Cinninae genera sampled (*Aniselytron* with type *A. treutleri*, *Cinna* L., monospecific *Cyathopus* Stapf with *C. sikkimensis* Stapf, *Simplicia* Kirk with *S. buchananii* (Zotov) Zotov; Fig. 3J) appeared in the main polytomy of the ABCV(+A) clade, except for *Cinna* and *Cyathopus*, which were supported sister in the nrDNA tree. Both share spikelets that are falling entire, whereas *Aniselytron* and *Simplicia* have spikelets disarticulating above the glumes. In all Cinninae genera, the spikelets are single-flowered, with occasional occurrence of a second floret reported for *Simplicia* (Watson & al., 1992 –; Edgar & Connor, 2000). Notwithstanding the established sister relations of each *Beckmannia*/*Pholiurus* and *Alopecurus*/*Cornucopiae*, the phylogenetic relationships of all genera of Alopecurinae, Beckmanniinae and Cinninae and the delineation of these subtribes certainly warrant future work.

Monospecific *Limnodea* (*L. arkansana*), sometimes placed near or included within *Cinna* (Clayton & Renvoize, 1986; Tucker, 1996), was placed very distant to this genus in the molecular trees, namely close to *Sphenopholis* within the Koeleriinae lineage of Aveninae (Figs. 4, 5, 8) (see also Döring, 2009; Hochbach & al., 2015; Saarela & al., 2017: suppl. 7; Barberá & al., 2019).

Brizochloa humilis (M.Bieb.) Chrtek & Hadač, with lemmas that are not cordate as in *Briza* or *Macrobriza* and upright pedicels of the spikelets, is a morphologically most striking species of the ABCV(+A) clade. The monospecific genus *Brizochloa* cannot be accommodated under any of the subtribes yet described, and we assign it to a new monogeneric subtribe, Brizochloinae. The exclusion of *B. humilis*, an annual distributed from the Eastern Mediterranean to Iran, from *Briza* had already been suggested by previous morphological and molecular studies (Jirásek & Chrtek, 1967; Tzvelev, 1968, 1976; Hoffmann & al., 2013; Persson & Rydin, 2016; Essi & al., 2017).

Festuceae. — *(1) Loliinae*. – The large and worldwide distributed subtribe Loliinae was represented in this study by a small sample of taxa. It has been investigated and shown to be monophyletic by several previous studies (see Introduction). Affiliation of former *Megalachne* Steud. and *Podophorus* Phil., endemics of the Juan Fernándes Islands (Chile), with Loliinae was established by Schneider & al. (2011, 2012). Subtribe Loliinae was characterized in this study by two supported main lineages in the plastid DNA data analyses (Fig. 4), one of which was formed by *Drymochloa sylvatica* (Pollich) Holub (= *Festuca altissima* All., type of *Drymochloa*) as clear sister to *Lolium* L. species, namely *L. perenne* L. (type of *Lolium*), *L. rigidum* Gaudin and *L. giganteum* (L.) Darbysh. (≡ *F. gigantea* (L.) Vill. ≡ *Schedonorus giganteus* (L.) Holub; Fig. 3A).

The second lineage was formed by *Castellia tuberculosa* (type of *Castellia*) as sister to a monophyletic lineage that corresponds to a narrowly defined genus *Festuca* that is equivalent to the "fine-leaved fescues" (Torrecilla & Catalán, 2002) as suggested (Kellogg, 2015; Soreng & al., 2015b, 2017). This lineage of *Festuca* s.str. was represented in our sample by species from several morphologically partly well-defined segregate genera, namely *F. berteroniana* Steud. (type of *Megalachne*), *F. floribunda* (Pilg.) P.M.Peterson & al. (type of *Dielsiochloa* Pilg.), *F. incurva* (Gouan) Gutermann (type of *Psilurus* Trin.), *F. lachenalii* (C.C.Gmel.) Spenn. (type of *Micropyrum* (Gaudin) Link; Fig. 2B), *F. masatierrae*, nom. nov. (type of *Podophorus*; no plastid DNA data available), *F. maritima* L. (= *Vulpia unilateralis* (L.) Stace), *F. myuros* L. (type of *Vulpia* C.C.Gmelin) and *F. salzmannii* (Boiss.) Boiss. ex Coss. (type of *Narduroides* Rouy).

The nrDNA results agreed widely with the trees of the plastid DNA data analyses; however, *Castellia* was differently placed, namely together with *Drymochloa* (Fig. 5) and not with the lineage of *Festuca* s.str. as just mentioned. This points to a hybrid origin of this odd monotypic, Mediterranean to mid-East genus (see above: Reticulations within major lineages).

The South American representatives sampled of *Festuca* s.str., namely *F. floribunda* from the Andes and the endemics of the Chilean Juan Fernández Islands, *F. berteroniana* and *F. masatierrae*, formed a monophyletic cluster in the nrDNA analysis. *Festuca floribunda* belongs to the group "American II" of the fine-leaved *Festuca* in the study on the historical biogeography of Loliinae by Minaya & al. (2017). Group "American II" has colonized South America in the Miocene, a time frame that makes sense also for the establishment of *F. berteroniana* and *F. masatierrae*. The islands started to originate in the Upper Miocene 5.8 million years ago (Stuessy & al., 1984).

(2) ADCP clade. – The species of the small sister subtribes Ammochloinae and Dactylidinae clade have spikelets arranged in dense clusters. The close relationship of both tribes (Figs. 4, 5) was already revealed by the plastid DNA data of Quintanar & al. (2007) and Orton & al. (2019), whereas the ITS data of *Ammochloa palaestina* Boiss. of the former study, used also by Saarela & al. (2010), were wrong and belonged to *Helictochloa* (Appendix 3). Ammochloinae are monogeneric (*Ammochloa*; type *A. palaestina*), whereas Dactylidinae encompass Eurasian *Dactylis* (type *D. glomerata* L.) und Mediterranean to mid-East monospecific *Lamarckia* Moench (type *L. aurea* (L.) Moench; Fig. 2M). The sister relation of the Ammochloinae/Dactylidinae to the Cynosurinae/ Parapholiinae clade was found in all analyses of this study (Figs. 4, 5) although without strong support, which agrees with the plastid DNA results of several previous studies (Davis & Soreng, 2007; Quintanar & al., 2007; Bouchenak-Khelladi & al., 2008).

The Cynosurinae species *C. cristatus* L. (type of *Cynosurus*; Fig. 2E) and *C. elegans* Desf. did not resolve as monophyletic but formed a grade basal to Parapholiinae.

Parapholiinae were strongly supported as monophyletic in all analyses (Figs. 4, 5), which is in agreement with several previous studies (Davis & Soreng, 2007; Quintanar & al., 2007; Bouchenak-Khelladi & al., 2008; Schneider & al., 2012). Its species are distributed from the Mediterranean to the Middle East and frequently grow on saline soil. Parapholiinae encompass six genera of annuals if, firstly, the former monotypic genus *Hainardia* Greuter (type *H. cylindrica* (Willd.) Greuter) is reduced to synonymy of *Parapholis* C.E. Hubb. (type *P. incurva* (L.) C.E.Hubb.) as suggested by our plastid and nrDNA analyses (Figs. 4, 5) and, secondly, the endemic Algerian monotypic and perennial genus *Agropyropsis*, which was not molecularly studied to date, belongs to Loliinae as suggested by morphological characters (Schneider & al., 2012). The remaining Parapholiinae genera in addition to *Parapholis* are *Catapodium* Link (type *C. marinum* (L.) C.E.Hubb.; Fig. 2A), *Cutandia* Willk., *Desmazeria* Dumort. (type *D. sicula* (Jacq.) Dumort.), *Sphenopus* Trin. (type *S. divaricatus* (Gouan) Rchb.) and *Vulpiella* (Batt. & Trab.) Burollet (type *V. stipoides* (L.) Maire).

Desmazeria philistaea (Boiss.) H.Scholz and *D. sicula* were sister taxa and monophyletic in the plastid (Fig. 4) but not in the nrDNA tree, in which *D. sicula* clustered with *Vulpiella* and *Cutandia* (Fig. 5) (see also Schneider & al., 2012). *Desmazeria sicula* is likely to be a hybrid, which may lead to a name change for this genus, pending further investigation.

Unplaced lineages. — The following subtribes have reticulate origin between tribes Aveneae and Festuceae, as documented by the incongruent placement in the plastid and nrDNA trees (Figs. 6, 7). Poeae have most likely not been involved in hybridizations with the other tribes according to the molecular phylogenetic results of this study.

(1) Sesleriinae. – The largely European subtribe Sesleriinae encompasses species with capitate or spiciform inflorescences, among them two small genera of short-lived annuals, *Mibora* with two species (type *M. minima* (L.) Desv.) and monospecific *Echinaria* (*E. capitata* (L.) Desf.). *Mibora* and *Oreochloa* Link (type *O. disticha* (Wulfen) Link) were sister in all analysis. They formed a sister clade to *Sesleria* (type *S. caerulea* (L.) Ard.) and monospecific *Sesleriella* (type *S. sphaerocephala* (Ard.) Deyl) in the plastid DNA tree (Figs. 4, 9), in which *Echinaria* clustered with monospecific *Psilathera* (type *P. ovata* (Hoppe) Deyl). In the nrDNA tree, *Mibora*/*Oreochloa* stood in a polytomy with *Sesleriella* and a supported clade of *Echinaria*, *Psilathera* and *Sesleria* (Figs. 5, 9). The origin of *Sesleria* through hybridization between a *Sesleriella*-like maternal ancestor and a *Psilathera*-like paternal ancestor (see Kuzmanović & al., 2017 and above) represents also a good example of allopolyploidy because *Sesleria* comprises consistently polyploid species (4*x*–12*x*), whereas *Sesleriella* (most likely monospecific) and *Psilathera* (monospecific) are diploid. Also, for *Oreochloa*, a genus with four species occurring in the European Alpine mountain system, only diploids are known so far. The relationships resolved by the plastid and the nrDNA analyses were congruent, and *Oreochloa* is not involved in the origin of *Sesleria* (Figs. 4, 5, 9).

(2) Scolochloinae. – Scolochloinae encompasses *Scolochloa* (two species; type *S. festucacea* (Willd.) Link) from the temperate regions of the Holarctic and monospecific Australian *Dryopoa* (*D. dives* (F.Muell.) Vickery). Both resemble one another morphologically (Clayton & Renvoize, 1986) and represent a remarkable example of bipolar distribution. The genera were not supported to be closely related by the plastid DNA analysis, in which *Scolochloa* aggregated with *Antinoria* and *Dryopoa* with Sesleriinae, although without strong support (Fig. 4). The nrDNA data analyses showed *Scolochloa* and *Dryopoa* as strongly supported sister (Fig. 5). The nrDNA revealed Scolochloinae in a common and considerably supported clade comprising Phalaridinae, Torreyochloinae, both with hybrid origin, and supersubtribe Agrostidodinae, which corroborates the findings of Birch & al. (2014), who noted a relationship of *Dryopoa* to Brizinae and Agrostidinae.

(3) Holcinae. – Monophyletic Holcinae with *Holcus* L. (Fig. 2J,K) and *Vahlodea* Fr. (type *V. atropurpurea* (Wahlenb.) Fr.) were sister to Airinae according to the nrDNA data analysis (Fig. 5) and in agreement with Quintanar & al.

(2007), sampling only *Holcus*, and Schneider & al. (2009), sampling both genera. Plastid DNA data showed Holcinae in a polytomy with Aristaveninae and Helictochloinae (Figs. 4, 6, 7) (similarly found by Quintanar & al., 2007; Schneider & al., 2009), as well as with Festuceae, Scolochloinae and Sesleriinae, whereas Airinae were more distant. This means that Holcinae share plastid DNA characters with a larger set of subtribes but to a lesser extent with Airinae, whereas nrDNA connects Holcinae with Airinae (Figs. 5, 6). This indicates that Holcinae are of ancient hybrid origin slightly different from that of Airinae although both subtribes share an overall similar pattern of conflicting placements with respect to the plastid and nrDNA trees (see above: Comparison of the plastid and nuclear DNA trees).

(4) Airinae and Helictochloinae. – Airinae as defined in this study were clearly monophyletic in all analyses (Figs. 4, 5). They encompass *Aira* L. (type *A. praecox* L.; Fig. 1D), *Avenella* Bluff ex Drejer (type *A. flexuosa* (L.) Drejer; Fig. 1H), *Corynephorus* P.Beauv. (type *C. canescens* (L.) P.Beauv.; Fig. 2C) and *Periballia* Trin. (type *P. involucrata* (Cav.) Janka; Fig. 3D).

Helictochloinae is newly established to accommodate *Helictochloa* (type *H. bromoides* (Gouan) Romero Zarco; Fig. 2H), a widespread Eurasian/Mediterranean perennial, and *Molineriella* (type *M. minuta* (L.) Rouy), a Mediterranean annual genus. Both genera had maximum support as sisters in all analyses and segregated consistently from Airinae s.l., which disintegrated further into Antinoriinae and Airinae (Figs. 4–6). Subtribe Helictochloinae is morphologically hard to define, because its genera differ substantially. However, their spikelets disarticulate below each floret, the lemma has a hairy callus and a dorsal awn though the latter not consistently in *Molineriella*. Lodicules of both genera have a lateral tooth (pers. obs.; Cebrino Cruz & Romero Zarco, 2017). The endosperm is soft in contrast to the Airinae genera *Aira*, *Avenella*, *Corynephorus*, and *Periballia*, which have hard endosperm (R.J. Soreng, pers. comm.). We consider the relationship of *Molineriella* and *Helictochloa*, which was similarly found by Soreng & al. (2007), not as artefact as discussed above (see Aveneae: (4) Brizinae and Macrobriza).

(5) Antinoriinae. – Subtribe Antinoriinae encompasses only *Antinoria* (type *A. agrostidea* (DC.) Parl.). In the nrDNA tree, the sampled *Antinoria* species were placed in the basal Poodae polytomy, whereas previous ITS studies found *A. agrostidea* closer to Loliinae (Quintanar & al., 2007) or Cynosurinae/Parapholiinae (Inda & al., 2008) though with moderate support. Together with the placement of *Antinoria* (plastid sequences only for *A. agrostidea*) near the species of Festuceae in the plastid DNA analyses, the molecular phylogenetic data seem to support the segregation of a Antinoriinae from Airinae.

