

Open access • Posted Content • DOI:10.1101/707588

Phylogeny, morphology and the role of hybridization as driving force of evolution in grass tribes Aveneae and Poeae (Poaceae) — Source link []

Natalia Tkach, Julia Schneider, Elke Döring, Alexandra Wölk ...+7 more authors Institutions: Martin Luther University of Halle-Wittenberg Published on: 18 Jul 2019 - bioRxiv (Cold Spring Harbor Laboratory) Topics: Pooideae, Poeae, Maximum parsimony, Phylogenetic tree and Phylogenetics

Related papers:

- Phylogeny and evolution of grammitid ferns (Grammitidaceae): a case of rampant morphological homoplasy
- Phylogeny of Spiraea (Rosaceae) based on plastid and nuclear molecular data: Implications for morphological character evolution and systematics
- A molecular phylogeny, morphology and classification of genera of Ranunculeae (Ranunculaceae)
- Phylogeny of Helieae (Gentianaceae): Resolving taxonomic chaos in a Neotropical clade.
- Grass Phylogeny and Classification: Conflict of Morphology and Molecules



bioRxiv preprint doi: https://doi.org/10.1101/707588; this version posted July 18, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Phylogeny, morphology and the role of hybridization as driving force of evolution in grass tribes Aveneae and Poeae (Poaceae)

- 3
- 4 Natalia Tkach,¹ Julia Schneider,¹ Elke Döring,¹ Alexandra Wölk,¹ Anne Hochbach,¹ Jana
- 5 Nissen,¹ Grit Winterfeld,¹ Solveig Meyer,¹ Jennifer Gabriel,^{1,2} Matthias H. Hoffmann³ &
- 6 Martin Röser¹
- 7
- 8 ¹ Martin Luther University Halle-Wittenberg, Institute of Biology, Geobotany and Botanical
- 9 Garden, Dept. of Systematic Botany, Neuwerk 21, 06108 Halle, Germany
- ¹⁰ ² Present address: German Centre for Integrative Biodiversity Research (iDiv), Deutscher
- 11 Platz 5e, 04103 Leipzig, Germany
- ³ Martin Luther University Halle-Wittenberg, Institute of Biology, Geobotany and Botanical
- 13 Garden, Am Kirchtor 3, 06108 Halle, Germany
- 14

Addresses for correspondence: Martin Röser, martin.roeser@botanik.uni-halle.de; Natalia
Tkach, natalia.tkach@botanik.uni-halle.de

17

18 ABSTRACT

19 To investigate the evolutionary diversification and morphological evolution of grass 20 supertribe Poodae (subfam. Pooideae, Poaceae) we conducted a comprehensive molecular 21 phylogenetic analysis including representatives from most of their accepted genera. We 22 focused on generating a DNA sequence dataset of plastid matK gene-3'trnK exon and trnL-23 trnF regions and nuclear ribosomal ITS1–5.8S gene–ITS2 and ETS that was taxonomically 24 overlapping as completely as possible (altogether 257 species). The idea was to infer whether 25 phylogenetic trees or certain clades based on plastid and nuclear DNA data correspond with 26 each other or discord, revealing signatures of past hybridization. The datasets were analysed 27 using maximum parsimony, maximum likelihood and Bayesian approaches. Instances of 28 severe conflicts between the phylogenetic trees derived from both datasets, some of which 29 have been noted earlier, unambiguously point to hybrid origin of several lineages (subtribes, 30 groups of genera, sometimes genera) such as Phalaridinae, Scolochloinae, Sesleriinae, 31 Torreyochloinae; Arctopoa, Castellia, Graphephorum, Hyalopodium, Lagurus, Macrobriza, 32 Puccinellia plus Sclerochloa, Sesleria, Tricholemma, American Trisetum, etc. and 33 presumably Airinae, Holcinae and Phleinae. 'Calamagrostis' flavens appears to be an 34 intergeneric hybrid between Agrostis and Calamagrostis. Most frequently there is good

35 agreement of other regions of the trees, apart from intrinsic different phylogenetic resolution 36 of the respective DNA markers. To explore the to date rather unclear morphological evolution 37 of our study group a data matrix encompassing finally 188 characters was analysed for 38 ancestral state reconstructions (ASR) using the tree from the combined molecular dataset as 39 presumably best approximation to the species phylogeny. For 74 characters ASRs were 40 feasible and yielded partly surprising results for the study group as a whole but also for some 41 of their subdivisions. Considering taxonomy and classification it became evident, that many 42 morphological characters show a very high degree of homoplasy and are seemingly able to 43 change within comparatively short timespans in the evolution of our grasses. Most of the 44 taxonomic units distinguished within our study group, e.g. as subtribes, are defined less by 45 consistent morphological characters or character combinations and should be rather 46 understood as clades revealed by molecular phylogenetic analysis. One reason for this 47 extreme homoplasy concerning traditionally highly rated characters of inflorescences or spikelets and their components might be that they have little to do with pollination (always 48 49 wind) or adaptation to pollinators as in other angiosperms but rather with dispersal and 50 diaspores. Easily changing structure of spikelet disarticulation, of glume, lemma or awn 51 characters might be advantageous in the rapid adaptation to different habitats and micro-52 habitats, which was evidently most successfully accomplished by these grasses. A partly 53 revised classification of Poodae is presented, including a re-instatement of tribes Aveneae and 54 Poeae s.str. Following a comparatively narrow delineation of preferably monophyletic 55 subtribes, Antinoriinae, Avenulinae, Brizochloinae, Helictochloinae, Hypseochloinae are 56 described as new. New genera are Arctohyalopoa and Hyalopodium. New combinations are 57 Arctohyalopoa lanatiflora, A. lanatiflora subsp. ivanoviae, A. lanatiflora subsp. momica, 58 Colpodium biebersteinianum, C. kochii, C. trichopodum, C. verticillatum, Deschampsia 59 micrathera, Dupontia fulva, Festuca masafuerana, Hyalopodium araraticum, Paracolpodium 60 baltistanicum, Parapholis cylindrica, P. ×pauneroi. Festuca masatierrae is a new name. 61 **Keywords** ancestral state reconstruction; ASR; *Arctohyalopoa*; Aveneae; classification; 62 63 *Hyalopodium*; phylogenetic character mapping; phylogeny; Poeae; taxonomy 64 Supporting Information may be found online in the Supporting Information section at the 65 66 end of the article.

- 67
- 68 INTRODUCTION

69 The grass supertribe Poodae with Poeae sensu lato (s.l.) as sole tribe (i.e., including 70 Aveneae) encompasses 106–121 genera, depending on the respective width of their 71 delineation, and 2562–2578 species (Kellogg, 2015; Soreng & al., 2017). It is a characteristic 72 group of C_3 grasses proliferating in the northern temperate and boreal regions and represented 73 by many annuals especially in the Mediterranean/Near East, a region that was also the cradle 74 of Avena with cultivated oat(s). Economically enormously significant are also the pasture and 75 forage grasses. Poodae are scarce in the subtropics and tropics but bridge them on the top of 76 high mountains and have a second centre of diversity in the temperate and cool zones of the 77 southern hemisphere. Concepts of relationship in this group of grasses based on 78 morphological characters were summarized by Genera graminum (Clayton & Renvoize, 79 1986) that served as an important basis for later molecular phylogenetic studies. Due to the 80 sheer size of the group, usually representative genera were selected since then for comparative 81 studies to gain an overview on the whole Poodae and their major groupings using traditional 82 Sanger and, more recently, plastid genome sequencing (Soreng & Davis, 2000; Davis & 83 Soreng, 2007; Döring & al., 2007; Ouintanar & al., 2007; Soreng & al., 2007; Schneider & 84 al., 2009; Saarela, & al., 2015, 2018; Pimentel & al., 2017; Orton & al., 2019). Other studies 85 focused on special groups using an in-depth sampling of taxa, for example, within Aveneae 86 (Grebenstein & al., 1998; Döring, 2009; Saarela & al., 2010, 2017; Wölk & Röser, 2014, 87 2017; Barberá & al., 2019) and Poeae sensu stricto (s.str.; Schneider & al., 2012; Birch & al., 88 2014, 2017), in which especially the subtribes Poinae (Hunter & al., 2004; Gillespie & 89 Soreng, 2005; Gillespie & al., 2007, 2008, 2009, 2010, 2018; Refulio-Rodríguez & al., 2012; 90 Hoffmann & al., 2013; Soreng & al., 2010, 2015a; Nosov & al., 2015, 2019), Loliinae (Torrecilla & Catalán, 2002, Catalán & al., 2004; Torrecilla & al., 2004; Catalán & al., 2007; 91 92 Inda & al., 2008; Cheng & al., 2016; Minaya & al., 2017), Brizinae and Calothecinae (Essi & 93 al., 2008; Persson & Rydin, 2016) or Sesleriinae (Kuzmanović & al., 2017) were studied. 94 Recent classifications of Poodae took up the progress made by molecular phylogenetic 95 studies and numerous changes in classification proposed relative to Genera graminum, which 96 was superseded by the comprehensive Poaceae treatment for *The families and genera of* 97 vascular plants (Kellogg, 2015). The recent taxonomic accounts on grasses of Soreng & al. 98 (2015, 2017) and Kellogg (2015) abandoned the traditional distinction of tribes Aveneae and Poeae s.str. since molecular phylogenetic data did not corroborate their separation according 99 100 to their previous circumscription based on morphology. Nevertheless, the occurrence of two 101 different plastid DNA sequences ("Aveneae type" and "Poeae type") led to the 102 nomenclaturally informal recognition of two lineages (Soreng & Davis, 2000), each of which

103 was divided in a number of subtribes (Soreng & al., 2007, 2017; Kellogg, 2015) as followed
104 also in the molecular phylogenetic account on the Aveneae type lineage of Saarela & al.
105 (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 may 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 classification
for Poodae (Soreng & Davis, 2000).

113 To address the role of hybridization as suspected factor in the evolution of several of 114 its lineages (Soreng & Davis, 2000; Quintanar & al., 2007; Soreng & al., 2007) and to 115 contribute to an improved classification we aimed at a comparative sequencing study of 116 representatives of most genera of Poodae, except for some lineages that were already shown 117 to be clearly monophyletic (e.g., Calothecinae, Loliinae, Poinae), in which we sampled only a 118 small selection of taxa. Due to the different inheritance of the plastid and the nuclear genome 119 we tried to generate a taxonomically overlapping dataset for both genomes, since incongruent 120 placement of taxa in phylogenetic trees derived from both individual datasets is a reliable 121 indicator of past hybridization events.

Secondly, 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 problem cases we have created ourselves
in previous publications from our lab.

Finally, we wanted to compare the molecular phylogenetic information with a morphological matrix for the molecularly studied taxa and performed an extensive analysis of available and newly collected morphological data. For characters sufficiently densely scored for our taxa in question we conducted an ancestral state reconstruction using the molecular phylogenetic information.

131

132 MATERIAL AND METHODS

Classification employed. — We follow in this study, as far as possible, the
 classification of 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

137 with the classification used by Kellogg (2015) for her account on Poaceae in *The families and*

- 138 *genera of vascular plants.* We also follow the treatment of genera and synonyms presented by
- 139 Soreng & al. (2017) unless otherwise stated. Genus names occasionally misapplied in the

140 literature are enclosed in the following by single quotation marks.