(6) Aristaveninae. – Segregation of this subtribe from Holcinae and Airinae as addressed earlier (Schneider & al., 2012; Saarela & al., 2017; Soreng & al., 2017) was supported by all analyses of this study. Aristaveninae encompass only *Deschampsia* P.Beauv. (type *D. cespitosa* (L.) P.Beauv.), in which the former monospecific genus *Scribneria* Hack. (*S. bolanderi* (Thurb.) Hack.), whose relationship with *Deschampsia* was established by Schneider & al. (2012), was included (Saarela & al., 2017).

■ NEW NAMES AND COMBINATIONS

Antinoriinae Röser & Tkach, **subtr. nov.** – Type: *Antinoria* Parl.

Description. – Annual or rarely (in *A. agrostidea*) perennial, caespitose or decumbent; leaf sheath margins free, leaf blades flat; ligule an unfringed membrane, 1–3 mm long; inflorescence paniculate; spikelets pedicellate, laterally compressed, 1–2 mm long, with 2 florets, disarticulating above the glumes and between the florets, with distinctly elongated rhachilla internode between the florets, glabrous, terminated by a female-fertile floret; glumes relatively large, more or less equal, exceeding the spikelets, awnless, carinate, 3-nerved; lemmas elliptic, widest near the tip, membranous, incised or blunt, awnless, glabrous, 5-nerved; palea relatively long, tightly clasped by the lemma, 2-nerved, 2-keeled; anthers 0.5–1 mm long; ovary glabrous; caryopsis pyriform, compressed dorsiventrally, smooth; hilum short; embryo less than 1/3 the caryopsis in length.

Included genus. – *Antinoria*.

Distribution. – Mediterranean.

Avenulinae Röser & Tkach, **subtr. nov.** – Type: *Avenula* (Dumort.) Dumort. ≡ *Trisetum* sect. *Avenula* Dumort.

Description. – Perennial, loosely caespitose, with creeping underground shoots; roots without sclerenchyma surrounding endodermis; culms with 1–3 visible nodes. Leaf sheaths closed over more than half their length from base; leaf blades flat or ± conduplicate, not furrowed, relatively soft but rigid, with long hairs; bulliform cells forming a row each side of the adaxial midrib; with abaxial midrib and margins scarcely evident; secondary nerves few; well-developed subepidermal sclerenchyma forming O-shaped girders at lateral nerves; inflorescence a lax panicle; spikelets 14–20 mm long, with 3–4 developed bisexual florets, the two upper florets not or scarcely exceeding the upper glume, apical floret reduced; glumes unequal, keeled on the back, somewhat scabrid on the central nerve at the base, the lower glume 1–3-nerved, the upper glume 3-nerved; rhachilla disarticulating above the glumes and between the florets; lemmas glabrous (except for the callus); dorsally awned, with a strongly twisted, rounded column, without pale margins; palea scarcely 2-keeled, with glabrous and smooth keels; lodicules as long or shorter than the ovary, ovate or obovate, 2–3-lobed or with a irregularly dentate apex; caryopsis furrowed; hilum linear, as long as caryopsis; endosperm soft, with lipid; embryo with a truncated epiblast and obtuse scutellum.

Included genus. – *Avenula*.

Distribution. – Europe to eastern Siberia, Caucasus, northern Central Asia, Mongolia.

Brizochloinae Röser & Tkach, **subtr. nov.** – Type: *Brizochloa* Jirás. & Chrtek

Diagnosis. – Differs from Brizinae and *Macrobriza* by upright pedicels of the spikelets, slightly scabrous rhachillas, non-cordate lemmas and punctifom caryopsis hilum.

Included genus. – Brizochloa.

Distribution. – Eastern Mediterranean to Caucasus and Iran.

Helictochloinae Röser & Tkach, **subtr. nov.** – Type: *Helictochloa* Romero Zarco

Description. – Perennial (*Helictochloa*) or annual (*Molineriella*); leaf sheaths split almost up to the base, leaf blades flat, conduplicate or convolute; inflorescence a lax panicle to (sometimes in *Helictochloa*) raceme-like; spikelets 10–36 mm (*Helictochloa*) or 1.5–2.5 mm (*Molineriella*), with (2–)3–9(–12) (*Helictochloa*) or 2 (*Molineriella*) developed, bisexual florets; glumes shorter than spikelets, the lower glume with (1–)3–5 (*Helictochloa*) or 1 (*Molineriella*) nerve, the upper glume with 3–5(–7) (*Helictochloa*) or 3 (*Molineriella*) nerves; rhachilla disarticulating above the glumes and between the florets; lemmas glabrous or sericeous towards the base, awned dorsally in the half (*Helictochloa*) or in the upper 1/3 of the lemma or awnless (*Molineriella*); awn with a loosely twisted column and a long subula (*Helictochloa*) or straight, extending by more than 10 mm (*Helictochloa*) or by 0.3–0.6 mm (*Molineriella*) beyond the lemma apex; palea 2-keeled, keels minutely ciliate (*Helictochloa*) or almost smooth (*Molineriella*); lodicules lanceolate, with a lateral lobe; caryopsis hilum linear, 1/3–2/3 the caryopsis in length (*Helictochloa*) or punctifom (*Molineriella*); endosperm soft, at least in *Helictochloa* with lipid.

Included genera. – Helictochloa, *Molineriella*.

Distribution. – Mediterranean, Eurasia, North America.

Hypseochloinae Röser & Tkach, **subtr. nov.** – Type: *Hypseochloa* C.E.Hubb.

Diagnosis. – Differs from Airinae by 1-flowered spikelets, 5-nerved glumes (the upper rarely 3-nerved), an apically deeply bifid lemma (about 1/3 incised), which is crustaceously indurated at maturity, the awn arising from the apical sinus; caryopsis hilum punctiform; endosperm hard, with lipid.

Included genus. – Hypseochloa.

Distribution. – Cameroon Mt. and Tanzania.

Anthoxanthum glabrum subsp. ***sibiricum*** (Tzvelev) Röser & Tkach, **comb. nov.** ≡ *Hierochloe odorata* subsp. *sibirica* Tzvelev in Novosti Sist. Vyssh. Rast. 1968: 21. 1968.

Anthoxanthum nitens subsp. **kolymense** (Prob.) Röser & Tkach, **comb. nov.** ≡ *Hierochloe odorata* subsp. *kolymensis* Prob. in Novosti Sist. Vyssh. Rast. 15: 69. 1979.

Arctohyalopoa Röser & Tkach, **gen. nov.** – Type: *Arctohyalopoa lanatiflora* (Roshev.) Röser & Tkach (≡ *Poa lanatiflora* Roshev. ≡ *Hyalopoa lanatiflora* (Roshev.) Tzvelev).

Diagnosis. – Differs from *Hyalopoa* by lemmas with copious and long hairs on the basal half and especially on nerves, calli copiously covered with long crinkly hairs and glabrous paleas with rarely a few hairs along keels.

Arctohyalopoa ivanovae (Malyschev) Röser & Tkach, **comb. nov.** ≡ *Colpodium ivanoviae* Malyschev in Novosti Sist. Vyssh. Rast. 7: 295. 1971 (‘1970’).

Arctohyalopoa jurtzevii **(**Prob. & V.V.Petrovsky) Röser & Tkach, **comb. nov.** ≡ *Hyalopoa jurtzevii* Prob. & V.V.Petrovsky in Novosti Sist. Vyssh. Rast. 46: 71. 2015.

Arctohyalopoa lanatiflora (Roshev.) Röser & Tkach, **comb. nov.** ≡ *Poa lanatiflora* Roshev. in Izv. Bot. Sada Akad. Nauk S.S.S.R. 30: 303. 1932.

Arctohyalopoa momica (Tzvelev) Röser & Tkach, **comb. nov.** ≡ *Colpodium lanatiflorum* subsp. *momicum* Tzvelev, Fl. Arct. URSS 2: 172. 1964 ≡ *Hyalopoa lanatiflora* subsp. *momica* (Tzvelev) Tzvelev in Novosti Sist. Vyssh. Rast. 1966: 32. 1966 ≡ *Hyalopoa momica* (Tzvelev) Czerep, Sosud. Rast. SSSR: 363. 1981.

Colpodium biebersteinianum (Claus) Röser & Tkach, **comb. nov.** ≡ *Agrostis biebersteiniana* Claus in Beitr. Pflanzenk. Russ. Reiches 8: 264. 1851 ≡ *Zingeria biebersteiniana* (Claus) P.A.Smirn. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 51(2): 67. 1946 ≡ *Zingeria trichopoda* subsp. *biebersteiniana* (Claus) Doğan in Notes Roy. Bot. Gard. Edinburgh 40(1): 86. 1982.

Colpodium kochii (Mez) Röser & Tkach, **comb. nov.** ≡ *Milium kochii* Mez in Notes Roy. Bot. Gard. Edinburgh 17: 211. 1921 ≡ *Zingeria kochii* (Mez) Tzvelev in Bot. Zhurn. (Moscow & Leningrad) 50: 1318. 1965.

Colpodium pisidicum (Boiss.) Röser & Tkach, **comb. nov.** ≡ *Agrostis pisidica* Boiss. in Ann. Sci. Nat., Bot., sér. 4, 2: 255. 1854 ≡ *Agrostis trichoclada* var. *pisidica* (Boiss.) Boiss., Fl. Orient. 5: 516. 1884 ≡ *Zingeria pisidica* (Boiss.) Tutin in Bot. J. Linn. Soc. 76(4): 365. 1978.

Colpodium trichopodum (Boiss.) Röser & Tkach, **comb. nov.** ≡ *Milium trichopodum* Boiss., Diagn. Pl. Orient., ser. 1, 13: 45. 1854 ≡ *Zingeria trichopoda* (Boiss.) P.A. Smirn. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 51: 67. 1946 ≡ *Zingeria biebersteiniana* subsp. *trichopoda* (Boiss.) R.R.Mill, Fl. Turkey 9: 365. 1985.

Colpodium verticillatum (Boiss. & Balansa) Röser & Tkach, **comb. nov.** ≡ *Milium verticillatum* Boiss. & Balansa in Bull. Soc. Bot. France 5: 169. 1858 ≡ *Zingeria verticillata* (Boiss. & Balansa) Chrtek in Novit. Bot. Delect. Seminum Horti Bot. Univ. Carol. Prag. 1963: 3. 1963 ≡

Zingeriopsis verticillata (Boiss. & Balansa) Prob. in Novosti Sist. Vyssh. Rast. 14: 12. 1977.

Dupontia fulva (Trin.) Röser & Tkach, **comb. nov.** ≡ *Poa fulva* Trin. in Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1(4): 378. 1830.

Festuca dolichathera Röser & Tkach, **nom. nov.** ≡ *Megalachne dantonii* Penneck. & Gl.Rojas in Phytotaxa 418: 295. 2019, non *Festuca danthonii* Asch. & Graebn., Syn. Mitteleur. Fl. 2(1): 550. 1901.

Etymology. – The epithet is derived from Greek "dolichós" (long) and "ather" (awn) and refers to the long lemma awn (Penneckamp Furniel & Rojas Villegas, 2019) of this species.

Festuca masafuerana (Skottsb. & Pilg. ex Pilg.) Röser & Tkach, **comb. nov.** ≡ *Bromus masafueranus* Skottsb. & Pilg. ex Pilg. in Repert. Spec. Nov. Regni Veg. 16: 385. 1920 ≡ *Megalachne masafuerana* (Skottsb. & Pilg. ex Pilg.) Matthei in Bol. Soc. Biol. Concepción 48: 171, fig. 1a, c–e. 1974.

Festuca masatierrae Röser & Tkach, **nom. nov.** ≡ *Podophorus bromoides* Phil. in Bot. Zeitung (Berlin) 14: 649. 1856, non *Festuca bromoides* L., Sp. Pl.: 75. 1753.

Etymology. – The epithet refers to Masatierra Island (Robinson Crusoe Island) of the Juan Fernández Archipelago, on which this extinct taxon (Baeza & al., 2002) previously occurred.

Festuca robinsoniana (C.M.Peña) Röser & Tkach, **comb. nov.** ≡ *Megalachne robinsoniana* C.M.Peña in Gayana Bot. 74(1): 198. 2017.

Graphephorum canescens (Buckley) Röser & Tkach, **comb. nov.** ≡ *Trisetum canescens* Buckley in Proc. Acad. Nat. Sci. Philadelphia 14: 100. 1862.

Graphephorum cernuum (Trin.) Röser & Tkach, **comb. nov.** ≡ *Trisetum cernuum* Trin. in Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1(1): 61. 1830.

Hyalopodium Röser & Tkach, **gen. nov.** – Type: *Hyalopodium araraticum* (Lipsky) Röser & Tkach (≡ *Catabrosa araratica* Lipsky).

Description. – Perennial, caespitose, with creeping underground shoots; aerial shoots enclosed at the base by reticulately fibrous sheaths of dead leaves; culms erect, 20–55 cm long; ligule an eciliate membrane, 3–5 mm long, acute; leaf blades 4–11 cm long, 1–3 mm wide, midrib prominent beneath, surface glabrous, margins cartilaginous; inflorescence a panicle, contracted, linear, interrupted, 4–11 cm long, 0.5–1.5 cm wide; primary panicle branches short, 0.2–0.6 cm long; spikelets solitary, pedicelled, comprising 2(–3) fertile florets, without rhachilla extension, cuneate, laterally compressed, 6–7 mm long, disarticulating below each fertile floret; glumes persistent, similar, shorter than spikelet, similar to fertile lemma in texture, gaping; lower glume oblong, 4.5 mm long, 3/4 to as long as the upper glume, membranous, much thinner above and on the margins, purple, 1-keeled, 1-veined, lateral veins absent, apex acute; upper glume elliptic, 4.5–6 mm long, as long as the adjacent fertile lemma, membranous, much thinner above, with hyaline margins, purple, 1-keeled, 3-veined, apex acute; lemma elliptic, 4–6 mm long, membranous, much thinner above, purple and yellow, tipped with yellow, keeled, 5-veined; lateral veins less than 2/3length of lemma; lemma surface pubescent, hairy below; lemma apex erose, obtuse; callus very short, pilose; palea keels smooth, eciliate; anthers 3.3–4.5 mm long, yellow or purple; caryopsis about 3 mm long; hilum elliptic, 1/3–1/2 of the grain.

Hyalopodium araraticum (Lipsky) Röser & Tkach, **comb. nov.** ≡ *Catabrosa araratica* Lipsky in Trudy Imp. S.-Peterburgsk. Bot. Sada 13(2): 358. 1894.