141

142 Plant material and choice of study taxa. — For the molecular phylogenetic study we 143 tried to sample as complete as possible all currently acknowledged genera and important 144 segregate genera of Poodae except for subtribes Calothecinae, Loliinae and Poinae (see 145 Introduction). The types of the genera were preferably included. For information retrieval on 146 nomenclatural types we consulted the *Index nominum genericorum* (ING; botany.si.edu/ing/), 147 Tropicos (tropicos.org), Clayton & Renvoize (1986), Clayton & al. (2002 onwards), 148 Catalogue of New World grasses (Soreng & al., 2000 onwards) and other taxonomic sources 149 (see References). In non-monospecific genera we tried to investigate two or more species. 150 Sometimes, we used more than one accession for the same taxon. In total, 117 accepted 151 genera and 257species were treated in this study. No plant material has been obtained in the 152 genera Agropyropsis A.Camus, Agrostopoa Davidse, Soreng & P.M.Peterson, and 153 Pseudophleum Doğan. Taxa selected from the lineages next to Poodae, namely Hordelymus 154 europaeus (L.) O.E.Harz, Hordeum marinum Huds. subsp. gussoneanum (Parl.) Thell. and 155 Secale sylvestre Host from Triticeae subtribe Hordeinae in the sense of Schneider & al. 156 (2009), Boissiera squarrosa (Sol.) Nevski and Bromus erectus Huds. from Triticeae subtribe 157 Brominae, Littledalea tibetica Hemsl. from Triticeae subtribe Littledaleinae as well as 158 Brachypodium distachyon (L.) P.Beauv. from Brachypodieae were selected as suitable 159 outgroup taxa based on previous studies (Davis & Soreng, 1993; Catalán & al., 1997; Hilu & 160 al., 1999; Schneider & al., 2009, 2011; GPWG, 2012; Blaner & al., 2014; Hochbach & al., 161 2015). The molecular phylogenetic studies were conducted using silica gel-dried leaf material 162 collected in the field from living plants or leaves from specimens of the following herbaria: 163 AD, ALTB, B, BBG, C, CAN, CHR, COL, FI, HAL, HO, ICN, JACA, K, LE, LISU, MEXU, 164 MO, NS, NSK, NSW, NU, NY, PRE, RO, RSA, SGO, TROM, UPS, US (abbreviations 165 according to Index herbariorum; http://sweetgum.nybg.org/science/ih/). Information on 166 origin, collectors, collection details and ENA/GenBank sequence accession numbers of the 167 analysed taxa is given in Appendices 1, 2.

168

Molecular methods and sequence alignment. — FastPrep FP120 cell disrupter
 (Qbiogene, Heidelberg, Germany) was used to homogenize 20–45 mg leaf tissue per sample.

171 Extraction of total genomic DNA was conducted with the NucleoSpin Plant Kit in accordance 172 to the manufacturer's protocol (Macherey-Nagel, Düren, Germany). The concentration of the 173 DNA samples was checked with a NanoDrop spectrophotometer (Thermo Fisher Scientific, 174 Waltham, USA). The entire internal transcribed spacer region (ITS) of the nuclear ribosomal 175 (nr) DNA (ITS1–5.8S rRNA gene–ITS2) and the matK gene–3'trnK exon of the plastid DNA 176 were PCR-amplified following the protocols described by Schneider & al. (2009) and Wölk & 177 Röser (2014). The 3' end of the external transcribed spacer region (ETS) of the nrDNA was 178 amplified with primers 18S-Rcyper (Starr & al., 2003), RETS4-F (Gillespie & al., 2010) and 179 RETS-B4F (Alonso & al., 2014) under conditions following Tkach & al. (2008). For 180 amplification of the plastid non-coding region of the *trnL–trnF*, including *trnL*(UAA) intron 181 and adjacent intergenic spacer between the trnL(UAA) 3'exon and trnF(GAA) gene, were 182 used primers c, d, e and f and the PCR protocol of Taberlet & al. (1991). Additional new 183 primers created for this region (cps ACGGACTTGATTGTATTGAGCC; dps 184 CTCTCTCTTTGTCCTCGTCCG; eps CGGACGAGGACAAAGAGAGAG; fps AACTGAGCATCCTGACCTTTTCTTG) were used in combination with the primers cited. 185 186 PCR was carried out on a thermocycler manufactured by Eppendorf (Hamburg, Germany). 187 Purification and sequencing of all PCR products were performed in our lab or by StarSEQ 188 (Mainz, Germany), Eurofins MWG Operon (Ebersberg, Germany) and LGC Genomics 189 (Berlin, Germany) with the same primers as used for amplifications. PCR products of the ITS 190 region with ambiguous sequence peaks were cloned. Cloning was performed using the 191 pGEM-T Easy Vector System (Promega Mannheim, Germany). Ligation and transformation 192 of the relevant purified amplicons were carried out according to the technical manual. The 193 plasmid DNA was isolated using the GeneJET Plasmid Miniprep Kit (Fermentas, St. Leon-194 Rot, Germany) according to the manufacturer's protocol. The PCR products were quantified 195 spectrophotometrically. Highly similar ITS clone sequences were combined to one consensus 196 sequences to reduce the number of singletons in the alignment. All sequences were edited by 197 eye in Sequencher 5.0 (Gene Codes Corporation, Ann Arbor, USA). The automatically 198 performed alignments by using ClustalW2 (Larkin & al., 2007) were manually adjusted in 199 Geneious 9.1.6 (https://www.geneious.com; Kearse & al., 2012). 200

201 Phylogenetic analysis. — Sequences generated in this or previous studies of our lab 202 could be used in many taxa (Appendix 1). For comparison with our own data and to complete 203 our datasets we included publicly available sequences for the taxa and sequence regions in 204 question in the alignments (Appendix 2). The nuclear (including ITS and ETS sequences) and plastid (including *matK* gene–3'*trnK* exon and *trnL–trnF*) DNA sequence datasets were first
analysed separately using the phylogenetic approaches of Maximum Likelihood (ML),
Maximum Parsimony (MP) and Bayesian Inference (BI) following Tkach & al. (2019). All
trees were visualized with FigTree 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).

211 To avoid redundancy and to improve the clarity of the phylogenetic trees we finally 212 omitted unnecessary duplicate sequences for the same taxon from the alignments. The final 213 DNA sequence matrices for Poodae and outgroups are provided as fasta files in the supporting 214 information (suppl. Appendix S1). The tree topologies obtained from the individual nuclear 215 and plastid DNA sequence alignments were examined visually for incongruity. The node 216 bootstrap support of \geq 70 in ML analysis was chosen as value for supported incongruence 217 (Wiens, 1998; Schneider & al., 2009; Baker & al., 2011; Pirie, 2015; Tkach & al., 2015, 218 2019). Since significantly conflicting relationships occurred as localized incongruences 219 caused by specific taxa or clades in the individual phylogenetic trees, we combined the 220 sequences of the nuclear and plastid markers in a second round of analyses to a concatenated 221 dataset. It was analysed as described above to obtain a molecular total evidence tree that 222 served as guideline for taxonomic classification.

223

224 Morphological analysis and character mapping. — For morphological analysis we 225 compiled for our study group a data matrix of 188 characters in total. Supplementary 226 Appendix S2 is the character list with coding of character states used to assess character 227 evolution. Supplementary Fig. S2 graphically displays the characters states for the taxa 228 studied. Morphological characteristics were gathered from various published resources, 229 especially the genus and species data of GrassBase (Clayton & al., 2006 onwards), data from 230 Grass genera of the world (Watson & al., 1992 onwards; Watson & Dallwitz, 1994) and from 231 own observations using an incident light microscope Stemi 508doc equipped with a digital 232 camera AxioCam ERc (Zeiss, Oberkochen, Germany).

We commonly used the genus data in the morphological character matrix. Exceptions were made when genus boundaries did not match our genus circumscriptions or when no data were available for a genus. Then we used species data and checked them for their applicability for the whole genus and eventually modified them accordingly. Character mapping on the molecular phylogenetic tree derived from the concatenated plastid and nuclear DNA sequence dataset was conducted in R version 3.5.0 with the package Phytools(Revell, 2012, 2013).

240

241 **Ancestral state reconstruction.** — For ancestral state reconstruction (ASR; suppl. 242 Appendix S3) we selected 74 sufficiently variable of the 188 morphological characters 243 studied. To avoid exceedingly large uncertainties, we considered for ASR only characters that 244 were known in more than 145 (67%) of the 218 taxa scored for morphological data. ASR was 245 also conducted in R version 3.5.0 using package phytools (Revell, 2012) by stochastic 246 character mapping (Huelsenbeck & al., 2003). Therefore, we generated 1.000 stochastic 247 character maps from the dataset using the ER (equal rate) model and obtained posterior 248 probabilities for the nodes by averaging the state frequencies across all maps. In the case of 249 unknown states, we used a prior probability distribution on the tips that is flat across all 250 possible states. According to Revell (see http://blog.phytools.org/2016/10/stochastic-251 mapping-discrete-character.html) this leaves the posterior probabilities at internal nodes 252 largely unaffected compared to just dropping tips with unknown states from the tree.

253

254 Scanning electron microscopes (SEM) observation. — Lemmas and awns of 255 selected representatives of major lineages were investigated using scanning electron 256 microscopy. The lemmas of the samples (legends to Figs. 9–11) were mounted under an 257 incident light microscope on aluminium stubs covered by double stick carbon conductive tabs 258 (Plano, Wetzlar, Germany). Samples were gold-coated using sputter coater MED010 (Balzers 259 Union, Balzers, Liechtenstein). Images were taken on the tabletop scanning electron 260 microscope TM-3030Plus (Hitachi Europe, Maidenhead, UK) with 5 kV acceleration voltage 261 and the secondary electron detector.

262

263 **RESULTS**

Plastid DNA analysis. — The plastid *matK* gene–3'*trnK* exon DNA sequence dataset
for 208 taxa included 2,530, the *trnL–trnF* DNA dataset for 199 taxa included 1,414 aligned
positions, respectively. The combined data matrix of the two plastid DNA markers for 214
taxa included a total of 3,927 aligned positions, of which 1,470 were variable (*matK* gene–
3'*trnK* exon: 984, *trnL–trnF*: 488) and 907 parsimony-informative (*matK* gene–3'*trnK* exon:
622, *trnL–trnF*: 286).

Poodae were corroborated a monophyletic lineage (100/100/1.00), using our extended
set of outgroup taxa. It split in two main clades, which were supported by 100/98/1.00 and

100/99/1.00, respectively (Fig. 1). One of the lineages agreed with the "Poeae chloroplast
group 1 (Aveneae type)" as termed by Soreng & al. (2007) or tribe Aveneae as suggested here
to use a taxonomic rank.

275 Aveneae showed more or less a polytomy of six lineages. Following the recent 276 classification of Soreng & al. (2017) and new names coined in this study (see below New 277 names and combinations) these lineages corresponded to subtribes Torreyochloinae and 278 Phalaridinae unified in a common clade (93/87/1.00), Aveninae (100/100/1.00), 279 Anthoxanthinae (100/100/1.00), new subtribe Hypseochloinae (only Hypseochloa 280 C.E.Hubb.), Brizinae with Macrobriza (Tzvelev) Tzvelev (97/98/1.00), Echinopogoninae 281 (100/99/1.00) and a well-supported common clade (90/71/1.00) of Calothecinae and 282 Agrostidinae. 283 Within Aveninae, Lagurus ovatus L., assigned to monogeneric subtribe Lagurinae by 284 Saarela & al. (2017), and Tricholemma jahandiezii (Litard. ex Jahand. & Maire) Röser were 285 opposed to a larger clade (91/95/1.00) formed of supported Aveninae s.str. (98/88/1.00) and a 286 lineage (99/97/1.00) sometimes referred to as separate subtribe Koeleriinae (Quintanar & al., 287 2007; Saarela & al., 2017; Barberá & al., 2019). 'Calamagrostis' rigida (Kunth) Trin. ex 288 Steud., member of the Central to South American 'Calamagrostis' Adans. or 'Deyeuxia'

289 Clarion ex P.Beauv. species, was nested among Aveninae and not Agrostidinae as

290 *Calamagrostis* s.str. and *Deyeuxia* s.str. It was placed in Koeleriinae in agreement with the

291 previous findings (Saarela & al., 2010, 2017; Wölk & Röser, 2014). Monospecific *Limnodea*

292 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

294 in its Koeleriinae lineage. Strongly supported Echinopogoninae encompassed among others

295 (Dichelachne Endl., Echinopogon P.Beauv., Pentapogon R.Br., Relchela Steud.) also

296 'Deyeuxia' contracta (F.Muell. ex Hook.f.) Vickery as representative of Australasian

297 'Deyeuxia' or 'Calamagrostis'. Altogether, supersubtribe Agrostidodinae (Soreng & al.,

298 2017) encompassing Agrostidinae, Brizinae, Calothecinae, Echinopogoninae and

299 Hypseochloinae received some support (75/-/0.96).

The second main lineage of the plastid DNA tree was the "Poeae chloroplast group 2 (Poeae type)" or tribe Poeae s.str. as suggested in this study. It 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

304 Puccinelliinae (= Coleanthinae), Poinae, Alopecurinae and Miliinae (Gillespie & al., 2008,

305 2010), supported by 71/67/0.99.