Paracolpodium baltistanicum (Dickoré) Röser & Tkach, **comb. nov.** ≡ *Colpodium baltistanicum* Dickoré in Stapfia 39: 114. 1995.

Parapholis cylindrica (Willd.) Röser & Tkach, **comb. nov.** ≡ *Hainardia cylindrica* (Willd.) Greuter in Boissiera 13: 178. 1967.

Parapholis ×pauneroi (Castrov.) Röser & Tkach, **comb. nov.** ≡ ×*Hainardiopholis pauneroi* Castrov. in Anales Jard. Bot. Madrid 36: 238. 1980 ('1979').

■ CONCLUSIONS

Our survey of the molecular phylogenetic differentiation of supertribe Poodae, including most of its genera and based on plastid and nrDNA sequence markers that were investigated in an almost overlapping set of taxa, provides a robust and well-resolved topology for most regions of the phylogenetic trees. Some major polytomies remain and should be resolved in future studies. Notably, the plastid and nrDNA trees agree in wide portions and show congruent branching patterns, making it likely that they reflect the actual phylogenetic relationships of the taxa in these tree portions. Severe conflict between the trees, however, occurs in sometimes larger stretches of the trees and is interpreted to be indicative of past hybridization (Figs. 4, 5, 7). Taxonomic groups with hybrid background are subtribes Airinae, Anthoxanthinae, Antinoriinae, Aristaveninae, Avenulinae, Helictochloinae, Holcinae, Phalaridinae, Scolochloinae, Sesleriinae and Torreyochloinae. Major reticulation processes across subtribes include *Macrobriza* and *Arctopoa*. Well-identifiable infrasubtribe hybrid origins, which partly encompass lineages with several genera, were found, for example, within Agrostidinae, Aveninae, Coleanthinae, Loliinae and Sesleriinae (Figs. 4, 5, 7–10) but may be more frequent if denser sampling of taxa will be implemented and tree resolution will be improved by further investigations.

Our analyses revealed deep phylogenetic incongruence within Poodae, pointing to a hybridization event in its early evolution. Regarding this, we suggest to distinguish three main lineages, namely tribes Aveneae, Poeae and Festuceae. This implies several further changes in classification, including a revised arrangement of subtribes. Poeae is seemingly of reticulate origin as revealed by its cytonuclear discordance. Within Poeae, the ABCV clade, representing a comparatively large lineage with several subtribes, is a further example of likely hybrid origin. This pattern is therefore encountered on different taxonomic levels ranging from shallow to deep phylogenetic levels and must be regarded as an important and recurrent evolutionary incident in Poodae. Different levels of reticulate origins (tribes, subtribes, genera, etc.) corroborate the discussed significance of hybridization processes in grasses and underline their potential to give rise even to major evolutionary lineages. The likely hybrid character of several taxa and lineages offers a detailed hypothesis for evolutionary relationships within Poodae than can be tested in future studies employing larger sets of nuclear and organellar DNA markers, for example, by next-generation sequencing approaches. Moreover, the morphological differentiation of Poodae can be analysed using the new phylogenetic framework. From the current data it is obvious that there is a high degree of homoplasy in many morphological characters as seen, for example, in traditionally highly ranked characters for classification such as the presence of a dorsal lemma awn, which occur in Aveneae (for example, Agrostidinae, Anthoxanthinae, Aveninae, Torreyochloinae; Figs. 1A,C,E,F,M,O, 2D,F,I, 3E,G,I,K,L), Poeae (for example, Alopecurinae, Avenulinae, Ventenatinae; Figs. 1I,J, 3H) and some of the unplaced (hybrid) subtribes (for example, Airinae, Aristaveninae, Helictochloinae, Holcineae; Figs. 1D,H, 2H,K). We assume, that the overall strong variation in spikelet and floret characters of Poodae relates to a high degree of selective pressure acting on these structures. They have little to do with pollination as an important factor for the floral structures in many other angiosperms because all grass taxa in question are wind-pollinated. We suppose they are rather significant for the efficient dispersal of diaspores, which is highly varied in grasses (Davidse, 1987). It can be supposed that the variety of dispersal mechanisms caused by spikelet structures (spikelet disarticulate or fall entire, different types of disarticulation, types of awns, animal dispersal, hygroscopic movement, bristles and hairs, lemma and palea structure, release of caryopses, etc.) are one of the important evolutionary factors that enabled Poodae to colonize successfully almost any habitat type in the temperate and cold zones of the world.

■ NOTE ADDED IN PROOF

The name *Festuca berteroniana* Steud. was not correctly applied in our study since it is not a synonym of *Megalachne berteroniana* Steud. The following new name is suggested:

Festuca megalachna Röser & Tkach, **nom. nov.** ≡ *Megalachne berteroniana* Steud., Syn. Pl. Glumac. 1(3): 237. 1854, non *Festuca berteroniana* Steud., Syn. Pl. Glumac. 1(3): 311. 1854.

Etymology. – The epithet is derived from Greek "megas" (large) and "achne" (scale).

■ AUTHOR CONTRIBUTIONS

MR, JS and NT designed the study. MR guided the sampling, contributed taxonomic knowledge and wrote the manuscript. JS, NT, ED, AW, AH, GW, JG and JN contributed lab work. NT and JS contributed data by supervising students in the lab. NT, JS and MR undertook the phylogenetic analyses. NT and MHH contributed to write the manuscript. — NT, https://orcid.org/0000-0002-4627-0706; GW, https://orcid.org/0000-0002-9866-335X; MR, https://orcid.org/0000-0001-5111-0945.

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Appendix 1. Taxa studied in our lab for DNA sequences.

Taxon, geographical origin, voucher information with collectors and herbarium code and ENA/GenBank accession numbers for plastid *matK* gene–3′*trnK* exon; plastid *trnL-trnF*; nuclear ribosomal ITS1–5.8S gene–ITS2 and nuclear ribosomal ETS. Sequences LR606315–LR607006, LR655821 and LR655822 were newly generated for this study. Missing sequence data are indicated by a dash. BG: Botanical Garden. MR: herbarium of G. & S. Miehe deposited at the Institute of Geography, University Marburg, Germany.

Acrospelion distichophyllum (P.Beauv.) Barberá: Austria, High Tauern, Glockner Alps, Pasterzen Kees, 19.07.2000, *G. Winterfeld 26* (HAL); LR606806, LT159704; LR606607; LT159798; LR606315. ***Agrostis alopecuroides*** Lam.: Cultivated in BG Halle, Germany, from seed obtained from BG Dijon, France (no. 2001-1096), s.d., *M. Röser 11078* (HAL); LR606807, AM234719; LR606608; LR606513; LR606316. ***A. avenacea*** J.F.Gmel.: Australia, New South Wales, Great Dividing Range, 13.09.1998, *M. Röser 10762* (HAL); LR606808; LR606609; LR606514; LR606317. ***A. capillaris*** L.: Germany, Saxony, Upper Lusatia, 30.07.1998, *M. Röser 10660/2* (HAL); LR606809, AM234560; LR606610; FM179384; LR606318. ***A. linkii*** Banfi, Galasso & Bartolucci: Cultivated in BG Halle, Germany, from seeds obtained from BG Copenhagen, Denmark, s.d., *s.coll.*. (HAL0140383); LR606810; LR606611; LR606515; LR606319. ***A. pallens*** Trin.: U.S.A., Oregon, Clackamas County, Mt. Hood, 26.08.2000, *R.J. Soreng 6361* (US); –; LR606612; LR606516; LR606320. ***A. ramboi*** Parodi: Brazil, Sta Catarina, Campo dos Padres, 22.01.1957, *B. Rambo 60074* (B 10 0448888); LR606811; –; –; LR606321. ***A. scabra*** Willd.: U.S.A., Alaska, Kenai Peninsula, Resurrection River, 08.07.2000, *R.J. Soreng 6078* (US Catalog No.: 3682815, Barcode: 01259848); –; LR606613; LR606517; –. ***A. tandilensis*** (Kuntze) Parodi: Brazil, Rio Grande do Sul, Garibaldi, 13.10.1957, *O. Camargo 62575* (B 10 0448889); –; –; LR606518; LR606322. ***Aira elegans*** Willd. ex Roem. & Schult. (1): Cultivated in BG Halle, Germany, from seed obtained from BG Munich-Nymphenburg, Germany, 02.07.2002, *s.coll.* (HAL0140286); –; –; LR606519; –; (2): Austria, Tyrol, Paznaun, Verwall Alps; cultivated in BG Halle, Germany, from seed obtained from BG Berlin-Dahlem, Germany (no. 2001-3947), 14.10.2002, *Royl & Hempel* (HAL); LR606812; LR606614; –; LR606323. ***A. praecox*** L.: Germany, Mecklenburg-Vorpommern, Müritz Lake, 28.05.2003, *M. Röser 11009/1* (HAL); LR606813, AM234540; LR606615; FM179385; LR606324. ***Airopsis tenella*** (Cav.) Coss. & Durieu: France, Montpellier, Bellargues, 01.05.1956, *R. Schubert* (HAL0080969); LR606814; LR606616; LR606520; LR606325. ***Alopecurus aequalis*** Sobol.: Germany, Baden-Württemberg, near Tübingen, 28.06.1984, *M. Röser 1892* (HAL); LR606815; LR606617; LR606521; LR606326. ***Ammochloa palaestina*** Boiss.: Spain, Andalucía, Province Almería, Tabernas, 13.04.1965, *F. Bellot & S. Rivas Goday* (C); LR606816; LR606618; LR606522; LR606327. ***A. pungens*** Boiss.: Algeria, between Djelfa and Bou-Saâda, 06.04.1965, *V.P. Bochantsev 1238* (LE); LR606817; LR606619; LR606523; LR606328. ***Amphibromus nervosus*** (Hook.f.) Baill.: Australia, New South Wales, Great Dividing Range, 23.05.2002, *M. Röser 10770* (HAL); LR606818; LR606620; LR606524; LR606329. ***Ancistragrostis uncinioides*** S.T.Blake: New Guinea, Central District, Papua, Mount Victoria, 10.07.1974, *L.A. Craven 3006* (L0533422); –; –; LR606525; –. ***Aniselytron treutleri*** (Kuntze) Soják: China, Yunnan, Fugong Province, Bilou Mts., 08.09.1997, *R.J. Soreng 5229, P.M. Peterson & Sun Hang* (US); LR606819; LR606621; –; –. ***Anthoxanthum arcticum*** Veldkamp: Russia, Yakutia, lower reaches of the Kolyma River, 27.07.1975, *V.V. Petrovskiy & I.A. Mikhaylova* (LE); LR606820; –; LR606526; –. ***A. australe*** (Schrad.) Veldkamp (1): Austria, Burgenland, Bernstein, upper area of Steinstückel range, 13.05.1992, *M. Röser 9089* (HAL); LR606821; –; LR606527; –; (2): France, Hautes-Alpes, 05.08.1984, *M. Röser 2206* (HAL); –; LR606622; –; LR606330. ***A. glabrum*** (Trin.) Veldkamp (1): Russia, Khakassia, Ust-Abakan District, 08.06.1968, *I. Neyfeld* (LE); LR606822; LR606624; LR606529; LR606331; (2): Russia, Kemerovo Oblast, 23.05.2003, *s.coll.* (LE); –; LR606623; LR606528; –; (3) subsp. ***sibiricum*** (Tzvelev) Röser & Tkach: Russia, Tomsk Oblast, 03.06.1912, *L. Utkin* (LE); LR606823; LR606625; LR606530; –. ***A. monticola*** (Bigelow) Veldkamp: Russia, Sibiryakova Island, 19.06.2016, *M.B. Matveeva & I.I. Zanokha 2730* (LE); LR606824; LR606626; LR606531; LR606332. ***A. nitens*** (Weber) Y.Schouten & Veldkamp subsp. ***kolymense*** (Prob.) Röser & Tkach: Russia, Yakutia, Nizhnekolymskiye Kresty, 30.06.1950, *G. Nemlin 340* (LE); LR606825; LR606627; LR606532; LR606333. ***A. odoratum*** L.: Russia, Irkutsk Oblast, Trehgolovyy Golez Mount, 04.07.1986, *K. Baykov 298* (NS/NSK); LR606826; LR606628; LR606533; LR606334. ***A. redolens*** (Vahl) P.Royen: Chile, Chiloe Island; cultivated in BG Halle, Germany, from seed obtained from BG Olomouc, Czech Republic, s.d., *s.coll.* (HAL); LR606827; LR606629; LR606534; LR606335. ***A. repens*** (Host) Veldkamp: Russia, Tomsk Oblast, Barnaul District, 05.06.1890, *S. Korshinskiy* (LE); LR606828; LR606630; LR606535; LR606336. ***Antinoria agrostidea*** (DC.) Parl.: Portugal, Province Beira Alta, Serra da Estrela, Lagoa do Paixão, 15.08.1986, *Arriegas, Loureiro, Santos & Seleiro 192* (COI); LR606829; –; LR606536; LR606337. ***A. insularis*** Parl.: Greece, Crète, Nomos Hania, plateau d'Omalos, 23.05.1998, *A. Charpin 25346* (G86517); –; –; LR606537; LR606338. ***Apera spica-venti*** (L.) P.Beauv.: Germany, Mecklenburg-Vorpommern, Müritz Lake, 26.07.2001, *M. Röser 11005* (HAL); LR606830, AM234542; LR606631; LR606538; LR606339. ***Arctagrostis latifolia*** (R.Br.) Griseb.: Norway, Finnmark, Nesseby, 23.08.1997, *T. Alm & A. Often 563* (TROM 64713); LR606831; LR606632; HE802200; LR606340. ***Arctohyalopoa lanatiflora*** (Roshev.) Röser & Tkach (1): Russia, Yakutia, basin of Tompon River, 01.07.1956, *I.D. Kildyushevskiy 18/1* (LE); LR606833, AM234604; LR606633; LR606540; LR606341; (2): Russia, Yakutia, Verkhoyanskiy Range, 17.07.1985, *E. Rybinskaya 395* (NS/NSK); LR606832; –; LR606539; –. ***Arctopoa eminens*** (J.Presl) Prob.: Russia, Far East, Kuril Islands, Iturup, 25.07.1959, *E. Pobedimova & G. Konovalova 986* (LE); LR606834; LR606634; HE802201; LR606342. ***Arrhenatherum elatius*** (L.) P.Beauv. ex J.Presl & C.Presl: Germany, Saxony, Leipzig, s.d., *G. Winterfeld 77* (HAL); LR606835, AM234543, HG797415; LR606635; FM179388; LR606343. ***Avellinia michelii*** (Savi) Parl.: Spain, Valencia, Devesa de l'Albufera, s.d., *J.B. Peris & G. Stubing 1977* (RO); LR606836; LR606636; LT159736; LR606344. ***Avena hispanica*** Ard.: Cultivated in BG Halle, Germany, from seed obtained from Agriculture Canada, Ottawa, Canada (no. CAV 6604); s.d., *s.coll.* (HAL); LR606837; LR606637; LR606541; LR606345. ***A. macrostachya*** Balansa ex Coss. & Durieu: Algeria; cultivated in BG Halle, Germany, from seed obtained from M. Leggett, Institute of Grassland and Environmental Research, Aberystwyth, UK (no. CC7068); s.d., *s.coll.* (HAL); FM253118, FM957002, HG797416; LR606638; FM179443; LR606346. ***Avenella flexuosa*** (L.) Drejer: Germany, Mecklenburg-Vorpommern, Müritz Lake, 27.07.2001, *M. Röser 11008* (HAL); LR606838, AM234545; LR606639; FM179389; LR606347. ***Avenula pubescens*** (Huds.) Dumort.: Hungary, Vezsprem, between Csabrendek and Sümeg, 23.05.1999, *M. Röser 10928/2* (HAL); FM253118, FM957003, HG797417; LR606640; FM956100, HG797487; LR606348. ***Beckmannia eruciformis*** (L.) Host: Russia, Yakutia, Ordzhonikidzevskiy District, 22.08.1982, *Bolshakov & Vlasova 4377* (NS/NSK); LN554423; LR606641; HE802171; LR606349. ***Bellardiochloa polychroa*** (Trautv.) Roshev.: Armenia, Agaraz Mount, 10.08.1969, *V.E. Voskonjan* (LE); LR606839, FM253119; LR606642; FM179390; LR606350. ***B. variegata*** (Lam.) Kerguélen subsp. ***aetnensis*** (C.Presl) Giardina & Raimondo: Italy, Sicily, Catania Province, Mount Etna, 29.10.1987, *M. Röser 6032* (HAL); LR606840, AM234605; LR606643; FM179391; LR606351. ***Boissiera squarrosa*** (Sol.) Nevski (1): Iran, Gilan, Zandjan, 09.05.1969, *H. Eckerlein* (HAL0022065); LR606841, FM253120, LN554424; –; FM179392; –; (2): Israel; cultivated in BG Halle, Germany, from seed obtained from Kew's Millennium Seed Bank, UK (no. 537580), s.d., *s.coll.* (HAL); –; LR606644; LR606542; LR606352. ***Brachypodium distachyon*** (L.) P.Beauv.: Spain, Andalucía, Province Almería, Cabo de Gata, 11.04.1986, *M. Röser 4359* (HAL); LR606842, AM234568, LN554426; LR606645; –; LR606353. ***Briza media*** L.: Germany, Thuringia, NE Jena, Tautenburger Forest, 21.05.2005, *M. Röser 11072* (HAL); AM234610, HG797418, LN554427; –; FM179393; LR606354. ***B. minor*** L.: Italy, Abruzzo; cultivated in BG Halle, Germany, from seed obtained from Kew's Millennium Seed Bank, UK (no. 6150), 19.08.1977, *P. Newman, P.A. Thompson, E.A.M. Ormerod & R.H. Sanderson* (HAL); LR606843; LR606646; KJ598892; LR606355. ***Brizochloa humilis*** (M.Bieb.) Chrtek & Hadač: Russia, Krym, Peninsula Tarkhankut, 25.05.1984, *N.N. Tzvelev, D.V. Geltman, N.A. Medvedeva & G.V. Mustafina 1110* (LE); LR606844; –; HE802178; LR606356. ***Bromus erectus*** Huds.: France, Hérault, Causses du Larzac, 07.06.1984, *M. Röser 1721* (HAL); AM234570, FM956476; LR606647; FM179394, FM956470; –. ***Calamagrostis arenaria*** (L). Roth subsp. ***arundinacea*** (Husn.) Banfi, Galasso & Bartolucci: Portugal, Odemira, Vila Nova de Milfontes; cultivated in BG Halle, Germany, from seed obtained from BG Lisbon, Portugal, s.d., *M. Röser 11055* (HAL); LR606845, AM234561; LR606648; LR606543; LR606357. ***C. arundinacea*** (L.) Roth: Germany, Lower Saxony, Harz Mts., Siebertal above Herzberg, 02.08.1983, *M. Röser 1232* (HAL); LR606846; LR606649; LR606544; LR606358. ***C. canescens*** (Weber) Roth: Germany, Saxony, Freiberger Mulde, 01.08.2005, *S. Schiebold & A. Golde* (HAL0004118); LR606847; LR606650; LR606545; LR606359. **'*C.*'** ***flavens*** (Keng) S.L.Lu & Z.L.Wu: China, Qinghai, surroundings of Maqen, 06.08.2004, *I. Hensen* (HAL); LR606882; LR606680; LR606561; LR606393. ***C. macrolepis*** Litv.: Mongolia, s.d., *K. Wesche 4279* (HAL); LR606848, AM234559; LR606651; LR606546; LR606360. ***C. neglecta*** (Ehrh.) G.Gaertn., B.Mey. & Scherb. subsp. ***borealis*** (C.Laest.) Selander: U.S.A., Alaska, Barrow, Gas Well Road, 01.08.2000, *R.J.*