306 The large lineage with 81/61/- support encompassed Holcinae (100/100/1.00), 307 Aristaveninae (100/98/1.00), Sesleriinae (81/62/0.99), Loliinae (100/99/1.00), Ammochloinae 308 (only Ammochloa), Dactylidinae (100/100/1.00), Cynosurinae, Parapholiinae (100/99/1.00) 309 and the new subtribe Helictochloinae (100/100/1.00) with Helictochloa Romero Zarco and 310 Molineriella Rouy, two genera previously accommodated in Airinae. Antinoria Parl., (new 311 monogeneric subtribe Antinoriinae), was closer to Scolochloa Link (86/70/0.68). Dryopoa 312 Vickery, the second Scolochloinae genus, was placed separate from Scolochloa with 313 Sesleriinae (63/50/0.98). Ammochloinae and Dactylidinae were sister clades (97/95/1.00). 314 Cynosurinae with Cynosurus species forming a grade and Parapholiinae were placed in a 315 common clade (100/100/1.00). Ammochloinae/Dactylidinae and Cynosurinae/Parapholiinae 316 are acknowledged here as AD and CP clades, altogether as ADCP clade, which had weak 317 support (57/52/0.70). 318 The PPAM clade split into subtribe Coleanthinae and supersubtribe Poodinae (Soreng 319 & al., 2017), both of which gained strong support (100/99/1.00 and 100/95/1.00, 320 respectively). The latter agrees with the PAM clade, an acronym derived from the subtribe 321 names Poinae, Alopecurinae and Miliinae (Gillespie & al., 2008), or with subtribe Poinae as 322 broadly delineated by Kellogg (2015). It included the subtribes Miliinae (only Milium), 323 Phleinae (only *Phleum*) and Poinae (only *Poa*; 86/76/1.00), *Arctopoa* (Griseb.) Prob., 324 monospecific Avenula (Dumort.) Dumort. assigned to the monogeneric new subtribe 325 Avenulinae and a considerably supported lineage (84/68/1.00) termed here ABCV clade. It 326 encompassed a large polytomy Alopecurinae, Beckmanniinae, Cinninae, Ventenatinae 327 (85/60/1.00), along with Brizochloa V.Jirásek & Chrtek (monogeneric new subtribe 328 Brizochloinae) and a number of genera not classed as to subtribe, including Arctohyalopoa 329 Röser & Tkach, a new monospecific genus harboring former Hyalopoa lanatiflora (Roshev.) 330 Tzvelev. Moreover, Alopecurinae, Beckmanniinae and Cinninae did not resolve as 331 monophyletic. Only a sister relation of Alopecurinae genera Alopecurus L. and Cornucopiae 332 L. was strongly supported (100/100/1.00), whereas Beckmannia Host. and Pholiurus Trin. 333 (Beckmanniinae) obtained weak support as sister (59/57/0.98). The DAD clade, an acronym 334 originally derived from Dupontia, Arctophila and Dupontiopsis (Soreng & al., 2015a), in this 335 study encompassing Dupontia including Arctophila, Dupontiopsis and new Arctohyalopoa, 336 was obvious within the ABCV clade but with low support (72/-/-), whereas the HSAQN clade 337 (Soreng & al., 2015b; Gillespie & al., 2010; Kellogg, 2015) was unresolved. 338

339 **Nuclear DNA analysis.** — The nuclear ITS DNA sequence dataset for 215 taxa 340 included 673 and the ETS DNA dataset for 200 taxa included 1,135 aligned positions, 341 respectively. The combined data matrix of two nuclear DNA markers for 218 taxa included a 342 total of 1,808 aligned positions, of which 1,093 were variable (ITS: 383, ETS: 710) and 863 343 parsimony-informative (ITS: 320, ETS: 543). 344 Poodae was supported by the nr ITS and ETS sequence data as monophyletic 345 (100/88/1.00). The tree backbone consisted of a polytomy of six clades (Fig. 2) comprising 346 Antinoriinae, Helictochloinae (100/100/1.00), Aristaveninae (100/96/1.00) and a supported 347 lineage (100/79/1.00) harboring Loliinae (70/-1.00) and the ADCP clade (69/-1.00). This 348 well-supported lineage of the latter two elements, unresolved in the plastid DNA tree, 349 represented supersubtribe Loliodinae (Soreng & al., 2017). The remaining two clades of the 350 backbone polytomy were the PPAM clade (95/74/1.00), and a large clade with 85/-/1.00 351 support. The PPAM clade consisted of Miliinae, a common lineage of Phleinae with Poinae 352 (84/-/0.99) that had not been resolved in the plastid DNA tree, Coleanthinae (68/-/0.98),

353 Avenulinae and a lineage termed ABCV+A clade (83/67/1.00), which corresponded to the

354 ABCV clade in the plastid tree complemented by Arctopoa. Supersubtribe Poodinae (~PAM

355 clade) was not resolved within the PPAM clade. The HSAQN clade was well-defined

356 (97/97/1.00) within the ABCV+A clade. Sister relations of *Alopecurus* and *Cornucopiae*

357 (Alopecurinae) and of *Beckmannia* and *Pholiurus* (Beckmanniinae) were supported

358 (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 supported 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

363 tree, and a clade supported by 93/55/1.00. It was formed by Scolochloinae with *Dryopoa* and

364 *Scolochloa* (100/97/1.00), Phalaridinae, Torreyochloinae (100/98/1.00) and supersubtribe

365 Agrostidodinae (81/-/0.99), which contained Hypseochloinae, Brizinae (54/-/0.93),

366 Calothecinae (89/88/1.00) as well as species and small clades of Agrostidinae and

367 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 *'Calamagrostis' rigida*.

376

Analysis of the combined DNA dataset. — Following the rationale outlined in
Material and Methods we analyzed also a concatenated dataset of plastid and nuclear DNA
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 nuclear DNA sequences for 218 taxa included a total of 5,736 aligned positions of which 2,564 were variable and 1,770 parsimonyinformative.

385 The backbone of the Poodae tree showed the same deep dichotomy as the plastid DNA 386 tree, which reflected the Aveneae and Poeae s.str., whereas further tree resolution was overall 387 low. Fig. 3 gives a simplified overview of the tree as a cladogram, the detailed phylogram is 388 shown in suppl. Fig. S1. Within the clade of Aveneae (100/67/1.00)), a series of clades 389 arranged in a polytomy was found. Anthoxanthinae (100/100/1.00), Aveninae (100/92/1.00), 390 Torreyochloinae (100/100/1.00) and Phalaridinae (100/99/1.00) were well-supported, to a 391 lesser extent Brizinae excluding Macrobriza (75/-/1.00) and Calothecinae (82/90/1.00). 392 Agrostidinae and Echinopogoninae did not resolve as monophyletic, respectively, but were 393 part of a polytomy. Supersubtribe Agrostidodinae under exclusion of Macrobriza was slightly 394 supported (62/-/1.00). Aveninae showed an internal structure of two main clades (Aveninae 395 s.str., Koeleriinae) with Tricholemma sister to one of these (93/90/1.00) and Lagurus to the 396 other (69/61/1.00).

Within the clade of Poeae (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

401 supersubtribe Loliodinae (100/68/1.00) containing Loliinae (99/67/1.00) and the ADCP clade

402 (80/56/1.00) and, finally, the PPAM clade (100/96/1.00). The latter encompassed

403 Coleanthinae (100/99/1.00) and supersubtribe Poodinae (~PAM clade; 100/82/1.00), in which

404 also Avenulinae was placed. Within Poodinae, the ABCV+A (97/97/92/1.00), the HSAQN

405 (99/98/1.00) and the DAD clade (96/91/1.00) were supported.

406

407 **DISCUSSION**

408 Molecular phylogenetics.

409 *Comparison of the plastid and nuclear DNA trees.* – Both phylogenetic trees agreed 410 widely in the resolution of minor clades, whose support values were frequently comparatively 411 high (Figs. 1, 2, 4). The larger clades, by contrast, corresponded only partly and disagreed 412 strikingly in some instances.

413 Concordant groupings were (1) supersubtribe Agrostidodinae, which was resolved in 414 both individual analyses although excluding Macrobriza in the nuclear tree, in which it was 415 sister to a clade of Aveninae and Sesleriinae; (2) the PPAM clade; (3) the ADCP clade. There 416 were (4) many congruent clades, which corresponded to subtribes, for example, Phalaridinae, 417 Torreyochloinae, Anthoxanthinae, Holcinae, Aristaveninae, Loliinae, Ammochloinae, 418 Dactylidinae, Parapholiinae, Coleanthinae, Phleinae, Miliinae, Poinae and Ventenatinae. (5) 419 Former subtribe Airinae (Airinae s.l.) was non-monophyletic in both analyses but its 420 subgroups were resolved and congruent (Airinae, Antinoriinae, Helictochloinae).

421 Several clades were monophyletic in one of the individual plastid and nuclear DNA 422 analyses, whereas they were unresolved in the other, appearing as a polytomy or a grade. We 423 consider this not as severe conflict. Supersubtribe Loliodinae was clearly monophyletic in the 424 nuclear DNA tree but formed a polytomy with several other lineages in the plastid DNA tree. 425 Calothecinae and the DAD clade were likewise monophyletic in the nuclear but paraphyletic 426 in the plastid DNA tree. Conversely, supersubtribe Poodinae (~PAM clade) including Avenula 427 as well as subtribes Echinopogoninae, Agrostidinae and Sesleriinae were clearly 428 monophyletic in the plastid DNA tree but form polytomies with other lineages in the nuclear 429 DNA tree.

430 Discordant groupings occurred starting with the backbone of the trees since the 431 bifurcation of the plastid DNA tree into Aveneae and Poeae s.str. was not reflected in the 432 nuclear tree, which represented a polytomy. Sesleriinae from the Poeae lineage of the plastid 433 were placed along with Aveninae in the nuclear DNA tree (Quintanar & al., 2007; Saarela & 434 al., 2017). Subtribe Holcinae and Airinae as part of Poeae in the plastid DNA tree were placed 435 in the nuclear DNA tree close to subtribes of Aveneae such as Aveninae, Agrostidinae, etc. 436 The same pattern was encountered in Scolochloinae as belonging to Poeae (plastid) but nested 437 (nuclear) in a common clade with subtribes of Aveneae such as Phalaridinae, 438 Torreyochloinae, Echinopogoninae, Agrostidinae etc. A number of further subtribes showed 439 different affiliations depending on the individual tree: Phalaridinae and Torreyochloinae were 440 sister in the plastid but not in the nuclear DNA analyses (Saarela & al., 2017). Subtribe

441 Aveninae was monophyletic in the plastid DNA tree but disintegrated in the nuclear tree into
442 two lineages, one of which (Aveninae s.str. with *Tricholemma*) aggregated with the taxa of
443 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 nuclear tree. Furthermore, *Arctopoa* was placed in
a clade along with Poinae in the plastid but within the ABCV+A clade in the nuclear 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*).

450

451 Tree of the combined plastid and nuclear DNA dataset. - This tree obtained from the 452 concatenated dataset all in all combined features of the individual plastid and nuclear DNA 453 trees. Lineages that were retrieved in both individual analyses were present also in the 454 combined tree, for example, the PPAM clade, supersubtribe Agrostidodinae (except for Macrobriza), the ADCP, AD and CP clades (Fig. 4, suppl. Fig. S1). Also many subtribes were 455 456 recovered in the combined analyses such as Anthoxanthinae, Torreyochloinae and 457 Phalaridinae, Aristaveninae, Holcinae, Loliinae, Dactylidinae, Ammochloinae, Parapholiinae, 458 Coleanthinae, Miliinae, Phleinae, Poinae, Ventenatinae and the monophyletic subdivisions of 459 former Airinae s.l., namely Airinae, Antinoriinae and Helictochloinae. Occasionally, the clade 460 support values of concordant lineages were higher in the analysis of the combined dataset 461 than in the individual analyses, for example, for the PPAM clade (combined 100/96/1.00, 462 plastid 71/67/0.99, nuclear 95/74/1.00), the ABCV(+A) clade (combined 97/92/1.00, plastid 463 84/68/1.00, nuclear 83/67/1.00) or the ADCP clade (combined 80/56/1.00, plastid 57/52/0.70, 464 nuclear 69/-/1.00).

465 The combined tree contained most well-resolved groups from the individual trees, 466 even if they were supported only in one of them. It followed this way the main dichotomy of 467 Aveneae and Poeae s.str. observed in the plastid tree and resolved supersubtribe Poodinae and 468 subtribe Agrostidinae, which were likewise supported only in the plastid DNA tree. 469 Conversely, supersubtribe Loliodinae, the ABCV+A and the HSAQN clade, subtribes 470 Calothecinae, Scolochloinae and the Koeleriinae lineage combined with *Lagurus* found within 471 Aveninae were present in the combined tree although they were supported only in the nuclear

472 but not the plastid DNA tree.

473 Lineages with a discordant grouping in the individual analyses followed one of these474 placements in the combined tree. Sesleriinae were nested within the Poeae clade as in plastid

475 DNA tree and not together with Aveninae as in the nuclear DNA tree. Torreyochloinae and 476 Phalaridinae built a clade sister to supersubtribe Agrostidodinae as similarly encountered in 477 the nuclear DNA tree, whereas they were sister to Aveninae in the plastid DNA tree. Subtribe 478 Aveninae resolved monophyletic as in the plastid DNA tree, however, the placement of 479 Lagurus and Tricholemma was different. Lagurus was sister to the Koeleriinae lineage as in 480 the nuclear DNA tree. Tricholemma belonged to the Aveninae s.str., although its position was 481 new relative to the nuclear DNA tree. Subtribe Scolochloinae grouped within Poeae as in the 482 plastid DNA tree, whereas it was affiliated with supersubtribe Agrostidodinae, namely 483 subtribes Torreyochloinae and Phalaridinae, in the nuclear DNA tree. Finally, Macrobriza 484 was sister to the lineage of Aveninae and Sesleriinae in the nuclear but was placed within 485 Brizinae in the plastid DNA tree.

486

Hybrid origin of major lineages or subtribes and genera derived from hybridization
between them. – The examples of discordant grouping are best explained by 'chloroplast
capture', which means hybridization (Rieseberg & Soltis, 1991). Some lineages and genera
have seemingly reticulate origin documented by the incongruent placement in the plastid and
nuclear trees (Figs. 1, 2, 4).

492 (1) The whole lineage of Sesleriinae had one ancestor with Poeae s.str. plastid DNA 493 (Figs. 1, 4). Due to the usually maternal inheritance of plastids in angiosperms, this ancestor 494 was supposedly the maternal parent. The paternal parent inherited the Aveninae-like rDNA 495 (Figs. 2, 4). This can be stated even more precisely because it was an Aveninae s.str.- and not 496 Koeleriinae-like parent. Maternal rDNA seemingly is no longer present in Sesleriinae or at 497 least was not detected by our approach using direct sequencing of PCR products, presumably 498 due to sequence homogenization of this repetitive rDNA in favor of one parental copy type, a 499 well-documented process of unidirectional loss (Winterfeld & al., 2009, 2012; Kotseruba & 500 al., 2010; Wölk & al., 2015; Tkach & al., 2019).

501 (2) Subtribes Phalaridinae and Torreyochloinae had a maternal ancestor with
502 Aveninae-like plastid DNA, whereas the paternal parent was close to supersubtribe
503 Agrostidodinae (Figs. 1, 2, 4).

(3) Scolochloinae had a maternal parent inheriting the plastid DNA from Poeae s.str.,
most likely from outside the PPAM clade, namely from relatives of Loliinae and Sesleriinae
(Figs. 1, 4). The paternal parent as indicated by the nuclear rDNA was distantly related and
was close to supersubtribe Agrostidodinae such as seen in Phalaridinae and Torreyochloinae
(Figs. 2, 4).

509 (4) The position of Phleinae is intriguing, because this subtribe is sister lineage to 510 Poinae in the nuclear DNA analyses (84/-/0.99), whereas in the plastid DNA analyses it is part 511 of a polytomy with Miliinae, Poinae, the ABCV clade, Avenula and Arctopoa within the 512 strongly supported supersubtribe Poodinae (~PAM clade; Figs. 1, 2, 4). The placements of 513 Phleinae might actually bear witness of a further instance of reticulation. 514 (4) Macrobriza and Arctopoa are examples of genera with hybrid origin. Monospecific 515 Macrobriza had a maternal parent with Brizinae plastid DNA and a paternal parent with 516 Aveninae-/Sesleriinae-like rDNA (Figs. 1, 2, 4). Arctopoa had a maternal parent (plastid 517 donor) related with, or from, Poinae, whereas its paternal parent inheriting its rDNA belonged 518 to the ABCV clade in accordance with Gillespie & al. (2008, 2010), while the maternal rDNA 519 is no longer detectable, at least by our direct sequencing of PCR products. Further examples 520 of genera originating from hybridization across major lineages were discussed also in the 521 instances of Avenula, Helictochloa and Aniselytron Merr. In the latter, a strongly divergent, 522 *Poa* L.-like ITS copy was found in addition to the regular type, pointing to either hybrid 523 origin of Aniselytron or recent hybridization with Poa (Soreng & Davis, 2000; Gillespie & al., 524 2008, 2010; Soreng & al., 2017). Our results, however, indicate a largely concordant 525 placement of these genera in the plastid and nuclear DNA trees, respectively. Only in 526 monospecific Avenula, which was consistently placed in all our analyses within the PPAM 527 clade, there are slight differences but seem to be too small to corroborate hybrid origin of 528 Avenula (see below PAM clade...).

529

530 *Reticulations within major lineages.* – (1) Within Aveninae, *Tricholemma* and 531 *Lagurus*, with a plastid DNA seemingly characteristic of early-branching Aveninae as a whole 532 (Figs. 1, 5; Wölk & Röser, 2017), have rDNA sequences with characteristics of either 533 Aveninae s.str. or the lineage of Koeleriinae. In the nuclear DNA tree, Lagurus was sister to 534 the remaining genera of the latter and represents an early-branching offspring (Figs. 2, 5). 535 Tricholemma was nested amidst the taxa of Aveninae s.str. Within the Koeleriinae lineage, 536 there were several further instances of non-concordant placements of taxa, the most 537 remarkable being that of American Trisetum Pers. species and Graphephorum Desv. (Wölk & 538 Röser, 2017; see below Aveninae).

(2) Sesleria Scop. (Sesleriinae) was sister to Sesleriella Deyl according to the plastid
DNA data (Figs. 1, 6), whereas the nuclear rDNA of Sesleria points to a close relation with *Psilathera* Link and Echinaria Desf. (Figs. 2, 6; see below Sesleriinae and Scolochloinae). As
suggested by Kuzmanović & al. (2017), Sesleria originated most likely from hybridization

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

547 (3) The new Coleanthinae genus Hyalopodium Röser & Tkach, gen. nov., comprises 548 only *H. araraticum* (Lipsky) Röser & Tkach, comb. nov. [= *Colpodium araraticum* (Lipsky) 549 Woronow ex Grossh.]. With respect to the nuclear rDNA, Hyalopodium largely agreed with 550 Colpodium Trin. (Figs. 1, 7; Rodionov & al., 2008; Kim & al., 2009), whereas it shared 551 plastid DNA characteristics with *Hyalopoa* (Tzvelev) Tzvelev [*H. pontica* (Balansa) Tzvelev] 552 and Paracolpodium (Tzvelev) Tzvelev [P. altaicum (Trin.) Tzvelev, P. baltistanicum 553 Dickoré; Figs. 2, 7], indicative of hybrid background. 554 The incongruent tree position of the sister genera *Puccinellia* Parl. and *Sclerochloa*

554 The incongruent tree position of the sister genera *Puccinetita* Pari. and *Scierochioa*555 P.Beauv. also points to hybrid origin because they clustered with *Catabrosa* P.Beauv. and
556 *Catabrosella* (Tzvelev) Tzvelev in the plastid but with *Coleanthus* Seidel ex Roem. & Schult.
557 and *Phippsia* (Trin.) R.Br. in the nuclear DNA tree (Figs. 1, 2, 7; Schneider & al., 2009).

(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 (Figs. 1, 2; see below *Loliinae*).

562

563 **Circumscription of lineages or genera.** — Our molecular phylogenetic data support 564 the circumscription of many lineages that have been recognized already previously. However, 565 due to the inclusion of several taxa that have not been sampled before and the sampling 566 strategy including a comparatively broad representative set of taxa used for both plastid and 567 nuclear DNA sequence data some re-arrangements and emendations are required.

568

569 Anthoxanthinae, Torreyochloinae and Phalaridinae. - Cumarin-scented subtribe 570 Anthoxanthinae was corroborated as clearly monophyletic and distinct from scentless 571 Phalaridinae (Figs. 1, 2, 4) as suggested by several previous molecular phylogenetic studies 572 (Döring & al., 2007; Quintanar & al., 2007; Döring, 2009; Saarela & al., 2015, 2017; 573 Rodionov & al., 2017; Orton & al., 2019). Species traditionally assigned to Hierochloe R.Br. 574 [including the type *H. odorata* (L.) P.Beauv. = Anthoxanthum nitens (Weber) Y.Schouten & 575 Veldkamp], namely *H. australis* (Schrad.) Roem. & Schult. [$\equiv A.$ australe (Schrad.) 576 Veldkamp], H. glabra Trin. $[\equiv A. glabrum (Trin.) Veldkamp], H. pauciflora R.Br. (= A.$

577 arcticum Veldkamp), H. redolens (Vahl) Roem. & Schult. [= A. redolens (Vahl) P.Royen] 578 and *H. repens* $[\equiv A. repens$ (Host) Veldkamp; not all shown in Figs. 1, 2], were not 579 consistently separated from Anthoxanthum L.: A. odoratum (type of Anthoxanthum) was sister 580 to traditional *H. australis* (plastid DNA tree) or was placed between species of traditional 581 Hierochloe (nuclear DNA tree). The peculiar tree position of A. australe, a species not 582 sampled by Pimentel & al. (2013), agreed with that obtained by Rodionov & al. (2017) on 583 ITS. All in all, the findings support to assign preliminarily the species of *Hierochloe* to 584 Anthoxanthum (Schouten & Veldkamp, 1985) as suggested also by Pimentel & al. (2013: 585 1025) in view of the intermediate floral characters of A. sect. Ataxia (R.Br.) Stapf between 586 typical Anthoxanthum and Hierochloe (Connor, 2012). 587 Subtribe Torreyochloinae consists of south hemispheric Amphibromus Nees and North 588 American/East Asian Torreyochloa Church. They shared a plastid DNA type with Phalaris L. 589 (Döring, 2009; Saarela & al., 2015; Orton & al., 2019), the only genus of holarctic 590 Phalaridinae, but were more distant to each other in nuclear ITS since Torreyochloinae were 591 supported sister to supersubtribe Agrostidodinae, whereas Phalaridinae were closer to 592 Scolochloinae (Figs. 1, 2, 4). Interestingly, the three subtribes share eco-morphological 593 characteristics because Amphibromus, Torreyochloa, Phalaris, Scolochloa and Dryopoa have 594 rather tall, sometimes reed-like perennial species, which prefer aquatic habitats or wet 595 mountain forests (Dryopoa), except for the annuals of Phalaris, some of which are adapted to 596 seasonally dry Mediterranean-type climate (Baldini, 1995).

597

598 Aveninae. – This large lineage encompasses two main subgroups, namely Aveninae 599 s.str. and the Koeleriinae lineage. Additionally, there are two somewhat isolated genera with 600 hybrid background (see above *Reticulations within major lineages*), namely monospecific 601 Lagurus (type L. ovatus) and Tricholemma (two species; type T. jahandiezii; Röser, 1989, 602 1996; Röser & al., 2009; Gabriel & al., 2019), which makes a separation of Aveninae s.str. 603 and Koeleriinae as distinct subtribes not straightforward (Figs. 1, 2, 5), even if Lagurus is 604 accommodated under a monogeneric subtribe Lagurinae (Saarela & al., 2017). For this reason 605 we argue for summarising all of them under a single subtribe, i.e., Aveneae, in the 606 classification below.