Appendix 1. Continued.

Soreng 6204 (US); –; LR606652; LR606547; LR606361. ***C. nutkaensis*** (J.Presl) Steud.: U.S.A., Alaska, Kenai Peninsula, Seward, 08.07.2000, *R.J. Soreng 6062* (US); LR606849; LR606653; LR606548; LR606362. ***C. purpurascens*** R.Br. (1): Canada, Yukon, Marsh Lake, 14.06.2000, *R.J. Soreng 5996b* (US); LR606850, LT222486; LR606655; FM179395; LR606363; (2): Canada, Yukon, Kluane Lake, Duke River Bridge, 14.08.2000, *R.J. Soreng 6301* (US); –; LR606654; LR606549; –. ***C. rivalis*** H.Scholz: Germany, Saxony, Mulde River, 30.09.2002, *M. Röser 11054/D* (HAL); LR606852, AM234564; LR606657; LR606550; LR606365. ***Catabrosa aquatica*** (L.) P.Beauv.: Germany, Baden-Württemberg, Zollhausried near Blumberg, 18.07.1984, *M. Röser 2007* (HAL); LR606853, AM234589; –; FM179396; LR606366. ***Catabrosella humilis*** (M.Bieb.) Tzvelev: Kazakhstan, Ili River, 08.05.1934, *N.I. Rubtsov* (LE); LR606854; –; HE802182; LR606367. ***C. variegata*** (Boiss.) Tzvelev: Russia, Kabardino-Balkar Republic, Caucasus, Mount Elbrus' foot, 24.07.1939, *E.V. Schiffers & T.A. Moreva* (LE); LR606855; –; HE802181; –. ***Catapodium marinum*** (L.) C.E.Hubb.: Spain, Valencia, Province Alicante, Cabo de Santa Pola, 10.04.1986, *M. Röser 4299* (HAL); LR606856, HE646574; LR606658; HE646600; LR606368. ***C. rigidum*** (L.) C.E.Hubb.: Greece, Macedonia, Thessaloniki, Chalcidice, 25.05.1985, *M. Röser 2571* (HAL); LR606857, AM234586; LR606659; FM179399; –. ***Chascolytrum bulbosum*** (Parodi) Essi, Longhi-Wagner & Souza-Chies: Brazil, Rio Grande do Sul, Pirationi, 16.11.2003, *L. Essi 50, J.F.M. Valls, A. Guglieri & S. Hefler* (ICN); LR606858; LR606660; LR606551; LR606369. ***C. rhomboideum*** (Link) Essi, Longhi-Wagner & Souza-Chies: Chile, Linares Province, Department Loncomilla, 12.10.1954, *R. Avendaño T.* (SGO071551); LR606859; LR606661; LR606552; LR606370. ***C. subaristatum*** (Lam.) Desv.: Argentina, Buenos Aires Province; cultivated in BG Halle, Germany, from seed obtained from BG Berlin-Dahlem, Germany (no. 2001-3817), s.d., *M. Röser 11079* (HAL); LR606860, AM234608; LR606662; LR606553; LR606371. ***C. uniolae*** (Nees) Essi, Longhi-Wagner & Souza-Chies: Paraguay, Department Paraguarí, National Park Ybycui, 31.10.1989, *Zardini & Guard 14580* (MO3879842); LR606861; LR606663; LR606554; LR606372. ***Cinna latifolia*** (Trevir. ex Göpp.) Griseb.: Finland, South Savo, Rantasalmi, 13.08.1977, *M. Isoviita* (HAL0050605); LR606862; LR606664; HE802198; LR606373. ***Cinnagrostis rigida*** (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá: Bolivia, Department La Paz, Province Murillo, 12.02.1989, *S.G. Beck 14738* (B 10 0448895); LR606851, HG797422; LR606656; HG797492; LR606364. ***Coleanthus subtilis*** (Tratt.) Seidel ex Roem. & Schult.: Austria, Lower Austria, 30.08.2006, *H. Rainer & M. Röser 11082* (HAL); LR606863; LR606665; HE802180; LR606374. ***Colpodium biebersteinianum*** (Claus) Röser & Tkach: Cultivated in BG Halle, Germany, from seed obtained from Institute of Plant Genetics and Crop Plant Research, Gatersleben, Germany, 28.05.2003, *s.coll.* (HAL); AM234551, LN554457; LR606666; HE802184; LR606375. ***C. chionogeiton*** (Pilg.) Tzvelev: Tanzania, Kilimanjaro, above Mawengi hut, 25.11.1967, *D.G. King 6* (UPS:BOT:V-652825); LR606864; –; HE802185; LR606376. ***C. hedbergii*** (Melderis) Tzvelev: Ethiopia, Bale Province, Bale Mountains National Park, Saneti Plateau; cultivated in BG Uppsala, Sweden, 07.06.1905, *O. Hedberg 5618* (UPS:BOT:V-652843); LR606865; –; HE802186; LR606377. ***C. trichopodum*** (Boiss.) Röser & Tkach: Cultivated in BG Halle, Germany, from seed obtained from Institute of Plant Genetics and Crop Plant Research, Gatersleben, Germany, 28.05.2003, *M. Röser 11074* (HAL); LR606866, AM234551; LR606667; FM179441; LR606378. ***C. versicolor*** (Steven) Schmalh.: Georgia, South Ossetia, Ermany., 23.08.1938, *E.A. & N.A. Bush* (LE); LR606867, FM253122; –; FM179397; LR606379. ***Cornucopiae cucullatum*** L.: Cultivated in BG Halle, Germany, from seeds obtained from Botanical Garden Frankfurt, Germany (no. 2005-926), s.d., *E. Döring* (HAL0100582); LR606868; LR606668; HF564627; LR606380. ***Corynephorus canescens*** (L.) P.Beauv. (1): Portugal, Province Estremadura, Vieria, Pinhal de Leira, 14.07.1992, *M. Röser 9483* (HAL); LR606869; –; HE802179; –; (2): Germany, Saxony-Anhalt, Harz Mts., 14.05.2016, *M. Röser 11230 & N. Tkach* (HAL); –; LR606669; LR606555; LR606381. ***Cutandia maritima*** (L.) Barbey: France, Hérault, Etang d'Ingril, 30.05.1977, *A. Dubuis* (HAL0048831); LR606870, HE646572; LR606670; HE646601; LR606382. ***Cyathopus sikkimensis*** Stapf: China, Yunnan, Fugong Province, s.d., *R.J. Soreng 3224, P.M. Peterson, Sun Hang* (US); LR606871, AM234553; LR606671; HE802199; LR606383. ***Cynosurus cristatus*** L.: Germany, Baden-Württemberg, Ettenheim, 16.06.1989, *M. Röser 9965* (HAL); LR606872, HE646575; –; HE646602; LR606384. ***C. elegans*** Desf.: France, Corsica, Forêt d'Aitone, 28.06.1987, *M. Röser 5420* (HAL); LR606873, HG797427; LR606672; LR606556; LR606385. ***Dactylis glomerata*** L.: Greece, Macedonia, Serron, Vrondus range, 31.05.1985, *M. Röser 2948* (HAL); LR606874, AM234595; LR606673; LR606557; –. ***Deschampsia bolanderi*** (Thurb.) Saarela: U.S.A., California, Monterey County, Hanging Valley, Santa Lucia Mts., 11.06.2003, *D.H. Wilken 16163 & E. Painter* (RSA 695253); LR606875, HE646588; –; HE646612; LR606386. ***D. cespitosa*** (L.) P.Beauv.: Germany, Brandenburg, Niederspree, s.d., *M. Röser 10737/1* (HAL); LR606876, AM234546; LR606674; AF532929; LR606387. ***D. danthonioides*** (Trin.) Munro: U.S.A., California, Siskiyou, Klamath River, 03.06.2000, *R.J. Soreng 5965* (US); LR606877; LR606675; LR606558; LR606388. ***D. elongata*** (Hook.) Munro: Argentina, Neuquén Province, Los Lagos, Correntoso, 27.01.1990, *Z. Rúgolo 1245* (B 10 0448863); LR606878, LT159689; –; LT159754; LR606389. ***Desmazeria philistaea*** (Boiss.) H.Scholz: Israel, Philistean Plain, 21.03.1989, *A. Danin & al. 03.074* (B 10 0240417); LR606879, HE646573; LR606676; HE646603; LR606390. ***D. sicula*** (Jacq.) Dumort. (1): Malta, Dwejra Point, 01.04.1975, *A. Hansen 490* (C); LR606880, HE646576; LR606677; HE646604; –; (2): Malta, Gozo; cultivated in BG Halle, Germany, from seed obtained from Kew's Millennium Seed Bank, UK (no. 17332), 02.08.1981, *J. Newmarch* (HAL); –; LR606678; LR606559; LR606391. **"*Deyeuxia*" *contracta*** (F.Muell. ex Hook.f.) Vickery: Australia, Tasmania; cultivated in BG Halle, Germany, from seed obtained from Kew's Millennium Seed Bank, UK (no. 391131), 21.02.2007, *E. Brüllhardt & M. Visoiu* (HAL); LR606881; LR606679; LR606560; LR606392. ***Dichelachne crinita*** (L.f.) Hook.f.: New Zealand, Canterbury, Banks Peninsula, Pigeon Bay, 03.12.1990, *J.R. Bulman* (CHR 477794); LR606883; LR606681; LR606562; LR606394. ***D. micrantha*** (Cav.) Domin: Australia, New South Wales, Thirlmer Lakes area, 04.10.1998, *R.J. Soreng 5901, P.M. Peterson, S.W.L. Jacobs* (US); LR606884, FM253124; LR606682; FM179401; LR606395. ***Drymochloa sylvatica*** (Pollich) Holub: Germany, Lower Saxony, Harz Mts., Siebertal above Herzberg, 02.08.1983, *M. Röser 1227* (HAL); LR606885, AM234585; LR606683; FM179404; LR606396. ***Dryopoa dives*** (F.Muell.) Vickery (1): Australia, Tasmania, Hobart District, 04.12.1980, *T. Walker* (AD98132291); LR606886; LR606684; LR606563; LR606397; (2): Australia, Victoria; cultivated in BG Halle, Germany, from seed obtained from Kew's Millennium Seed Bank, UK (no. 333531), 15.02.2006, *M.J. Hirst & S. Hodge* (HAL); –; LR606685; LR606564; –. ***Dupontia fisheri*** R.Br. subsp. ***psilosantha*** (Rupr.) Hultén: Russia, Yakutia, estuary of Yana River, near Nizhneyansk, 27.07.1988, *Doronkin & Bubnova 439* (NSK); LR606887, AM234601; LR606686; AY237848; LR606398. ***Dupontia fulva*** (Trin.) Röser & Tkach: Russia, Yakutia, estuary of Yana River, near Nizhneyansk, 21.07.1988, *Doronkin & Kulagin 81* (NSK); LR606888, AM234606; LR606687; FM179387; LR606399. ***Echinaria capitata*** (L.) Desf.: Spain, Andalusia, Province Granada, Sierra Nevada, 14.06.1985, *M. Röser 3336* (HAL); LR606889, AM234599, LN554434; LR606688; LR606565; LR606400. ***Echinopogon caespitosus*** C.E. Hubb.: Australia, New South Wales, Thirlmer Lakes area, 04.10.1998, *R.J. Soreng 5900, P.M. Peterson, S.W.L. Jacobs* (US); LR606890, AM234609; LR606689; FM179403; LR606401. ***Festuca berteroniana*** Steud.: Chile, Juan Fernandez, Masatierra, Corrales de Molina, 24.01.1990, *D. Wiens, P. Penailillo, R. Schiller, A. Andaur* (MO5259377); LR606891, HE646581; LR606690; FR692028; LR606402. ***F. floribunda*** (Pilg.) P.M.Peterson, Soreng & Romasch.: Peru, Department Moquegua, Province Mariscal Nieto, 01.03.1999, *P.M. Peterson 14566, N. Refulio Rodriguez & F. Salvador Perez* (NY); LR606892; LR606691; LR606566; LR606403. ***F. incurva*** (Gouan) Gutermann: Spain, Provincia of Salamanca, 31.05.1987, *F. Amich & J.A. Sánchez 19923* (RO); LR606893, HE646587; LR606692; HE646611; LR606404. ***F. lachenalii*** (C.C.Gmel.) Spenn.: France, Corsica, 29.06.1987, *M. Röser 5470* (HAL); LR606894; –; LR606567; –. ***F. maritima*** L.: France, Montpellier, Bois de Boscares, 01.04.1956, *R. Schubert* (HAL0081028); LR606895, HE646590; LR606693; AY118095; –. ***F. masatierrae*** Röser & Tkach: Chile, Valparaíso Region, Juan Fernándes, s.d., *R.A. Philippi* (HAL0052812); –; –; FR692035; –. ***F. myuros*** L.: Cultivated in BG Halle, Germany, from seed obtained from BG Dijon, France (no. 1060), 02.07.2002, *s.coll.* (HAL); LR606896; LR606694; –; –. ***F. salzmannii*** (Boiss.) Boiss. ex Coss.: Spain, Andalucía, Province Malaga, Sierra de Mijas, Alhaurín el Grande, 08.05.1989, *S. Rivas-Martínez 17742* (BASBG); LR606897, HE646583; LR606695; HE646608; LR606405. ***Gastridium nitens*** (Guss.) Coss. & Durieu: Greece, Crete, Agios Nikolaos, 01.05.1983, *G. van Buggenhout* (ROM); LR606898; LR606696; LR606568; LR606406. ***G. phleoides*** (Nees & Meyen) C.E.Hubb.: Lebanon, North Lebanon; cultivated in BG Halle, Germany, from seed obtained from Kew's Millennium Seed Bank, UK (no. 241421), 28.07.2004, *M. van Slageren & Khairallah, S.* (HAL); LR606899; LR606697; LR606569; LR606407. ***G. ventricosum*** (Gouan) Schinz & Thell.: France, Corsica, 30.06.1987, *M. Röser 5491* (HAL); LR606900; LR606698; LR606570; LR606408. ***Gaudinia fragilis*** (L.) P.Beauv.: Spain, Andalucía, Province Cádiz, NW Gibraltar, 20.06.1985, *M. Röser 11070* (HAL); LN554436; LR606699; LT159737; –. ***Graphephorum canescens*** (Buckley) Röser & Tkach: U.S.A., Oregon, Josephine, Cave Creek, 02.06.2000, *R.J. Soreng 5956* (US); LR606997, AM234611; LR606797; LR606603; LR606504. ***G. cernuum*** (Trin.) Röser & Tkach: U.S.A., Montana, Glacier County, Alon Continental Divide, 19.07.2003, *P. Lesica*