607 The taxa of Aveninae have several flowers per spikelet, but there are exceptions with 608 only a single flower such as *Lagurus*, *Limnodea* or Mexican to South American members of 609 *'Calamagrostis'* or *'Deyeuxia'*, for which the genus name *Cinnagrostis* Grieseb. recently has 610 been suggested (Soreng & al., 2017; see Saarela & al., 2017; Barberá & al., 2019). The 611 phylogenetic trees of the Aveninae s.str. showed a rather narrowly delineated genus 612 Helictotrichon Besser after exclusion of Tricholemma, Subsaharo-African to Southeast Asian 613 Trisetopsis Röser & A.Wölk [type T. elongata (Hochst. ex A.Rich.) Röser & A.Wölk] and 614 East Asian Tzveleviochloa Röser & A.Wölk [type T. parviflora (Hook.f.) Röser & A.Wölk], 615 which are members of the Aveninae but belong to the Koeleriinae lineage. Excluded from 616 Helictotrichon were also Helictochloa and Avenula, which were placed even more distantly in 617 the molecular phylogenetic analyses in the clade of Poeae. Further excluded was the 618 nothogenus ×Trisetopsotrichon Röser & A.Wölk. The redefined genus Helictotrichon [type 619 H. sempervirens (Vill.) Pilg.; studied also by Wölk & Röser, 2014, 2017; Wölk & al. 2015] 620 encompasses the former genus *Pseudarrhenatherum* Rouy [type *H. thorei* Röser = *P.* 621 longifolium (Thore) Rouy] and was corroborated in this circumscription as monophyletic 622 (data not shown; Appendix 1; Schneider & al., 2009). Avena L., a genus with consistently 623 annual species except for perennial A. macrostachya Balansa ex Coss. & Durieu, was close to 624 Arrhenatherum P.Beauv. [type A. elatius (L.) P.Beauv. ex J.Presl & C.Presl] according to the 625 plastid DNA but not the nuclear DNA trees, in which Arrhenatherum clustered with 626 Tricholemma and Helictotrichon.

627 The delineation of genera within the Koeleriinae lineage is still an insufficiently 628 solved problem as there are seemingly intermediates between traditionally acknowledged 629 genera and a considerable degree of hybrid speciation and allopolyploid evolution (Quintanar 630 & al., 2010; Saarela & al., 2010, 2017; Wölk & Röser, 2014, 2017; Wölk & al., 2015; Soreng 631 & al., 2017; Barberá & al., 2019). As a possible consequence, all genera of Koeleriinae 632 widely accepted at the present time and additionally Leptophyllochloa Calderón ex Nicora 633 were unified by Kellogg (2015) under a single genus, Trisetaria Forssk. More detailed 634 investigations using a broad phylogenetic sampling of taxa are evidently still necessary to 635 delineate well-defined genera within Koeleriinae or, alternatively, infrageneric entities in 636 broadly delineated Trisetaria.

637 The backbone of the plastid DNA tree showed largely a polytomy for Koeleriinae 638 (excluding *Lagurus*) if not considering the unsupported placement of *Sibirotrisetum* Barberá, 639 Soreng, Romasch., Quintanar & P.M.Peterson (Figs. 1, 5). One maximally supported clade 640 (100/99/1.00) contained the sampled species of *Graphephorum* [type *G. melicoides* (Michx.) 641 Desv.], Limnodea (type L. arkansana), Peyritschia E.Fourn. [the type P. koelerioides (Peyr.) 642 E.Fourn. together with P. pringlei (Scribn.) S.D.Koch used in this study and P. deyeuxioides (Kunth) Finot studied by Wölk & Röser (2017) showing their monophyly], Sphenopholis 643 644 Scribn. [type S. obtusata (Michx.) Scribn.], Trisetopsis as well as Trisetum canescens

645 Buckley, T. cernuum Trin. and 'Calamagrostis' rigida as representative of the Mexican to 646 South American taxa of 'Calamagrostis'/'Deyeuxia'. This clade agreed largely with 647 Koeleriinae clade B of Saarela & al. (2017) and Barberá & al. (2019). This lineage was 648 present in principle also in the nuclear DNA analyses (98/92/1.00; Figs. 2, 5) but without 649 Graphephorum spp., Trisetum canescens and T. cernuum. They assembled in a strongly 650 supported clade (ML 98/97/1.00) with Avellinia Parl. [type A. michelii (Savi) Parl.], Gaudinia 651 J.Gay [type G. fragilis (L.) P.Beauv.], Rostraria Trin. [type R. pubescens Trin. = R. cristata 652 (L.) Tzvelev], Trisetaria, Koeleria Pers. [type K. pyramidata (Lam.) P.Beauv.] including the 653 former genus Parafestuca E.B.Alexeev [type P. albida (Lowe) E.B.Alexeev $\equiv K$. loweana 654 Quintanar, Catalán & Castrov.], Trisetum [type T. flavescens (L.) P.Beauv.], Acrospelion 655 Besser [type A. distichophyllum (Vill.) Barberá] and Tzveleviochloa This clade agreed with 656 Koeleriinae clade A (Saarela & al., 2017; Barberá & al., 2019) despite different sampling. The 657 changing position of American Graphephorum species, Trisetum cernuum and T. canescens 658 in plastid and nuclear analyses (Figs. 1, 2, 5; Wölk & Röser, 2014, 2017; Saarela & al., 2017) 659 points to their likely hybrid origin. 660 Sibirotrisetum sibiricum (Rupr.) Barberá, type of Sibirotrisetum, segregated from the 661 species currently ascribed to genera Trisetum and Acrospelion in both the plastid and the 662 nuclear DNA analysis. It was part of the backbone polytomy or placed in an unsupported

clade with clade A genera (Figs. 1, 5) in the former analysis and sister to the Koeleriinae clade
B (74/68/0.86) in the latter (Figs. 2, 5). Most likely due to the different taxon sampling, *S. sibiricum* stood in the study of Barberá & al. (2019) in a polytomy with clades A and B
according to the nuclear DNA, whereas it was sister to clade B according to their plastid DNA
data.

668

669 Brizinae and Macrobriza. – Monospecific Airopsis Desv. (A. tenella) was a supported 670 member of subtribe Brizinae. It segregated from the representatives of the genus Briza L. 671 (type B. minor L.) in the molecular phylogenetic trees and is also morphologically distinct 672 enough to be acknowledged as separate genus (Figs. 1, 2, suppl. Fig. S1). Remarkable is its 673 long branch in the trees, comparable to that of other annual taxa in this study such as 674 Echinaria Desf., Mibora Adans. (Sesleriinae), Ammochloa Boiss. (Ammochloinae), 675 Rhizocephalus Boiss. (Beckmanniinae), Brizochloa (Brizochloinae) and annual species of Poa 676 (Figs. 1, 2, suppl. Fig. S1). Briza media L., B. minor L. and Macrobriza maxima (L.) Tzvelev 677 were placed in a common lineage according to the plastid DNA data, whereas Macrobriza 678 deviated clearly in the nuclear DNA tree (see above *Hybrid origin of major lineages...*). This

discordant placement is implicitly obvious also in the study of Persson & Rydin (2016),

680 which showed *M. maxima* together with *B. marcowiczii* Woronow, *B. media* L. and *B. minor*

681 L. placed in a common clade according to the plastid DNA data, whereas *M. maxima*

682 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

684 Chascolytrum Desv. but no taxa of Aveninae. Macrobriza clustered with Briza minor in the

ITS/GBSSI tree of their Fig. 2, whereas *B. media* clustered with taxa of *Chascolytrum*, which
may be due to insufficient taxon sampling as noted by Saarela & al. (2017).

687 Considering morphology, monospecific *Macrobriza* by and large resembles *Briza* but 688 differs by its overall tall size, comparatively few-flowered spikelets and a linear hilum of the 689 caryopsis, which induced Tzvelev to treat it firstly as *Briza* subsect. *Macrobriza* Tzvelev and 690 later as a genus (Tzvelev, 1970, 1993). Its hybrid origin between ancestors from Brizinae 601 (relactid doner) and Augringer/Sectoringer on discussed shows appreciate its evolution from

691 (plastid donor) and Aveninae/Sesleriinae as discussed above suggests its exclusion from692 Brizinae.

693

694 Echinopogoninae and Calothecinae. - These are subtribes of the southern hemisphere. 695 Australasian Echinopogoninae were strongly supported (100/99/1.00) as monophyletic by the 696 plastid DNA data (not available for New Guinea to Queensland Ancistragrostis; Fig. 1) but 697 formed to a large extent a polytomy with other subtribes of supersubtribe Agrostidodinae in 698 the nuclear and combined data (Figs. 2, 3, suppl. Fig. S1). Echinopogoninae were represented 699 in this study by monospecific Ancistragrostis, two species of Dichelachne, Echinopogon, 700 Relchela (monospecific), two accessions of Pentapogon (monospecific) and 'Deveuxia' 701 contracta. A placement within Echinopogoninae was reported also for the species of 702 'Deveuxia' from Australia and New Zealand studied by Saarela & al. (2017). They belong to 703 the ~40 species of this region unified under the genus name 'Deyeuxia' (Vickery, 1940; 704 Weiller & al., 2009; Edgar & Connor, 2000) as a presumed segregate of *Calamagrostis*. 705 'Deveuxia' contracta was closer to Pentapogon than to Dichelachne according to the plastid 706 and nuclear DNA data (Figs. 1, 2). Merging *Dichelachne* with '*Deyeuxia*' (Kellogg, 2015) 707 therefore was not supported, unless Pentapogon would likewise be abandoned as a genus. For 708 nomenclature reasons, the genus name 'Deveuxia' is not applicable anyway (see following 709 chapter). 710

Calothecinae (Mexico to South America) encompasses only *Chascolytrum* Desv. [type *C. subaristatum* (Lam.) Desv.] after inclusion of several segregate genera such as *Erianthecium* (type *E. bulbosum* Parodi), *Rhombolytrum* Link (type *R. rhomboideum* Link),

713 *Poidium* Nees [*P. uniolae* (Nees) Matthei sampled] and others (Essi & al., 2017).

- 714 Chascolytrum proved monophyletic in this study according to the nuclear DNA data
- 715 (89/88/1.00; Fig. 2) such as found by Persson & Rydin (2016) for their set of taxa, whereas
- 716 Briza media was nested among New World Chascolytrum taxa in the ITS/GBSSI tree of Essi
- 718 insufficient taxon sampling.
- 719

720 Agrostidinae and Hypseochloinae; Calamagrostis and Deyeuxia. - Subtribe 721 Agrostidinae, characterized by single-flowered spikelets, is well-supported as monophyletic 722 by the plastid DNA (83/79/1.00) but not the nuclear and combined data analyses, due to the 723 polytomy mentioned. African Hypseochloa deviating from Agrostidinae in all analyses (Figs. 724 1, 2, 4) belongs to supersubtribe Agrostidodinae but it may be best to assign it to a new 725 monogeneric subtribe, Hypseochloinae, which is morphologically supported by peculiar 726 lemma characters not found elsewhere in supersubtribe Agrostidodinae (Hubbard, 1936, 727 1981; Clayton & Renvoize, 1986; Kellogg, 1995; see below New names and combinations). 728 Agrostidinae comprised three well-supported lineages in the plastid DNA tree, which 729 were arranged largely in a polytomy with the remainder of this subtribe and, in the nuclear 730 DNA tree, even in an even more extended polytomy with taxa of Brizinae, Calothecinae and 731 Echinopogoninae.

732 One of these well-supported Agrostidinae lineages in both analyses (plastid and 733 nuclear DNA; 100/100/1.00 and 100/0.99/1.00, respectively) was composed of Gastridium 734 phleoides (Nees & Meyen) C.E.Hubb., G. ventricosum (Gouan) Schinz & Thell. (type of 735 Gastridium P.Beauv.) and G. nitens (Guss.) Coss. & Durieu (type of Triplachne Link) as 736 similarly found in several previous studies (Davis & Soreng, 2007; Quintanar & al., 2007; 737 Soreng & al., 2007; Döring, 2009; Saarela & al., 2010, 2017; Orton & al., 2019). Species of 738 Gastridium and former Triplachne even were intermingled in the plastid DNA tree. This 739 supports to assign them to a single genus, which is emphasized also by their strong 740 morphological similarity (Clayton & Renvoize, 1986).