Appendix 1. Continued.

8714 (NY1819808); LR606998, LT159703; LR606798; LT159797; LR606505. ***G. melicoides*** (Michx.) Desv.: Canada, New Brunswick, Madawaska County, 04.08.1990, *G. Flanders & R. Hinds 981* (CAN550357); LR606901, HG797428; LR606700; HG797505; LR606409. ***G. wolfii*** J.M.Coult.: U.S.A., Colorado, San Juan County, 06.08.1982, *R.J. Soreng* (NY); LR606902, HG797429; LR606701; HG797506; LR606410. ***Helictochloa aetolica*** (Rech.f.) Romero Zarco: Greece, Epirus, Tomaros Mts., 23.02.2004, *M. Röser 10726/3* (HAL); FM957008; –; LR606571; LR606411. ***H. bromoides*** (Gouan) Romero Zarco subsp. ***bromoides***: France, Vaucluse, 19.08.1997, *M. Röser 10630/2* (HAL); LR606903, AM234721, FM956474, HG797430; LR606702; FM956463; LR606412. ***H. compressa*** (Heuff.) Romero Zarco: Greece, Macedonia, Drama, Orvilos region, 16.08.1998, *M. Röser 10707/8* (HAL); FM957009; LR606703; –; LR606413. ***H. hookeri*** (Scribn.) Romero Zarco (1) subsp. ***hookeri:*** Canada, Yukon, Kluane Lake, Duke River Bridge, 14.08.2000, *R.J. Soreng 6305* (US); LR606904; LR606704; LR606572; LR606414; (2) subsp. ***schelliana*** (Hack.) Romero Zarco: Mongolia, Chentej Aimag, 02.08.2002, *K. Wesche 4333* (HAL); LR606905, AM234550; LR606705; FM179409, FN984915; LR606415. ***H. levis*** (Hack.) Romero Zarco: Spain, Andalusia, Province Granada, Sierra Nevada, 23.04.2001, *G. Winterfeld 50* (HAL); FM958418; LR606706; LR606573; LR606416. ***H. marginata*** (Lowe) Romero Zarco: Portugal, Province Beira Alta, Serra da Estrela, between São Romão and Torre, 12.07.1992, *M. Röser 9421* (HAL); FM957007; –; LR606574; LR606417. ***H. versicolor*** (Vill.) Romero Zarco: France, Haute Garonne, Pyrenees, Pic de Cécire, 21.08.1985, *M. Röser 3937* (HAL); LR606906, FM957011; –; FM956467; LR606418. ***Helictotrichon convolutum*** (C.Presl) Henrard: Greece, Peloponnese, Arkadia, Menalon, 10.08.1998, *M. Röser 10697* (HAL); LR606907, AM234557, HG797431; LR606707; FM179406, FM956461; LR606419. ***H. mongolicum*** (Roshev.) Henrard: Russia, E Sayan Mts., Large Kishta River source, 14.08.1962, *L. Malyshev 795* (NS/NSK); LR606908, HG797439; LR606708; HG797516; LR606421. ***H. parlatorei*** (Woods) Pilg.: Austria, Carinthia, 16.10.2001, *B. Heuchert 11-08* (HAL); AM234566, FM957005, HG797442; LR606709; FM179408, LT159741; LR606422. ***H. sarracenorum*** (Gand.) Holub: Spain, Andalucía, Province Granada, between Guadix and Granada, 13.06.1985, *M. Röser 3266* (HAL); LR606909, FM956473, HG797443; LR606710; FM956462, HG797519; –. ***H. sedenense*** (DC.) Holub: France, Pyrénées-Orientales, Mount Canigou, 09.08.1997, *M. Röser 10545* (HAL); LR606910, FM957004, HG797444; LR606711; FM956104, HG797520; LR606423. ***H. sempervirens*** (Vill.) Pilg.: France, Drôme, 22.08.1984, *M. Röser 2429* (HAL); HG797445; LR606712; HG797521; –. ***H. setaceum*** (Vill.) Henrard subsp. ***petzense*** (H.Melzer) Röser: Austria, Carinthia, Karavankes near Bleiburg, Petzen, 09.07.1998, *M. Röser 10646* (HAL); LR606911, FM957010; LR606713; FM956468; –. ***H. thorei*** (Duby) Röser: Portugal, Province Minho, 02.07.2002, *M. Röser 9322/3A* (HAL); LR606912, AM234565, HG797448; LR606714; FM956102, FM179430; LR606424. ***H. ×krischae*** Melzer: Austria, Carinthia, Karavankes near Bleiburg, Petzen, 09.07.1998, *M. Röser 10648* (HAL); LR606913, FM958417, HG797451; LR606715; FM958415, HG797513; LR606420. ***Holcus mollis*** L.: Germany, Saxony, Upper Lusatia, 04.07.2002, *M. Röser 10658/2* (HAL); LR606914, AM234554; LR606716; FM179411; LR606425. ***Hookerochloa eriopoda*** (Vickery) S.W.L.Jacobs: Australia, Southern Tablelands, 30.01.1964, *R. Pullen 4003* (AD96435171); LR606915, HE646578; –; HE646605; LR606426. ***H. hookeriana*** (F.Muell. ex Hook.f.) E.B.Alexeev: Australia, Tasmania, Macquarie Rivulet, 01.02.2011, *A.M. Buchanan 15711* (HO 507299); LR606916, HE646579; LR606717; HE646606; LR606427. ***Hordelymus europaeus*** (L.) O.E.Harz: Germany, Baden-Württemberg, Suebian Alb, Urach, 01.08.1982, *M. Röser 708* (HAL); AM234596, LN554438; –; FM179412; LR606428. ***Hordeum marinum*** Huds. subsp. ***gussoneanum*** (Parl.) Thell.: Italy, Sardinia, Nuoro Province, Altipiano de Campeda, 09.05.1993, *M. Röser 10131* (HAL); FR694880, HG797452; LR606718; FR692026; –. ***Hyalopoa pontica*** (Balansa) Tzvelev: Russia, Balkaria, moraine of Karachiran glacier, 29.07.1925, *E. Bush & N. Bush* (LE); –; –; LR606575; –. ***Hyalopodium araraticum*** (Lipsky) Röser & Tkach: Armenia, Geghama Mts., Spitak-Syr, 21.08.1960, *Arverdyaev & Mirzaeva* (HAL0008785); LR606917; LR606719; HE802183; LR606429. ***Hypseochloa cameroonensis*** C.E.Hubb.: Cameroon, Cameroons Mountain, 01.12.1929, *T.S. Maitland 874* (B 10 0448883); LR606918; LR606720; LR606576; LR606430. ***Koeleria capensis*** Nees: Uganda, Mount Elgon, Sasa Trail, s.d., *K. Wesche 20026* (HAL); LR606919, AM234558, HG797453; LR606721; FM179413; –. ***K. loweana*** Quintanar, Catalán & Castrov.: Portugal, Madeira, 05.09.1983, *L. Dalgaard & V. Dalgaard 13276* (C); LR606920, HE646580; LR606722; HE646607; –. ***K. pyramidata*** (Lam.) P.Beauv.: Mongolia, Central Aimag, N to Ulan-Bator, 15.05.1944, *Ju.A. Yunatov 4381* (LE); LR606921, LT159683; LR606723; LT159743; LR606431. ***K. spicata*** (L.) Barberá, Quintanar, Soreng & P.M.Peterson: U.S.A., Alaska, Dalton Hwy, Chandler Shelf, 05.08.2000, *R.J. Soreng 6221* (US Catalog No.: 3682816, Barcode: 01259847), LR607000, LT159707; LR606800; LT159801; LR606507. ***Lagurus ovatus*** L.: Portugal, Minho Province, coastal area at Eposende; cultivated in BG Halle, Germany, from seed, 19.08.2002, *M. Röser 9271* (HAL); LR606922, AM234563, HG797455; LR606724; FM179414; –. ***Lamarckia aurea*** (L.) Moench: Spain, Murcia, between Murcia and Lorca, 11.04.1986, *M. Röser 4383* (HAL); LR606923; LR606725; LR606577; –. ***Limnas malyschevii*** O.D.Nikif.: Russia, Putorana plateau, Haya-Kuyol Lake, 10.08.1972, *S. Andrulajtis 1204* (NS/NSK); LR606924; LR606726; HE802176; LR606432. ***L. stelleri*** Trin.: Russia, Yakutia, Mirninskiy District, Mogdy River, 15.08.1975, *N. Vodopyanova, E. Ammosov, V. Strelkov 813* (NS/NSK); LR606925; LR606727; HE802175; –. ***Limnodea arkansana*** (Nutt.) L.H.Dewey: U.S.A., Texas, Washington County, 01.05.1976, *T.F. Daniel 69* (NY); LR606926, LN554440; LR606728; LR606578; –. ***Littledalea racemosa*** Keng: China, Qinghai, Kunlun Shan, 27.07.1994, *R.J. Soreng, P.M. Peterson, Sun Hang 5487-90-94* (US); LR606927, AM234572, LN554441; LR606729; FM179416; LR606433. ***Lolium giganteum*** (L.) Darbysh.: Germany, Lower Saxony, Harz Mts., Wolfshagen, 23.07.1987, *M. Röser 5719* (HAL); LR606928, AM234720; LR606730; HE646615; LR606434. ***Macrobriza maxima*** (L.) Tzvelev: France, Languedoc-Roussillon, Gard; cultivated in BG Halle, Germany, from seed obtained from Kew's Millennium Seed Bank, UK (no. 69618), 22.08.1988, *J. Feltwell* (HAL), LR606929; LR606731; LR606579; LR606435. ***Mibora minima*** (L.) Desf.: Cultivated in BG Halle, Germany, from seeds, origin unknown, *s.coll*. (HAL0107426); LR606930, FR694894; LR606732; FR692030; LR606436. ***Milium effusum*** L.: France, Alpes-Maritimes, 21.07.1989, *M. Röser 6723* (HAL); LR606931, AM234598, HG797456; –; FM179419; LR606437. ***M. transcaucasicum*** Tzvelev: Armenia, Gukasyan District, Caucasus, Javakheti range's foot, 27.06.1960, *N.N. Tzvelev & S. Czerepanov 425* (LE); LR606932; –; HE802197; –. ***Molineriella laevis*** (Brot.) Rouy: Spain, Province of Madrid, Manzanares el Real, 15.05.1984, *P. Montserrat* (C); LR606933; LR606733; LR606580; LR606438. ***M. minuta*** (L.) Rouy: Greece, Lesbos, 03.04.1994, *Nielsen & Skovgaard 9613* (C); LR606934; LR606734; LR606581; LR606439. ***Nephelochloa orientalis*** Boiss.: Turkey, between Denizli and Aydin, 22.06.1976, *C. Simon 76900* (BASBG); LR606935, HE646584; –; HE646609; LR606440. ***Oreochloa blanka*** Deyl: France, Pyrénées-Orientales, Massif du Puigmal d'Err, 10.07.1991, *J. Lambinon 91/205* (B 10 0448884); LR606936; LR606735; LR606582; LR606441. ***O. disticha*** (Wulfen) Link: Romania, Jud. Hunedoara, Retezat Mts., 31.07.1992, *M. Röser 9588* (HAL); LR606937, AM234592; –; FM179421; LR606442. ***Paracolpodium altaicum*** (Trin.) Tzvelev: Russia, Altai, Kosh-Agach, Saylyugem range, 12.08.1982, *V. Khanminchun & N. Friesen 8* (ALTB); LR606938; LR606736; HF564629; LR606443. ***P. baltistanicum*** (Dickoré) Röser & Tkach: Pakistan, Baltistan, E part of Deosai plateau, 15.07.1991, *G. Miehe & S. Miehe 5105* (MR); LR606939; LR606737; LR606583; LR606444. ***Parapholis cylindrica*** (Willd.) Röser & Tkach: Cultivated in BG Halle, Germany, from seed obtained from BG Copenhagen, Denmark, 08.03.2010, *s.coll*. (HAL0140597); LR606940, HE646577; LR606738; LR606584; –. ***P. filiformis*** (Roth) C.E.Hubb. (1): France, Montpellier, 05.06.1957, *Streitberg & Stohr* (HAL0081242); LR606941, HE646585, LN554446; –; HE646610; LR606446; (2): France, Languedoc-Roussillon, Hérault; cultivated in BG Halle, Germany, from seed obtained from Kew's Millennium Seed Bank, UK (no. 63085), 06.08.1986, *J. Feltwell* (HAL); –; LR606739; LR606585; LR606445. ***P. incurva*** (L.) C.E.Hubb.: Greece, Macedonia, Thessaloniki, Chalcidice, 25.05.1985, *M. Röser 2517* (HAL); LR606942, AM234583; LR606740; FM179422; LR606447. ***P. marginata*** Runemark: Greece, Lasithiou, Eparchia Sitia, Xerocampos, Katsouria, 19.06.1905, *N. Böhling 5292b* (B 10 0199860); LR606943; LR606741; LR606586; LR606448. ***Parvotrisetum myrianthum*** (Bertol.) Chrtek: Greece, Macedonia, 21.06.1970, *A. Strid 221* (C); LR606944, LT159690; LR606742; HE802174; LR606449. ***Pentapogon quadrifidus*** (Labill.) Baill. (1) var. ***quadrifidus***: Australia, South Australia, Southern Tableland, 29.10.1998, *I. Crawford & N. Taws 4887* (NSW463696); LR606946; LR606744; LR606587; LR606451; (2) var. ***parviflorus*** (Benth.) D.I.Morris: Australia, Tasmania, South West Tasmania, Nye Bay, 09.01.1986, *A. Moscal 11543* (HO 95925); LR606945; LR606743; –; LR606450. ***Periballia involucrata*** (Cav.) Janka: Portugal, Minho, Portela do Homem, Cruz do Louro, 02.06.1990, *A.I.D. Correia & A. Fernandes* (LISU 160284); LR606947; LR606745; LR606588; LR606452. ***Peyritschia pringlei*** (Scribn.) S.D.Koch: Mexico, Puebla, Mun. S. Nícolas de los Ranchos Buenavista, 05.02.1988, *P. Tenorio 15095* (MEXU 542571); LR606948, HG797458; LR606746; HG797528; LR606453. ***Phalaris arundinacea*** L.: Russia, Yakutia, middle course of Kolyma, Lobuy, 30.07.1983, *Doronkin & Bubnova 2264* (NS/NSK); LR606949; LR606747; HF564628; LR606454. ***P. canariensis*** L.: Italy, Napoli Province, Campania; cultivated in BG Halle, Germany, from seed obtained from BG Berlin-Dahlem, Germany (no. 2001-3939), 15.05.2003, *Royl*