- The second supported lineage in the plastid DNA tree (96/81/1.00; Fig. 1) 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.], A. capillaris L., A. linkii Banfi, Galasso & Bartolucci [= Chaetopogon
 fasciculatus (Link) Hayek, type of Chaetopogon Janch.], A. pallens Trin., A. ramboi Parodi [≡
- 746 Bromidium ramboi (Parodi) Rúgolo] and A. scabra Willd. In the nuclear DNA tree, the

747 lineage disintegrated into a polytomy with strongly supported *A. avenacea* and *A.*

- 748 *alopecuroides* as sister (100/100/1.00) and a monophyletic lineage of the remaining species
- 749 (100/97/1.00), which was complemented by a further species of former genus *Bromidium*

750 Nees & Meyen [A. tandilensis (Kuntze) Parodi; only ITS]. Agrostis linkii was sister to A.

751 *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*

753 (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

8 4 al. (2010, 2017). The same applies to former *Polypogon*, which shares spikelets falling

756 entire and other characters with former *Chaetopogon*. Barely separable are also

757 Lachnagrostis, a richly evolved group in temperate Australasia encompassing ~38 species

758 (Jacobs & Brown, 2009), and *Bromidium*, which encompasses 5 species in South America

759 (Rúgolo de Agrasar, 1982).

The third well-supported lineage of Agrostidinae (plastid 94/94/1.00, nuclear

761 99/98/1.00) was represented by two species sampled of *Podagrostis* (Griseb.) Scribn. &

762 Merr., P. aequivalvis (Trin.) Scribn. & Merr. (type of Podagrostis) and P. thurberiana

763 (Hitchc.) Hultén. It was separate from *Agrostis* in both analyses, which supports to maintain

764 *Podagrostis* as a distinct genus (Figs. 1, 2).

The holarctic, temperate species of Calamagrostis sampled in this study (Old and New 765 766 World) belonged to Agrostidinae, whereas the Mexican to South American and Australasian 767 taxa sampled were nested in the lineages of Aveninae and Echinopogoninae, respectively 768 (Figs. 1, 2; Saarela & al., 2010, 2017; Wölk & Röser, 2014, 2017). The latter were usually 769 treated under either *Calamagrostis* or more frequently *Deveuxia* (for example, Bor, 1960; 770 Nicora & Rúgolo de Agrasar, 1987; Villavicencio, 1995; Renvoize, 1998; Edgar & Connor, 771 2000; Sharp & Simon, 2002; Rúgolo de Agrasar, 2006, 2012a; Weiller & al., 2009). None of 772 both genus names can be used for them because the type of *Calamagrostis* is *Arundo* 773 calamagrostis L., a synonym of C. canescens (Weber) Roth, which was nested within 774 Agrostidinae (Figs. 1, 2). The type of Deyeuxia Clar. ex P.Beauv. is D. montana (Gaud.) 775 P.Beauv., a synonym of C. arundinacea (L.) Roth, which likewise belongs to Agrostidinae. 776 Moreover, Deyeuxia is synonymous with Calamagrostis (Wölk & Röser, 2014; Saarela & al., 777 2017), if C. canescens and C. arundinacea belong to a single genus, which is more than likely 778 considering the plastid and nuclear DNA analyses, in which both species were placed with all

other species of *Calamagrostis* sampled from Eurasia and North America in a polytomy (Figs.

780 1, 2).

781 An exception was Tibetan 'Calamagrostis' flavens (Keng) S.L.Lu & Z.L.Wu. This 782 species clustered in the plastid DNA tree together with *Podagrostis*, *Gastridium* and *Agrostis* 783 in a considerably supported clade (95/70/1.00), whereas it was part of the polytomy of 784 Agrostidinae/Brizinae/Calothecinae/Echinopogoninae in the nuclear DNA tree (Figs. 1, 2). 785 Morphologically, this species has an unusual combination of characters otherwise found in 786 Agrostis and Calamagrostis as noted by Lu & al. (2006), which seems to fit its ambiguous 787 placement in the trees and points to a possible intergeneric hybrid origin. 788 Calamagrostis arenaria (L.) Roth, type of the former genus Ammophila Host, fell 789 within *Calamagrostis* in the nuclear DNA data tree (Fig. 2) in agreement with Saarela & al.

790 (2017). Our plastid DNA tree was not decisive (Fig. 1), whereas that of Saarela & al. (2017) 791 clearly showed C. arenaria nested within traditional Calamagrostis species. Inclusion of this 792 awnless or shortly awned species in *Calamagrostis* agrees also with morphological data, 793 although previous literature mostly kept this ecologically notable species of coastal dune 794 sands separate (Tutin, 1980; Conert, 1979–1998, 2007). Species of the former genus 795 Ammophila, viz. C. arenaria in Europe and C. breviligulata (Fernald) Saarela in North 796 America, are known to hybridize with C. epigejos and C. canadensis (Michx.) P.Beauv., 797 respectively. Hybrids between the former species were named C. ×baltica (Flüggé ex Schrad.) 798 Trin. $[\equiv \times Calammophila \ baltica$ (Flüggé ex Schrad.) Brand $\equiv \times Ammocalamagrostis \ baltica$ 799 (Flüggé ex Schrad.) P.Fourn. = *Calamagrostis* × *calammophila* Saarela]. They form 800 amazingly extensive stands along the coasts of the North and the Baltic Sea (Conert, 1979– 801 1998; Tutin, 1980), where they are locally more abundant than the parental species.

802

Sesleriinae and Scolochloinae. – 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* [type *O. disticha*(Wulfen) Link] were sister in all analysis.

808 They formed a sister clade to *Sesleria* [type *S. caerulea* (L.) Ard.] and monospecific 809 *Sesleriella* [type *S. sphaerocephala* (Ard.) Deyl] in the plastid DNA tree (Figs. 1, 6), in which 810 *Echinaria* clustered with monospecific *Psilathera* [type *P. ovata* (Hoppe) Deyl]. In the 811 nuclear tree, *MiboralOreochloa* stood in a polytomy with *Sesleriella* and supported clade of 812 *Echinaria*, *Psilathera* and *Sesleria* (Figs. 2, 6). The origin of *Sesleria* through hybridization 813 between a *Sesleriella*-like maternal ancestor and a *Psilathera*-like paternal ancestor (see 814 Kuzmanović & al., 2017 and above) represents also a good example of allopolyploidy because *Sesleria* comprising consistently polyploid species (4x-12x), whereas *Sesleriella*

- 816 (most likely monospecific) and Psilathera (monospecific) are diploid. Also for Oreochloa, a
- 817 genus with four species occurring in the European Alpine mountain system, only diploids are
- 818 known so far. The relationships resolved by the plastid and the nuclear DNA analysis were
- 819 congruent and *Oreochloa* is not involved in the origin of *Sesleria* (Figs. 1, 2, 6).

820 Scolochloinae encompass Scolochloa [two species; type S. festucacea (Willd.) Link] 821 from the temperate regions of the Holarctic and monospecific Australian Dryopoa [D. dives 822 (F.Muell.) Vickery]. Both resemble one another morphologically (Clayton & Renvoize, 1986) 823 and represent a remarkable example of bipolar distribution. The genera were not supported to 824 be closely related by the plastid DNA analysis, in which Scolochloa aggregated with 825 Antinoria (86/70/0.68) and Dryopoa with Sesleriinae, although without strong support (Fig. 826 1). The nuclear and the combined DNA data analyses showed *Scolochloa* and *Dryopoa* as 827 strongly supported sister (100/97/1.00 and 100/100/1.00, respectively; Figs. 2, 3, suppl. Fig. 828 S1). The nuclear DNA revealed Scolochloinae in a common and considerably supported clade 829 comprising Phalaridinae, Torrevchloinae and supersubtribe Agrostidodinae, which 830 corroborates the findings of Birch & al. (2014) who noted a relationship of Dryopoa to 831 Brizinae and Agrostidinae.

832

833 Aristaveninae. - Segregation of this subtribe from Holcinae and Airinae as addressed 834 earlier (Schneider & al., 2012; Saarela & al., 2017; Soreng & al., 2017) was supported by all 835 analyses of this study. Aristaveninae encompass only *Deschampsia* P.Beauv. [type D. 836 cespitosa (L.) P.Beauv.], in which the former monospecific genus Scribneria Hack. [S. 837 *bolanderi* (Thurb.) Hack.], whose relationship with *Deschampsia* was established by Schneider & al. (2012), was included (Saarela & al., 2017). Deschampsia encompasses 838 839 seemingly also the former monospecific south Andean genus Leptophyllochloa as supported 840 by all analyses of this study (Figs. 1, 2, suppl. Fig. S1; Wölk & Röser, 2017). The accessions 841 of Leptophyllochloa studied by Saarela & al. (2017) and Barberá & al. (2019), however, 842 resolved within the Koeleriinae lineage of Aveninae. This induced us to re-examine the 843 voucher specimen we used. It had been collected and identified by Z. Rúgolo (Rúgolo 1245; 844 see Appendix 1) and we were able to ascertain the correct identification, such as for a second 845 accession examined (Rúgolo 1250, B 10 0448862). Transferring L. micrathera (É.Desv.) 846 Calderón ex Nicora to Deschampsia and placing Leptophyllochloa under synonymy of 847 Deschampsia (see below New names and combinations) also is in good agreement with their 848 morphology (pers. observ.; Nicora, 1978; Rúgolo, 2012b).

bioRxiv preprint doi: https://doi.org/10.1101/707588; this version posted July 18, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

849	
850	Helictochloinae, Antinoriinae, Airinae and Holcinae. – Helictochloinae is newly
851	established as subtribe to accommodate Helictochloa Romero Zarco [type H. bromoides
852	(Gouan) Romero Zarco], a widespread Eurasian/Mediterranean perennial, and Molineriella
853	[type M. minuta (L.) Rouy], a Mediterranean annual genus. Both genera had maximum
854	support as sisters in all analyses and segregated consistently from Airinae s.l., which
855	disintegrated further into Antinoriinae and Airinae (Figs. 1, 2, 3, suppl. Fig. S1). The subtribe
856	Helictochloinae is morphologically hard to define, because its genera differ substantially.
857	However, the spikelets disarticulate below each floret, the rhachilla is glabrous or sparsely
858	hairy, the lemma has a hairy callus and a dorsal awn though not consistently in Molineriella.
859	Lodicules have a lateral tooth (pers. observ.; Cebrino Cruz & Romero Zarco, 2017)
860	Subtribe Antinoriinae encompassing only Antinoria [type A. agrostidea (DC.) Parl.]
861	was close to Loliinae in all analyses (Figs. 1, 2, suppl. Fig. S1). In the nuclear and combined
862	DNA trees, it was weakly supported sister to supersubtribe Loliodinae, viz. the lineage with
863	subtribes Loliinae, Ammochloinae, Dactylidinae, Cynosurinae and Parapholiinae, a placement
864	agreeing with previous ITS studies (Quintanar & al., 2007; Inda & al., 2008).
865	Airinae as defined in this study were clearly monophyletic in all analyses (Figs. 1, 2,
866	suppl. Fig. S1). They encompass Aira L. (type A. praecox L.), Avenella Bluff ex Drejer [type
867	A. flexuosa (L.) Drejer], Corynephorus P.Beauv. [type C. canescens (L.) P.Beauv.] and
868	Periballia Trin. [type P. involucrata (Cav.) Janka].
869	Monophyletic Holcinae with Holcus and Vahlodea Fr. [type V. atropurpurea
870	(Wahlenb.) Fr.] were sister to Airinae as supported by the nuclear DNA data (95/84/1.00; Fig.
871	2) and the combined data analysis (88/88/1.00; suppl. Fig. S1) as similarly found by
872	Quintanar & al. (2007), who sampled only Holcus, and by Schneider & al. (2009) for Holcus
873	and Vahlodea. Plastid DNA data showed Holcinae in a polytomy with Aristaveninae and
874	Helictochloinae (Figs. 1, 4; similarly found by Quintanar & al., 2007; Schneider & al., 2009),
875	as well as with Loliinae, Scolochloinae, Sesleriinae and the ADCP clade, whereas Airinae
876	were more distant. This means that Holcinae share plastid DNA characters with a larger set of
877	subtribes but to a lesser extent with Airinae, whereas nuclear DNA connects Holcinae in
878	particular with Airinae. This indicates that Holcinae might have ancient hybrid origin slightly
879	different from that of Airinae although both tribes share an overall similar pattern of
880	conflicting placements with respect to the plastid and nuclear DNA trees (see above
881	Comparison of the plastid and nuclear DNA trees).
882	

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 and combined data analyses (Fig. 1, suppl. Fig.
S1), 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

891 Lolium), L. rigidum Gaudin and L. giganteum (L.) Darbysh. $[\equiv F. gigantea$ (L.) Vill. \equiv

892 Schedonorus giganteus (L.) Holub].

893 The second lineage was formed by Castellia tuberculosa (type of Castellia) as sister to 894 a monophyletic lineage, which corresponds to a narrowly defined genus *Festuca* that is 895 equivalent to the "fine-leaved fescues" (Torrecilla & Catalán, 2002) as suggested (Kellogg, 896 2015; Soreng & al., 2015b, 2017). This lineage of Festuca s.str. was represented in our 897 sample by species from several morphologically partly well-defined segregate genera, namely 898 F. berteroniana Steud. (type of Megalachne), F. floribunda (Pilg.) P.M.Peterson, Soreng & 899 Romasch. (type of *Dielsiochloa* Pilg.), F. incurva (Gouan) Gutermann (type of Psilurus) 900 Trin.), F. lachenalii (C.C.Gmel.) Spenn. [type of Micropyrum (Gaudin) Link], F. masatierrae 901 Röser & Tkach, nom. nov. (type of Podophorus; no plastid DNA data available), F. maritima 902 L. [= Vulpia unilateralis (L.) Stace], F. myuros L. (type of Vulpia C.C.Gmelin) and F. 903 salzmannii (Boiss.) Boiss. ex Coss. (type of Narduroides Rouy).