Appendix 1. Continued.

173 (HAL); LR606950; LR606748; HE802173; LR606455. ***P. coerulescens*** Desf.: Italy, Siena, cultivated in BG Halle, Germany, from seed obtained from BG Berlin-Dahlem, Germany (no. 2001-3940); 07.06.2004, *s.coll.* (HAL); LR606951; LR606749; HE802172; –. ***Phippsia algida*** (Sol.) R.Br.: Russia, E Taymyr, Nyunkarakutari River, Poymennoe Lake, 05.08.1998, *I.N. Pospelov 98-158* (NS); LR606952, AM234603; –; FM179424; LR606456. ***P. concinna*** (Th.Fr.) Lindeb.: Russia, Taymyr, Syndasko River, 23.07.1979, *N. Vodopyanova, R. Krogulevich, N. Frisen, V. Nikolayeva & N. Shumik 224* (NS); LR606953, AM234582; LR606750; FM179425; LR606457. ***Phleum alpinum*** L.: Austria, Styria, near St. Oswald, 31.07.2001, *M. Röser 11023* (HAL); LN554448; LR606751; LR606589; LR606458. ***P. crypsoides*** (d'Urv.) Hack.: Cyprus, Cape Greco, 15.04.1992, *F. Skovgaard* (C); LR606954; –; HE802187; LR606459. ***P. phleoides*** (L.) Karsten: Norway, Oslo; cultivated in BG Halle, Germany, from seed obtained from BG Oslo, Norway (no. 2003-669), 31.07.2003, *s.coll.* (HAL); LR606955, AM234552; LR606752; FM179426; LR606460. ***Pholiurus pannonicus*** (Host) Trin.: Hungary, Great Hungarian Plane (Alföld), Hortobágy Puszta, 13.06.1967, *W. Hilbig* (HAL0067272); LR606956, HE646586; LR606753; HE646616–HE646625 (clones consensus); LR606461. ***Poa annua*** L.: Germany, Saxony-Anhalt, 18.01.2005, *M. Röser 11065* (HAL); LR606957, AM234593; LR606754; FM179428; LR606462. ***P. bulbosa*** L.: Austria, Lower Austria, near Eggenburg, 28.04.1991, *M. Röser 7419* (HAL); LR606959, AM234594; LR606756; FM179429; LR606464. ***P. cyrenaica*** E.A.Durand & Barratte: Libya, Bengasi, 29.01.1924, *F. Lavara & L. Grande* (FI); LR606960; –; HE802196; LR606465. ***P. diaphora*** Trin.: Mongolia, Bajan Ölgi Aimak, 27.07.1977, *W. Hilbig* (HAL0044036);, LR606961; LR606757; HE802188; –. ***P. fax*** J.H.Willis & Court: Australia, South Australia, Coffin Bay Conservation Park, 08.10.1991, *D.E. Murfet 1278* (AD99151120); LR606962; LR606758; HE802191; LR606466. ***P. hitchcockiana*** Soreng & P.M.Peterson: Ecuador, Province Loja, Cajanuma, 05.03.1987, *I. Grignon* (MO5151808); LR606963; –; HE802195; –. ***P. labillardierei*** Steud.: Australia, Nora Creina, 11.10.1989, *P.C. Heyligers 89162* (AD99151199); LR606958; LR606755; HE802193; LR606463. ***P. lepidula*** (Nees & Meyen) Soreng & L.J.Gillespie (1): Peru, Department Moquegua, Provincia Mariscal Nieto, 01.03.1999, *P.M. Peterson* (MO5151809); LR606964, FR694884; LR606759; –; LR606467; (2): Chile, Tarapacá Region (Region I), Chungará, 04.04.2001, *P.M. Peterson 15759 & R.J. Soreng* (MO5698870); FR694884; –; FR692034; –. ***P. persica*** Trin.: Turkmenistan, Geok-Tepinskiy District, Central Kopet-Dag, 12.07.1969, *A.A. Mescheryakov* (LE); LR606965; LR606760; HE802189; LR606468. ***P. pratensis*** L.: Germany, Saxony-Anhalt, Dessau-Roßlau, 14.05.2009, *E. Willing 25.267 D* (HAL0109437); LR606966; LR606761; LR606590; LR606469. ***P. serpaiana*** Refulio: Chile, Tarapacá Region (Region I); Parinacota, 04.04.2001, *P.M. Peterson & R.J. Soreng* (MO5698869); LR606967; LR606762; HE802194; LR606470. ***P. sintenisii*** H.Lindb.: Cyprus, Ayios Nikolaos; Kew DNA Bank, London (no. 24200), 01.11.1988, *Meikle 2853* (K); LR606968; LR606763; HE802190; LR606471. ***Podagrostis aequivalvis*** (Trin.) Scribn. & Merr.: Canada, British Colombia, Queen Charlotte Islands, Moresby Island, 25.06.1957, *J.A. Calder 21762, D.B.O. Savile & R.L. Taylor* (B 10 0448891); LR606969; LR606764; LR606591; LR606472. ***P. thurberiana*** (Hitchc.) Hultén: U.S.A., Washington, Kittitas County, Beverly Creek, 25.08.2000, *R.J. Soreng 6356* (US); –; LR606765; LR606592; LR606473. ***Psilathera ovata*** (Hoppe) Deyl: Austria, Tyrol, Grossglockner Mountain, Hochtor, 05.09.2017, *M. Röser 11318 & N. Tkach* (HAL); –; LR606766; –; LR606474. ***Puccinellia fasciculata*** (Torr.) E.P.Bicknell: Hungary, Hajdú-Bihar county, Hortobágy Puszta, 27.05.1991, *M. Röser 7633* (HAL); LR606970, AM234588, LN554450; LR606767; FM179431; LR606475. ***P. vahliana*** (Liebm.) Scribn. & Merr.: Denmark, W Greenland, Disko, Nodfjord, Stordal, 14.08.1975, *L. Andersen & B. Fredskild* (LE); LR606971; LR606768; LR606593; LR606476. ***Relchela panicoides*** Steud.: Chile, Andes, Malleco Province, Fundo Solano, Los Alpes, 13.01.1958, *W.J. Eyerdam 10152* (NY); LR606972, LT159692; LR606769; LT159756; LR606477. ***Rhizocephalus orientalis*** Boiss. (1): Turkmenistan, Geok-Tepinskiy District, Central Kopet-Dag, 03.06.1952, *V.V. Nikitin* (LE); LR606974; LR606770; LR606594; LR606478; (2): Turkmenistan, Geok-Tepinskiy District, Central Kopet-Dag, 04.06.1952, *V.V. Nikitin & A.A. Mescheryakov* (LE); LR606975; LR606771; LR606595; LR606479. ***Rostraria cristata*** (L.) Tzvelev: Cultivated in BG Halle, Germany, from seed obtained from BG Dijon, France (no. 2001-1130), 19.08.2002, *M. Röser 11081* (HAL); LR606976, AM234670; LR606772; LT159757; LR606480. ***Sclerochloa dura*** (L.) P.Beauv. (1): Hungary, Veszprém, between Balatonakali and Balatonudvari, 25.05.1991, *M. Röser 7527* (HAL); LR606977, AM234587; LR606773; FM179433; LR606481; (2): Germany, Thuringia, Kyffhäuser, Gorsleben, 31.05.2016, *M. Röser 11255 & N. Tkach* (HAL); –; LR655822; LR655821; –. ***S. festucacea*** (Willd.) Link (1): Russia, Irkutsk Oblast, Kasachinskoye, 27.08.1982, *A. Kiseleva & T. Takmanova 403* (NS/NSK); LR606978, AM234600; –; LR606596; –; (2): Germany, Potsdam, 03.08.2016, *M. Röser 11281 & N. Tkach* (HAL); –; LR606774; –; LR606482. ***Secale sylvestre*** Host: Hungary, Bács-Kiskun, Bugac Puszta, 26.05.1999, *M. Röser 10954* (HAL); LR606979, AM234581, LN554452; LR606775; FM179434; LR606483. ***Sesleria argentea*** (Savi) Savi: Cultivated in BG Halle, Germany, from seed obtained Museum national d'histoire naturelle, Paris, France (no. 2008-44), no voucher; LR606980; LR606776; –; LR606484. ***S. caerulea*** (L.) Ard.: Germany, Thuringia, Harz Mts., 15.05.2016, *M. Röser 11239 & N. Tkach* (HAL); –; LR606777; LR606597; –. ***S. insularis*** Sommier: Italy, Sardinia, Nuoro Province, Golfo di Orosei, Mt. Tuttavista, 10.05.1993, *M. Röser 10166* (HAL); LR606981, AM234591; LR606778; FM179435; LR606485. ***S. varia*** (Jacq.) Wettst.: Austria, Tyrol, Grossglockner Mountain, Edelweissspitze, 05.09.2017, *M. Röser 11321 & N. Tkach* (HAL); –; LR606779; LR606598; LR606486. ***Sesleriella sphaerocephala*** (Ard.) Deyl (1): Slovenia, Gorenjska, Julian Alps, summit of Mt. Lanževica, s.d., *B. Frajman S024* (IB 12825); LR606983, LN554453; LR606781; LR606600; LR606488; (2): Austria, Carinthia, Karavankes, 16.06.1991, *M. Röser 7867* (HAL); LR606982, AM234590; LR606780; LR606599; LR606487. ***Sibirotrisetum sibiricum*** (Rupr.) Barberá (1): China, Qinghai, surroundings of Menyang, 29.07.2004, *I. Hensen* (HAL); –; LR606782; LT159800; –; (2): Russia, Lake Baikal, Olchon Island; cultivated in BG Halle, Germany, from seed, 25.07.2006, *H. Heklau* (HAL); LR606984, LT159706; LR606783; –; LR606489. ***Simplicia buchananii*** (Zotov) Zotov: New Zealand, Nelson Land District, 13.03.1984, *A.P. Druce* (CHR 394262); LR606985; LR606784; HE802177; LR606490. ***Sphenopholis intermedia*** (Rydb.) Rydb. (1): Canada, Little Manitou Lake, 20.08.1992, *Hudson 5083* (CAN565509); LR606986, HG797460; –; HG797530; –; (2): U.S.A., Illinois; cultivated in BG Halle, Germany, from seed obtained from Kew's Millennium Seed Bank, UK (no. 307008), 07.11.2005, *s.coll.* (HAL); –; LR606785; –; LR606491. ***S. obtusata*** (Michx.) Scribn.: U.S.A., Kansas; cultivated in BG Halle, Germany, from seed obtained from Kew's Millennium Seed Bank, UK (no. 408330); 08.06.2007, *J. Hansen* (HAL); LR606987, HG797462, LN554455; LR606786; HG797532; LR606492. ***Sphenopus divaricatus*** (Gouan) Rchb.: Spain, Aragon, Province Huesca, 11.05.1980, *G. Montserrat 38080* (RO); LR606988, HE646589; LR606787; HE646613; LR606493. ***Torreyochloa pauciflora*** (J.Presl) Church: U.S.A., Alaska, Haines, Chilkoot Lake Road, 17.08.2000, *R.J. Soreng 6327* (US Catalog No.: 3679690, Barcode: 01259790), LR606989; LR606788; LR606601; LR606494. ***Tricholemma jahandiezii*** (Litard. ex Jahandiez & Maire) Röser: Morocco, Moyen Atlas, 02.07.2002, *M. Röser 10297/1B* (HAL); LR606990, AM234556, HG797464; LR606789; FM179407, FM956101; LR606495. ***Trisetaria panicea*** (Lam.) Paunero: Portugal, Province Beira Alta, Serra da Estrela, Rio Zêzere-Tale, 12.07.1992, *M. Röser 9473* (HAL); LR606991, HG797465; LR606790; HG797534; LR606496. ***Trisetopsis aspera*** (Hook.f.) Röser & A.Wölk: Sri Lanka (Ceylon), Horton Plains, Badulla District, Province Uva, 27.01.1970, *D. Clayton 5505* (CANB); LR606992; LR606791; LR606602; LR606497. ***T. elongata*** (Hochst. ex A.Rich.) Röser & A.Wölk: Uganda, Mount Elgon, 23.02.2004, *K. Wesche* (HAL); LR606993, HG797469; LR606792; HG797566; LR606498. ***T. imberbis*** (Nees) Röser, A.Wölk & Veldkamp: South Africa, Western Cape, Betty's Bay, corner Kreupel hout street and Lipkin road, 25.10.2010, *A.C. Mudau & L. Smook 452* (PRE); LR606994, HG797483; LR606793; HG797631; LR606499. ***T. longa*** (Stapf) Röser & A.Wölk: South Africa, Western Cape, Table Mountain National Park, Jonkersdam, 23.10.2010, *A.C. Mudau & L. Smook 450* (PRE); LR606995, HG797475; LR606794; HG797597; LR606500. ***T. turgidula*** (Stapf) Röser & A.Wölk: Lesotho, Ligholong, Mine, 02.01.1900, *T. Edwards 7141* (NU4-2005/15), –; –; –; LR606501. ***T. virescens*** (Nees ex Steud.) Röser & A.Wölk: Pakistan, Hazara, Himalaya foothills, Indus Kohistan, 28.08.1995, *B. Dickoré 12063* (MSB); –; LR606795; LT159791; LR606502. ***×Trisetopsotrichon altius*** (Hitchc.) Röser & A.Wölk: China, Sechuan, Nereku River, 26.07.1885, *G.N. Potanin* (LE); LR606996; LR606796; LT159792; LR606503. ***Trisetum flavescens*** (L.) P.Beauv.: Germany, Baden-Württemberg, near Tübingen, 26.06.1984, *M. Röser 1871* (HAL); LR606999; LR606799; LR606604; LR606506. ***Tzveleviochloa parviflora*** (Hook.f.) Röser & A.Wölk: Bhutan, Thimphu, 18.07.2000, *G. Miehe & S. Miehe 00-223-32* (MR); LR607001, LT159708; LR606801; LT159802; LR606508. ***T. potaninii*** (Tzvelev) Röser & A.Wölk: China, NW Sichuan, Upper Yalong basin, Chola Shan, Dege-Garze, Manigango, 27.09.1994, *G. Miehe, S. Miehe & Wündisch 94-435-9* (MR); LT159709; –; LT159803; –. ***Vahlodea atropurpurea*** (Wahlenb.) Fr. ex Hartm.: Canada, British