The nuclear DNA results agreed widely with the trees of the plastid data analyses, however, *Castellia* was differently placed, namely together with *Drymochloa* (Fig. 2) 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 Chilean Juan Fernández Islands, *F. berteroniana* and *F. masatierrae*, formed a monophyletic cluster in the nuclear DNA analysis. *Festuca floribunda* belongs to the group "American II" of fine-leaved *Festuca* in the study on the historical biogeography of Loliinae by Minaya & al. (2017). Group "American II" has colonised 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

- 915 million years ago (Stuessy & al., 1984).
- 916

917 ADCP clade. - The species of the small sister subtribes Ammochloinae and 918 Dactylidinae forming the AD clade have spikelets arranged in dense clusters. The close 919 relationship of both tribes (Figs. 1, 2) was revealed already by the plastid DNA data of 920 Quintanar & al. (2007) and Orton & al. (2019), whereas the ITS data of Ammochloa 921 palaestina Boiss. of the former study used by Saarela & al. (2010) were wrong and belonged 922 to Helictochloa (Appendix 3). Ammochloinae are monogeneric (Ammochloa; type A. 923 palaestina), whereas Dactylidinae encompass Eurasian Dactylis (type D. glomerata L.) und 924 Mediterranean to mid-East monospecific Lamarckia Moench [type L. aurea (L.) Moench]. 925 The sister relation of the AD to the CP clade was found in all analyses of this study (Figs. 1, 926 2, 4, suppl. Fig. S1) although without strong support, which agrees with the plastid DNA 927 results of several previous studies (Davis & Soreng, 2007; Quintanar & al., 2007; Bouchenak-928 Khelladi & al., 2008). 929 The Cynosurinae species C. cristatus L. (type of Cynosurus L.) and C. elegans Desf. 930 were not resolved as monophyletic but formed a grade basal to Parapholiinae. 931 Parapholiinae were strongly supported as monophyletic in all analyses (Figs. 1, 2, 932 suppl. Fig. S1), in agreement with Davis & Soreng (2007), Quintanar & al. (2007) and 933 Bouchenak-Khelladi & al. (2008). Its species are distributed from the Mediterranean to the 934 Middle East and frequently grow on saline soil. Parapholiinae encompass six genera of 935 annuals if, firstly, the former monotypic genus *Hainardia* Greuter [type *H. cylindrica* (Willd.) 936 Greuter] is reduced to synonymy of *Parapholis* C.E.Hubb. [type *P. incurva* (L.) C.E.Hubb.] 937 as concordantly suggested by our plastid and nuclear DNA analyses (Figs. 1, 2) and, 938 secondly, the endemic Algerian monotypic and perennial genus Agropyropsis, which was not 939 molecularly studied to date, belongs to Loliinae as suggested by morphological characters 940 (Schneider at al., 2012). The remaining Parapholiinae genera in addition to *Parapholis* are 941 Catapodium Link [type C. marinum (L.) C.E.Hubb.], Cutandia Willk., Desmazeria Dumort. 942 [type D. sicula (Jacq.) Dumort.], Sphenopus Trin. [type S. divaricatus (Gouan) Rchb.] and 943 *Vulpiella* (Batt. & Trab.) Burollet [type V. stipoides (L.) Maire]. 944 Desmazeria philistaea and D. sicula were sister taxa and monophyletic (100/100/1.0) 945 in the plastid (Fig. 1) but not in the nuclear DNA tree, in which D. sicula clustered with 946 Vulpiella and Cutandia (96/95/1.00; Fig. 2; see also Schneider & al., 2012). Desmazeria 947 *sicula* is likely to be a hybrid, which may lead to a name change for this genus, pending 948 further investigation. 949

PPAM clade and Coleanthinae. – The PPAM clade was resolved in all analyses of this
study. It was more strongly supported in the nuclear than the plastid DNA analysis but
obtained maximum support in the combined data tree (see above *Tree of the combined plastid and nuclear DNA dataset*; Figs. 1, 2, suppl. Fig. S1).

- 954 Within the monophyletic subtribe Coleanthinae (= Puccinelliinae), several species 955 were repeatedly transferred from one genus to another and genus limits are still in dispute. 956 Our results support to recognize ten genera, which partly have a new delineation. A close 957 relationship of perennial Colpodium and annual species that usually were treated under 958 Zingeria P.A.Smirn. was suggested by all our trees and had already been noted by Tzvelev & 959 Bolkhovskikh (1965) and Soreng & al. (2017). The tree from the plastid DNA data showed 960 the sampled representatives of *Colpodium* and former *Zingeria* intermingled (Fig. 1), namely 961 C. biebersteinianum (Claus) Röser & Tkach, comb. nov. (type of Zingeria), C. versicolor 962 (Steven) Schmalh. (type of Colpodium), C. trichopodum (Boiss.) Röser & Tkach, comb. nov. 963 [= Z. trichopoda (Boiss.) P.A.Smirn.], C. hedbergii (Melderis) Tzvelev and C. chionogeiton 964 (Pilg.) Tzvelev, both of which occur in Africa and had sometimes been accommodated also 965 under Keniochloa Melderis [type K. chionogeiton (Pilg.) Melderis]. The nuclear DNA tree 966 showed the former Zingeria species in a grade with the other Colpodium species sampled 967 (Fig. 2) as similarly encountered by Kim & al. (2009). If their different life form is left aside 968 there are no striking differences between Colpodium and former Zingeria, both of which have 969 small spikelets with a single bisexual flower, and we suggest unifying them under a single 970 genus. *Colpodium* is the genus with the lowest monoploid chromosome number known in 971 grasses of x = 2. There are known diploids with 2n = 4 (*C. biebersteinianum*, *C. versicolor*) 972 and several polyploids, namely C. trichopodum and C. pisidicum (Boiss.) Röser & Tkach, 973 comb. nov., with 2n = 8 and *C. kochii* (Mez) Röser & Tkach, comb. nov., with 2n = 12. 974 Colpodium versicolor (2x) was shown to be the donor of one genome in allohexaploid C. 975 kochii (Kotseruba & al., 2010), whereas it is not represented in allotetraploid C. trichopodum
- 976 (Kotseruba & al., 2005).
- The nuclear 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 tree supported a deviant relationship of *Hyalopodium* (Figs. 2, 7), namely to *Paracolpodium* and *Hyalopoa* (*H. pontica*). These differences between the plastid and nuclear DNA analyses suggest an origin of *Hyalopodium* as a hybrid between two different lineages of Coleanthinae (Fig. 7). *Hyalopodium araraticum* has formerly been treated under *Catabrosa*, *Colpodium* or *Catabrosella*. It is long-known as

984 remarkable species because of its odd combination of morphological characters and had been 985 placed in a monospecific section of *Catabrosella*, namely *C*. sect. *Nevskia* (Tzvelev) Tzvelev 986 (see Tzvelev, 1976), which seemingly had never been validly raised to genus rank although 987 that was stated by Kim & al. (2008). Hyalopodium araraticum has spikelets with several 988 flowers such as found in Catabrosella and Hyalopoa s.str., has creeping underground shoots 989 like Paracolpodium and Hyalopoa, whereas Catabrosella and Colpodium are not creeping 990 (Tzvelev, 1964a). A conspicuous character of Hyalopodium among Coleanthinae are its aerial 991 shoots with reticulate-fibrous sheaths of dead leaves at the base, which, however, resemble 992 the filamentously, though not reticulately decaying basal leaf sheaths of Hyalopoa pontica 993 (pers. observ.; Mill, 1985). Chromosomally, it has a monoploid number of x = 7 like 994 *Paracolpodium* and *Hyalopoa* (CCBD, 2019), not x = 2 as in *Colpodium*. This makes it likely 995 that the paternal parent of *Hyalopodium* did not come from present-day *Colpodium*, but was 996 an ancestor still having the plesiomorphic monoploid chromosome number of x = 7 (Fig. 7). 997 Paracolpodium altaicum (type of Paracolpodium) and P. baltistanicum clustered 998 together with *Hyalopoa pontica* (type of *Hyalopoa*) in all analysis of this study although with 999 weak support (Figs. 1, 2, 7). Both genera consistently encompass species with creeping 1000 underground shoots in contrast to tufted Colpodium and Catabrosella. Paracolpodium and 1001 *Hyalopoa* also share further morphological characters such as comparatively long glumes, 1002 large lodicules, a caryopsis with a rostrate tip and ay long hilum and the margins of leaf 1003 sheaths fused for more than 1/3 from the base (Tzvelev, 1976, Cope, 1982). The main 1004 difference are the number of florets in the spikelets, which usually have a single but 1005 sometimes an additional sterile floret in *Paracolpodium* or the spikelet is two-flowered with 1006 the lower floret sterile (P. baltistanicum; Dickoré, 1995), whereas Hyalopoa has 3-4 flowered 1007 spikelets.

1008 Catabrosa [type C. aquatica (L.) P.Beauv.] and Catabrosella [type C. humilis

1009 (M.Bieb.) Tzvelev] were well-supported separate genera (see Appendices 1 and 2 for further

1010 species molecularly sampled). In the plastid DNA analyses, both genera formed a sister clade

1011 to *Puccinellia/Sclerochloa*. In the nuclear DNA tree, they were together with

1012 Hyalopoa/Paracolpodium sister to a clade of Puccinellia/Sclerochloa and

1013 Coleanthus/Phippsia as similarly found in other studies (Fig. 7; Rodionov & al., 2008;

1014 Schneider & al., 2009; Soreng & al., 2015b; Nosov & al., 2019). This suggests a reticulation

1015 process within Coleanthinae in way that the *Puccinellia/Sclerochloa* lineage has hybrid

1016 background, namely Coleanthus/Phippsia-like rDNA from its paternal ancestor while its

1017 maternal rDNA from *CatabrosalCatabrosella* was lost.

Monospecific holarctic annual *Coleanthus* [*C. subtilis* (Tratt.) Seidel ex Roem. &
Schult.]) was clear sister to 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.
1, 2, 7), even after inclusion of more species of the latter genus (data not shown; Appendix 2;
Hoffmann & al., 2013; Soreng & al., 2015b).

1028

PAM clade, Avenulinae, Miliinae and Phleinae. – The small subtribes Avenulinae
(*Avenula*), Miliinae (*Milium* L.) and Phleinae (*Phleum* L.) formed together with Poinae and
the elements of the ABCV(+A) clade the PAM clade (~supersubtribe Poodinae). It was
resolved in the plastid DNA and combined data analysis of this study and encompassed also *Avenula pubescens* (Huds.) Dumort., type of the monospecific genus *Avenula* (Fig. 1, suppl.
Fig. S1). The PAM clade was unresolved in the nuclear DNA tree since its subtribes did not
join together in a common clade but stood in a polytomy with Coleanthinae (Figs. 2, 4).