Appendix 1. Continued.

Columbia, Haines Hwy., Chilkat Pass, 15.08.2000, *R.J. Soreng 6316* (US); LR607002, AM234549; LR606802; FM179439; LR606509. ***Ventenata blanchei*** Boiss.: Syria, Djebel Ed Drouz, 09.05.1933, *G. Samuelsson* (C); LR607003; –; LR606605; LR606510. ***V. dubia*** (Leers) Coss.: Bulgaria, East Stara Planina Mts., 26.05.1999, *T. Raus, F. Pina Gata 21-1-5* (B 10 0417270); LR607004; LR606803; LR606606; –. ***V. macra*** (Steven ex M.Bieb.) Balansa ex Boiss.: Greece, Peloponnese, Achaia, 10.08.1998, *M. Röser 10688* (HAL); LR607005, AM234555; LR606804; FM179440; LR606511. ***Vulpiella stipoides*** (L.) Maire: Libya, Tripolitania, Jebel Nefoussa Zintan, 30.04.1965, *H. Eckerlein* (HAL0016576); LR607006, HE646591; LR606805; HE646614; LR606512.

Appendix 2. Publicly available DNA sequences from ENA/GenBank used in this study for comparison with our own data during the work process and to complete our datasets.

The taxon name is followed by ENA/GenBank accession numbers for plastid *matK* gene–3′*trnK* exon; plastid *trnL-trnF*; nuclear ribosomal ITS1–5.8S gene–ITS2; nuclear ribosomal ETS. A dash indicates unavailable or unused sequences. Sequences included in the final alignments (suppl. Appendix S1) for the phylogenetic reconstructions presented in the figures of this study are marked by an asterisk (see Material and Methods).

Agrostis alopecuroides Lam.: DQ786937; –; –; –. ***A. avenacea*** J.F.Gmel.: HE574415; –; –; –. ***A. capillaris*** L.: –; –; –; JX438119. ***A. linkii*** Banfi, Galasso & Bartolucci: –; DQ631457; –; –. ***A. scabra*** Willd.: DQ146807*; KX372376; –; –. ***Aira praecox*** L.: EF137480; EF137588; –; –. ***Airopsis tenella*** (Cav.) Coss. & Durieu: KJ529354; DQ631445; –; –. ***Alopecurus aequalis*** Sobol.: KM538789, KM523821; KM524037, EU639572; –; KM523673. ***Ammochloa palaestina*** Boiss.: –; DQ631451; –; –. ***Aniselytron treutleri*** (Kuntze) Soják: KM523839; EU792441; EU792373*; GQ324239*, GQ324240. ***Anthoxanthum arcticum*** Veldkamp: –; KC698978*; –; –. ***A. australe*** (Schrad.) Veldkamp: –; DQ631447; –; –. ***A. monticola*** (Bigelow) Veldkamp: –; DQ353953; –; GQ324241. ***A. nitens*** (Weber) Y.Schouten & Veldkamp: EF137503; –; –; KC898002. ***A. odoratum*** L.: DQ786884, EF137484; KC897747; –; –. ***A. redolens*** (Vahl) P.Royen: –; KC897757; –; KC898003. ***A. repens*** (Host) Veldkamp: –; KC698990; –; –. ***Antinoria agrostidea*** (DC.) Parl.: KJ529360; –; DQ539562; –. ***Apera interrupta*** (L.) P.Beauv.: EF137485*, KM523842; EU792439*; EU792364*; GQ324242*. ***Arctagrostis latifolia*** (R.Br.) Griseb.: DQ786885, KM523924, KM523844; DQ353969; –; GQ324243, GQ324244, GQ324245. ***Arctohyalopoa lanatiflora*** (Roshev.) Röser & Tkach: –; –; FJ178781; –. ***Arctopoa eminens*** (J.Presl) Prob.: KM523848; DQ353977; –; GQ324247, GQ324248, GQ324249. ***A. subfastigiata*** (Trin.) Prob.: KM523849*; EU792449*; EU792372*; GQ324250*. ***A. tibetica*** (Munro ex Stapf) Prob.: KM523850*; EU792444*; GQ324471*; GQ324252*. ***Arrhenatherum elatius*** (L.) P.Beauv. ex J.Presl & C.Presl: EU434292, EF137486, KJ529335; JF904748; –; –. ***Avellinia michelii*** (Savi) Parl.: KJ529340; DQ631465; –; –. ***Avena hispanica*** Ard.: GU367287, GU367288, EU833849; EU833874; –; –. ***A. macrostachya*** Balansa ex Coss. & Durieu: EU833852; EU833877; –; –. ***Avenella flexuosa*** (L.) Drejer: DQ786887; AY237913; –; –. ***Avenula pubescens*** (Huds.) Dumort.: EF137502; DQ631460; –; –. ***Bellardiochloa polychroa*** (Trautv.) Roshev.: –; –; –; GQ324256. ***B. variegata*** (Lam.) Kerguélen: DQ786890, KM523852; –; –; GQ324257. ***Boissiera squarrosa*** (Sol.) Nevski: EF137488; –; –; KJ632438, KP996869, KP996870. ***Brachypodium distachyon*** (L.) P.Beauv.: –; KU163229; AF303399; –. ***Briza media*** L.: –; EU395902*; –; –. ***B. minor*** L.: KJ599228, DQ786892; –; –; KJ599006. ***Bromus erectus*** Huds.: –; JX985261; –; –. ***Calamagrostis arenaria*** (L). Roth subsp. ***arundinacea*** (Husn.) Banfi, Galasso & Bartolucci: KJ529326; DQ631456; –; JX438118. ***C. arundinacea*** (L.) Roth: DQ786895; KX372396; GQ266675; –. ***C. canadensis*** (Michx.) P.Beauv.: –; –; FJ377628*; –. ***C. purpurascens*** R.Br.: –; FJ394570, FJ394568; –; –. ***Castellia tuberculosa*** (Moris) Bor: EF137492*; EF137596*; AF532954*; –. ***Catabrosa aquatica*** (L.) P.Beauv.: DQ786898, KM523853; DQ353958*; –; KM523697, GQ324258. ***C. werdermannii*** (Pilg.) Nicora & Rúgolo: –; EU792431*; EU792333*; GQ324259*. ***Catabrosella variegata*** (Boiss.) Tzvelev: KM523854; –; –; KM523698*. ***Catapodium marinum*** (L.) C.E.Hubb.: KJ529348; –; –; –. ***C. rigidum*** (L.) C.E.Hubb.: EF137491, KJ599274; AF533034; –; –. ***Chascolytrum bulbosum*** (Parodi) Essi, Longhi-Wagner & Souza-Chies: –; EU395894; –; –. ***C. subaristatum*** (Lam.) Desv.: DQ786899, KJ599293; –; –; KJ599067. ***C. uniolae*** (Nees) Essi, Longhi-Wagner & Souza-Chies: –; EU395874; –; –. ***Cinna latifolia*** (Trevir. ex Göpp.) Griseb.: KM523855; GQ324396; –; GQ324261. ***Colpodium versicolor*** (Steven) Schmalh.: KM523856; KM524063*; –; KM523699. ***Corynephorus canescens*** (L.) P.Beauv.: KJ529351; DQ631440; –; –. ***Cutandia maritima*** (L.) Barbey: KJ529370; AF487618; –; –. ***Cynosurus cristatus*** L.: DQ786901, HM453075, KJ599277; KF876179*; –; –. ***Dactylis glomerata*** L.: EF137494, KJ599276; AF533028; –; KJ599050*. ***Deschampsia cespitosa*** (L.) P.Beauv.: KM523858, DQ786903, EF137495; AY237912; –; –. ***D. setacea*** (Huds.) Hack.: –; DQ631479*; DQ539615*; –. ***Desmazeria sicula*** (Jacq.) Dumort.: DQ786904; EF592948; –; –. ***Dichelachne crinita*** (L.f.) Hook.f.: HE574411; –; –; –. ***D. micrantha*** (Cav.) Domin: DQ786906; –; –; –. ***Drymochloa sylvatica*** (Pollich) Holub: HM453070, KJ529372; AF478505; –; –. ***Dryopoa dives*** (F.Muell.) Vickery: KJ599286, KJ599326; KJ599438; –; –. ***Dupontia fisheri*** R.Br. subsp. ***psilosantha*** (Rupr.) Hultén: DQ786908, KM523859, KM523860, KM523925, KM523926; –; –; KM523702, KM523701, GQ324267, GQ324266. ***D. fulva*** (Trin.) Röser & Tkach: KM523845, KM523846, KM523847; KM524058; –; KM523694, KM523695, GQ324246. ***Dupontiopsis hayachinensis*** (Koidz.) Soreng, L.J.Gillespie & Koba: KM523861*; KM524066*; KM523779*; KM523703*. ***Echinaria capitata*** (L.) Desf.: KJ529361; DQ631453; –; –. ***Echinopogon caespitosus*** C.E. Hubb.: DQ786909, HE574414; –; –; –. ***Festuca floribunda*** (Pilg.) P.M.Peterson, Soreng & Romasch.: DQ786907, JF697821; JF904750; –; –. ***F. incurva*** (Gouan) Gutermann: KJ599280; AF478533; –; KJ599053. ***F. lachenalii*** (C.C.Gmel.) Spenn.: KJ529387; AF478534*; –; –. ***F. maritima*** L.: KJ529388; AY118107; –; –. ***F. myuros*** L.: KJ599273, AF164403; AY118103; KJ598937*; KJ599048*. ***F. salzmannii*** (Boiss.) Boiss. ex Coss.: –; AF478535; –; –. ***Gastridium nitens*** (Guss.) Coss. & Durieu: DQ786945, KJ529331; DQ336836; –; –. ***G. ventricosum*** (Gouan) Schinz & Thell.: FN908056, DQ786914; DQ336837; –; HE575740. ***Gaudinia fragilis*** (L.) P.Beauv.: DQ786915, EF137499; DQ631478; –; –. ***Graphephorum canescens*** (Buckley) Röser & Tkach: DQ786946; –; –; –. ***G. cernuum*** (Trin.) Röser & Tkach: DQ786946; –; –; –. ***G. wolfii*** J.M.Coult.: DQ786917; DQ336843; –; –. ***Helictochloa aetolica*** (Rech.f.) Romero Zarco: –; EU792437; –; KM523706. ***H. bromoides*** (Gouan) Romero Zarco subsp. bromoides: KJ529356; DQ631459; –; –. ***H. hookeri*** (Scribn.) Romero Zarco: DQ786888; HM590299; –; –. ***Helictotrichon convolutum*** (C.Presl) Henrard: DQ786919, KM523865; DQ353954; –; KM523707. ***H. sedenense*** (DC.) Holub: –; –; –; KC899016. ***H. sempervirens*** (Vill.) Pilg.: –; DQ353955; –; GQ324269*. ***Hookerochloa eriopoda*** (Vickery) S.W.L.Jacobs: DQ786913, KJ599294, KM523866; GQ324397*; –; GQ324270, GQ324271. ***H. hookeriana*** (F.Muell. ex Hook.f.) E.B.Alexeev: KJ599295, DQ786922, KM523867; EU792435; –; KJ599068, GQ324272, KM523708. ***Hordelymus europaeus*** (L.) O.E.Harz: –; EU119368*; –; –. ***Hordeum marinum*** Huds.: –; AB732935; –; KJ632437*. ***Hyalopoa pontica*** (Balansa) Tzvelev: KM523868*; KM524070*; EU792365, FJ196302, FJ196303; KM523709*. ***Koeleria pyramidata*** (Lam.) P.Beauv.: EF137505; EU119370; –; –. ***K. spicata*** (L.) Barberá, Quintanar, Soreng & P.M.Peterson: –; FJ394585; –; –. ***Lagurus ovatus*** L.: –; DQ631464; –; –. ***Lamarckia aurea*** (L.) Moench: KJ599279; KJ599392; –; KJ599052*. ***Limnas stelleri*** Trin.: –; –; –; KM523710*. ***Littledalea racemosa*** Keng: DQ786924; –; –; –. ***Lolium giganteum*** (L.) Darbysh.: HM453058; AF533043; –; –. ***L. perenne*** L.: DQ786925*; EF378973*; KJ598999*; KJ599109*. ***L. rigidum*** Gaudin: DQ786926*, KJ599336; EF378980*; KJ599000*; KJ599110*. ***Macrobriza maxima*** (L.) Tzvelev: FN908048; EU395901; –; –. ***Mibora minima*** (L.) Desf.: DQ786927, KJ529357; DQ631454; –; –. ***Milium effusum*** L.: KM523869, KM523870; KM524072*; –; KM523711, GQ324273. ***Molineriella laevis*** (Brot.) Rouy: DQ786929; KJ529413; –; –. ***Nephelochloa orientalis*** Boiss.: KM523873; KM524075*; –; KM523714. ***Nicoraepoa andina*** (Trin.) Soreng & L.J.Gillespie: DQ786934*, KM523874; DQ353971*; EU792354*; GQ324275*. ***Oreochloa disticha*** (Wulfen) Link: –; DQ631452*; –; –. ***Paracolpodium altaicum*** (Trin.) Tzvelev: KM523878; KM524076; –; KM523715. ***Parapholis cylindrica*** (Willd.) Röser & Tkach: EF137501, KJ599283, KJ529366; KJ599395; –; KJ599056*. ***P. filiformis*** (Roth) C.E.Hubb.: KJ529365; KJ529415; –; –. ***P. incurva*** (L.) C.E.Hubb.: DQ786931, EF137508, KJ599281; –; –; KJ599054. ***Periballia involucrata*** (Cav.) Janka: KJ529353; DQ631438; –; –. ***Peyritschia pringlei*** (Scribn.) S.D.Koch: –; FJ394581; –; –. ***Phalaris arundinacea*** L.: AF164396; JF951096; –; –. ***P. canariensis*** L.: –; DQ631443; –; –. ***P. coerulescens*** Desf.: KJ529325; JF951116; –; –. ***Phippsia algida*** (Sol.) R.Br.: KM523879, KM523880; KM524078*; –; KM523716, KM523717, GQ283228, GQ283229. ***Phleum alpinum*** L.: KM523881; KM524079; –; KM523718. ***P. phleoides*** (L.) Karsten: KM523884; KM524082; –; KM523718. ***Poa alpina*** L.: DQ786933*, KM523888; DQ353986*; EU792390*; –. ***P. annua*** L.: KJ599339, KJ599340;

Appendix 2. Continued.

EU792452; –; KJ599113, KJ599114. ***P. apiculata*** Refulio: –; EU792469*; EU792428*; KU763389*. ***P. bulbosa*** L.: KJ529342, KJ599341; AH015559; –; KJ599115, GQ324297, GQ324298. ***P. diaphora*** Trin.: –; KJ746808; –; GQ324311*. ***P. fax*** J.H.Willis & Court: KJ599238; EU792460; –; KJ599016, KJ599065, GQ324318. ***P. hitchcockiana*** Soreng & P.M.Peterson: –; –; –; KU763378 *. ***P. labillardierei*** Steud.: DQ786935, KJ599324; AH015564; –; KJ599097, GQ324296. ***P. lepidula*** (Nees & Meyen) Soreng & L.J.Gillespie: –; AH015563*, EU792471; –; GQ324343, GQ324344. ***P. pratensis*** L.: KJ599260, KJ599261; JF904790; –; GQ324369, KJ599036. ***P. serpaiana*** Refulio: –; AH015566; –; GQ324265, KU763451. ***Podagrostis thurberiana*** (Hitchc.) Hultén: DQ786936*; –; –; –. ***Puccinellia arctica*** (Hook.) Fernald & Weath.: –; –; GQ283100 –. ***P. borealis*** Swallen: –; –; GQ283160 –. ***P. ciliata*** Bor: –; –; KJ598984 –. ***P. distans*** (Jacq.) Parl.: –; –; KP711085 –. ***P. fasciculata*** (Torr.) E.P.Bicknell: KJ599321; –; KJ598985; KJ599094. ***P. frigida*** (Phil.) I.M.Johnst.: –; –; JF904809 –. ***P. glaucescens*** (Phil.) Parodi: –; –; EU792338 –. ***P. interior*** T.J.Sørensen ex Hultén: –; –; KM523808 –. ***P. longior*** A.R.Williams: –; –; KJ598961 –. ***P. magellanica*** (Hook.f.) Parodi: –; –; KM523810 –. ***P. parishii*** Hitchc.: –; –; GQ283123 –. ***P. perlaxa*** (N.G.Walsh) N.G.Walsh & A.R.Williams: –; –; KJ598986 –. ***P. phryganodes*** (Trin.) Scribn. & Merr.: –; –; GQ283157 –. ***P. pumila*** (Macoun ex Vasey) Hitchc.: –; –; GQ283158 –. ***P. stricta*** (Hook. f.) C.H.Blom: –; –; EU792339 –. ***P. tenella*** (Lange) Holmb.: –; –; GQ283110 –. ***P. tenuiflora*** (Griseb.) Scribn. & Merr.: –; –; KP711084 –. ***P. vahliana*** (Liebm.) Scribn. & Merr.: KM523915; –; –; GQ283185, GQ283186, GQ283187, GQ283188, GQ324285. ***P. vassica*** A.R.Williams: –; –; KJ598963 –. ***P. walkeri*** (Kirk) Allan subsp. ***chathamica*** (Cheeseman) Edgar: –; –; EU331103 –. ***Relchela panicoides*** Steud.: –; JF904801; –; –. ***Rostraria cristata*** (L.) Tzvelev: –; DQ336853, GQ324465; –; –. ***Saxipoa saxicola*** (R.Br.) Soreng, L.J.Gillespie & S.W.L.Jacobs: KJ599265, KM523917*; GQ324465*; GQ324558*; GQ324392*. ***Sclerochloa dura*** (L.) P.Beauv.: DQ786941, KJ599275, KM523918; KM524102; –; KM523745, KJ599049, KJ632435. ***Scolochloa festucacea*** (Willd.) Link: KM523919; KM524103; –; KM523746*. ***Sesleria argentea*** (Savi) Savi: –; AF533030; –; –. ***S. insularis*** Sommier: KM523920; DQ353957; –; KM523747. ***Sibirotrisetum sibiricum*** (Rupr.) Barberá: –; KX372500; –; –. ***Simplicia buchananii*** (Zotov) Zotov: –; HM191465; –; HM191451, HM191452, HM191453. ***Sphenopholis intermedia*** (Rydb.) Rydb.: –; DQ631466; –; –. ***S. obtusata*** (Michx.) Scribn.: –; EU119377; –; –. ***Sphenopus divaricatus*** (Gouan) Rchb.: DQ786943; AF533033; –; –. ***Sylvipoa queenslandica*** (C.E.Hubb.) Soreng, L.J.Gillespie & S.W.L.Jacobs: KJ599262*, KM523921; GQ324466*; GQ324559*; GQ324393*. ***Torreyochloa pauciflora*** (J.Presl) Church: DQ786944; –; –; –. ***Trisetaria panicea*** (Lam.) Paunero: –; DQ631474; –; –. ***Trisetum flavescens*** (L.) P.Beauv.: –; JQ041860; –; –. ***Vahlodea atropurpurea*** (Wahlenb.) Fr. ex Hartm.: DQ786947; AM041251; –; –. ***Ventenata dubia*** (Leers) Coss.: KM523922; KM524104; –; KM523748*. ***V. macra*** (Steven ex M.Bieb.) Balansa ex Boiss.: KM523863; KM524068; –; KM523705.

Appendix 3. Questionable or wrong DNA sequences in ENA/GenBank.

A. In the course of this study we came across some errors that we made in previous publications of our lab. The errata et corrigenda are as follows:

Dryopoa dives (F.Muell.) Vickery. – Our ITS sequence HE802192 submitted as *Poa dives* F.Muell. (Hoffmann & al., 2013) belongs to a species of *Poa* and not to *Dryopoa*.

Hierochloe occidentale Buckley. – The earlier published *matK* sequence (AM234562; Döring & al., 2007; Döring, 2009; Schneider & al., 2009) does not belong to *Hierochloe* or *Anthoxanthum* as evident from comparison with the DNA sequences of other species. A sample switching error in our lab or in the field seems likely.

Hyalopoa* (*Arctohyalopoa*) *lanatiflora (Roshev.) Tzvelev. – Our *matK* gene sequence AM234604 (Döring & al., 2007; Döring, 2009) obtained from leaves taken from the herbarium specimen "Russia, Yakutskaya SSSR, Ordzhonikidzevskiy rayon, surroundings of the village Kytyl-Dyura, 22.07.1988, *Zuev & Agaltsev 434*, det. O. Nikiforova" (NSK) belongs to a species of *Poa* and not to *Hyalopoa* (*Arctohyalopoa*). Although we do not have the voucher specimen at hand to verify the identification, a re-examination of a photograph taken clearly corroborates that the inflorescences belong to this taxon, but it cannot be ruled out that the very dense tufts of leaves, from which the sample for DNA study was gathered, is a mixture of different grasses. In this study, two other DNA extractions from herbarium specimens unambiguously representing *Arctohyalopoa lanatiflora* were used. They yielded ITS/ETS and chloroplast DNA sequences that were identical, respectively (see Appendix 1).

Leptophyllochloa micrathera (Hook.) Munro. – Sequences LT159689 and LT159754, published by Wölk & Röser (2017), were from wrongly identified specimens and belong to *Deschampsia elongata* (Hook.) Munro.

Littledalea tibetica Hemsl. – Sequences AM234572 and FM179416 (Döring & al., 2007; Schneider & al., 2009) actually belong to *L. racemosa* Keng (R.J. Soreng, pers. comm.).

B. DNA sequences taken from ENA/GenBank that turned out to be questionable or wrong according to the results of this study are as follows:

Ammochloa palaestina Boiss. – The ITS sequence DQ539587 (Quintanar & al., 2007: fig. 2) belongs to a species of the genus *Helictochloa* and not to *Ammochloa*.

Hyalopoa* (*Arctohyalopoa*) *lanatiflora. – The ITS sequence FJ178781 (Rodionov & al., 2008) clusters with the sequences of *Catabrosa aquatica*, *C. werdermannii* (EU792333) and further ENA/GenBank entries for *Catabrosa* (not shown) and disagrees with our sequences for true *H.* (*Arctohyalopoa*) *lanatiflora*.

Hyalopoa pontica (Bal.) Tzvelev. – Our ITS sequence of *H. pontica* generated in this study (LR606575) corresponds to sequences FJ196303 (Rodionov & al., 2008) and EU792365 (Gillespie & al., 2008), all of which are nested within Coleanthinae. A deviant ITS sequence reported for *H. pontica* (FJ196302; see Rodionov & al., 2008, Nosov & al., 2015, 2019) clusters among the sequences of *Poa*. The presumed occurrence of different ITS copies in *H. pontica* was discussed to rest on genetic introgression of *Poa* into *Hyalopoa* or allopolyploidy with subsequent loss of one of the parental *Hyalopoa* nrDNAs (Nosov & al., 2015; Rodionov & al., 2017). The issue warrants further investigation.

Macrobriza maxima (L.) Tzvelev. – The ETS sequence KJ599007 submitted as *Briza maxima* L. (Birch & al., 2014) belongs to a species of *Agrostis*.