1036 In the plastid and nuclear DNA analyses, monogeneric Miliinae and Avenulinae were 1037 more or less in a polytomy with the remainder of the PAM clade. Considering the plastid 1038 DNA tree (Fig. 1), this applies also to monogeneric Phleinae, in which three species of 1039 Phleum including P. crypsoides (d'Urv.) Hack., the type of Maillea Parl., were sampled. 1040 Phleinae, however, were sister to Poinae with considerable support according to the nuclear 1041 DNA analysis (Figs. 2, 4), which underpins a possible hybrid origin of this lineage. For 1042 Avenula, a suspected intergeneric hybrid (Soreng & Davis, 2000) between Helictotrichon 1043 (Aveninae) and Helictochloa (Helictochloinae), there was no supported incongruence 1044 between the placements in the plastid and nuclear DNA trees. Avenula is unsupported sister to 1045 Coleanthinae in the nuclear DNA tree (Figs. 2, 4), whereas it was part of the PAM clade 1046 resolved only in the plastid but unresolved in the nuclear DNA tree (Figs. 1, 4). The PAM 1047 clade was sister to Coleanthinae, which makes the conflicting placements rather negligible and does not give evidence on hybrid origin of this taxon. In- or exclusion of this taxon did 1048 1049 not fundamentally change the tree structure of the nuclear phylogram for the PPAM clade 1050 such as described by Gillespie & al. (2008) for their ITS analysis. Morphological 1051 characteristics of Avenula also speak against the hybrid hypothesis (Gabriel & al., 2019).

1	052
т	052

1052	
1053	Poinae The monogeneric subtribe Poinae was sampled in this study using a small
1054	selection of species of traditional Poa s.str., namely P. annua L., P. bulbosa L. and the type of
1055	the genus, P. pratensis L. This set of taxa was complemented by a several species of previous
1056	segregate genera that meanwhile were shown to belong to an enlarged but subsequently
1057	monophyletic genus Poa (see Introduction for references). Our results corroborate monophyly
1058	of Poa encompassing P. apiculata Refulio (type of Tovarochloa T.D.Macfarl. & P.But), P.
1059	labillardierei Steud. [type of Austrofestuca (Tzvelev) E.B.Alexeev], P. cyrenaica E.A.Durand
1060	& Barratte (type of Libyella Pamp.), P. fax J.H.Willis & Court (type of Neuropoa Clayton), P.
1061	hitchcockiana Soreng & P.M.Peterson [type of Aphanelytrum Hack.], P. lepidula (Nees &
1062	Meyen) Soreng & L.J.Gillespie (type of Anthochloa Nees & Meyen), P. persica Trin. (type of
1063	Eremopoa Roshev.), P. serpaiana Refulio (type of Dissanthelium Trin.), P. sintenisii
1064	H.Lindb. (type of Lindbergella Bor) and P. diaphora Trin., a second species of former
1065	Eremopoa.
1066	The plastid and nuclear DNA trees were widely congruent and showed sister relations
1067	of P. alpina and P. bulbosa, of P. annua and P. cyrenaica, of P. diaphora and P. persica,
1068	respectively, and the latter two species together with P. sintenisii (corresponding to Poa clade
1069	E in Gillespie & al., 2018) as sister to the remaining species of <i>Poa</i> included in our study
1070	(Figs. 1, 2). Nevertheless, there were some differences between the plastid and nuclear
1071	analyses. The nuclear DNA tree (Fig. 2), for example, revealed a supported sister relation
1072	between P. labillardierei and P. fax or between P. apiculata and P. hitchcockiana,
1073	respectively, whereas the plastid DNA tree placed them, along with others, in a polytomy
1074	(Fig. 1).
1075	

1076 *ABCV(+A) clade.* – This clade contains many monospecific or species-poor genera,
 1077 *Alopecurus* with ~40 species being the largest genus. *Arctopoa* joined this clade only in the
 1078 nuclear and combined analyses, whereas it was placed outside of it in the plastid DNA tree
 1079 and close to subtribe Poinae (see above *Comparison of the plastid and nuclear DNA trees*).

1080 Relationships within the ABCV(+A) clade were overall weekly resolved, except for
1081 well-supported monophyletic subtribe Ventenatinae, which was retrieved in all analyses. Our
1082 results support to abandon *Gaudinopsis* (Boiss.) Eig as monospecific genus [*G. macra*1083 (Steven ex M.Bieb.) Eig] distinct from *Ventenata* Koeler [type *V. dubia* (Leers) Coss. &
1084 Durieu]. Monospecific *Parvotrisetum* Chrtek [*P. myrianthum* (Bertol.) Chrtek] was clearly

1085 excluded from *Trisetaria*, a member of distantly related subtribe Aveninae. The monospecific

1086 genus Nephelochloa Boiss. (N. orientalis Boiss.) was sister to Apera Adans. [type A. spica-1087 venti (L.) P.Beauv.] in the nuclear analyses (Fig. 2; Hoffmann & al., 2013). With regards to 1088 the plastid DNA (Fig. 1), N. orientalis was even nested within the two species sampled of 1089 Apera (altogether ~5 species). Also morphologically, both genera share certain characters 1090 (usually richly branched inflorescences with numerous primary branches in whorls, similar 1091 shape of glumes and lemmas). The main difference is the number of flowers in the spikelets, 1092 one in Apera and three to six in Nephelochloa, which supports to maintain them as separate 1093 genera.

1094The HSAQN clade was well-supported only in the trees of the nuclear and combined1095DNA data, such as the DAD clade (Fig. 2, suppl. Fig. S1). The former is biogeographically1096characterized by bipolar distribution. *Arctagrostis* Griseb. [two species; type *A. latifolia*1097(R.Br.) Griseb.] is distributed in the boreal and arctic regions of the northern hemisphere,1098whereas the remaining taxa of the HSAQN clade occur in Australasia and southern South1099America.

1100 The taxa of DAD clade also occur in the boreal and the arctic regions of the northern 1101 hemisphere. The new genus Arctohyalopoa was nested in the nuclear and combined analyses 1102 within this clade (Fig. 2, suppl. Fig. S1), whereas the plastid DNA tree placed it along with many other taxa in the large polytomy of the ABCV clade (Fig. 1). Arctohyalopoa comprises 1103 1104 only A. lanatiflora (Roshev.) Röser & Tkach, comb. nov., which previously has been 1105 accommodated in the genus Hyalopoa together with H. pontica (Balansa) Tzvelev, the type of 1106 Hyalopoa, and few other species. Arctohyalopoa lanatiflora was not nested in the clade of 1107 Coleanthinae but in the ABCV or ABCV+A clade, respectively, in which it was part of a 1108 polytomy with many other taxa according to the plastid DNA data. It belongs to the DAD 1109 clade according to the nuclear and, with strong support, according to the combined DNA data 1110 along with Dupontia R.Br. (type D. fisheri R.Br.), which includes Arctophila (Rupr.) 1111 Andersson [type A. fulva (Trin.) Andersson] (see below New names and combinations), and 1112 with monospecific *Dupontiopsis* Soreng, L.J.Gillespie & Koba [D. hayachinensis (Koidz.) 1113 Soreng, L.J. Gillespie & Koba; Figs. 2, 3, suppl. Fig. S1]. This placement of Arctohyalopoa 1114 lanatiflora distant to Coleanthinae was verified in this study also by analyzing a second 1115 accession (data not shown; Appendix 1). In should be noted that our previously published 1116 sequence of Hyalopoa lanatiflora (Döring & al., 2007; Döring, 2009) is wrong such as seemingly a sequence of Rodionov & al. (2008), which was also used by Hoffmann & al. 1117 1118 (2013; for details see Appendix 3).

1119 The molecular phylogenetic results on Arctohyalopoa were supported also by 1120 morphological data because as pointed out by Tzvelev (1964a: 8) and (1964b: 14–15), A. 1121 *lanatiflora* [= *Colpodium lanatiflorum* (Roshev.) Tzvelev] differs from both the other species 1122 of *Colpodium* subg. *Hyalopoa* Tzyeley (\equiv *Hyalopoa*) as well as *Poa* by "lemmas ... on basal 1123 half especially on nerves with rather copious and long pubescence, with distal part of callus 1124 (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 1125 1126 lanatiflora refers to the conspicuous indumentum of the lemmas. Tzvelev (1964c, 1995b) also 1127 addressed that A. lanatiflora otherwise strikingly resembles Dupontia fulva (\equiv Arctophila 1128 *fulva*). Moreover, Arctohyalopoa lanatiflora is geographically separated as an eastern 1129 Siberian endemic from the species of *Hyalopoa*, which are Caucasian (5 species) and West 1130 Himalayan [only *H. nutans* (Stapf) E.B.Alexeev ex T.A.Cope] in distribution. It seems to be 1131 also ecologically different due to its preference of non-carbonatic bedrock (Tzvelev, 1964c, 1132 1995b). 1133 Merging the small genera *Dupontia* und *Arctophila* as already suggested by Kellogg

1134 (2015) was supported also by Hoffmann & al. (2013), who showed that the nuclear ITS 1135 sequences of both were intermingled in the molecular phylogenetic tree. It further agrees with 1136 their overall morphological similarity except for rather small difference in the shape of their 1137 lemmas (Clayton & Renvoize, 1986; Cayouette & Darbyshire, 2007a,b; see also Brysting & al., 2004) and the occurrence of hybrids between D. fisheri and D. fulva (Trin.) Röser & 1138 1139 Tkach, comb. nov. that were formerly regarded as intergeneric hybrid and treated under the 1140 nothogenus ×Arctodupontia Tzvelev (Tzvelev, 1973; Brysting & al., 2003; Darbyshire & 1141 Cayouette, 2007).

1142 Tribes Alopecurinae, Beckmanniinae and Cinninae in each case did not resolve as 1143 monophyletic. The species of *Limnas* Trin. sampled (type *L. stelleri* Trin. and *L. malyschevii* 1144 O.D.Nikif.) formed in none of the analysis (plastid, nuclear, combined data) a clade with the 1145 other species of Alopecurinae (*Alopecurus aequalis* Sobol., *Cornucopiae cucullatum* L., type 1146 of *Cornucopiae*). In the nuclear tree they even were closer to the DAD clade (73/94/1.00) than 1147 to *Alopecurus* and *Cornucopiae* (Fig. 2). The latter genera were always sister, which agrees 1148 with their common spikelet structure.

Beckmannia [type B. eruciformis (L.) Host] and monospecific Pholiurus [P.
pannonicus (Host) Trin.] were well-supported sister in the nuclear DNA tree in agreement
with Hoffmann & al. (2013) but less supported in the plastid DNA tree (Figs. 1, 2). *Rhizocephalus orientalis*, type of monospecific genus *Rhizocephalus* Boiss. and the third

1153 taxon of the tribe Beckmanniinae as delineated by Soreng & al. (2017), was placed in all 1154 analyses remotely from *Beckmannia* and *Pholiurus* in the main polytomy of ABCV(+A) 1155 clade. Spikelets in Alopecurus, Cornucopiae, Limnas and Rhizocephalus are single-flowered, 1156 in Beckmannia (the upper staminate) and Pholiurus two-flowered (Schneider & al., 2012). 1157 Also the Cinninae genera sampled [Aniselytron with type A. treutleri (Kuntze) Soják, 1158 Cinna L., monospecific Cyathopus Stapf with C. sikkimensis Stapf, Simplicia Kirk], appeared 1159 in the main polytomy of ABCV(+A) clade, except for Cinna and Cyathopus, which were supported sister in the nuclear and combined trees. Both share spikelets that are falling entire, 1160 1161 whereas Aniselytron and Simplicia have spikelets disarticulating above the glumes. In all 1162 Cinninae genera, the spikelets are single-flowered, with occasional occurrence of a second 1163 floret reported for Simplicia (Watson & al., 1992 onwards; Edgar & Connor, 2000). 1164 Notwithstanding the established sister relations of each Beckmannia/Pholiurus and 1165 Alopecurus/Cornucopiae, the phylogenetic relationships of all genera of Alopecurinae, Beckmanniinae and Cinninae and the delineation of these tribes certainly warrant future work. 1166 1167 Monospecific Limnodea (L. arkansana), sometimes placed near or included within 1168 Cinna (Clayton & Renvoize, 1986; Tucker, 1996), was placed very distant to this genus in the 1169 molecular trees, namely within Aveninae and close to Sphenopholis (Figs. 1, 2) within the 1170 Koeleriinae lineage (see also Döring, 2009; Hochbach & al., 2015; Saarela & al., 2017: suppl. 1171 7). 1172 Brizochloa humilis with lemmas that are not cordate as in Briza or Macrobriza and 1173 upright pedicels of the spikelets is a morphologically most striking species of the ABCV(+A) 1174 clade. Monospecific genus Brizochloa cannot be accommodated under any of the subtribes 1175 vet described and we assign it to a new monogeneric subtribe, Brizochloinae. The exclusion 1176 of B. humilis, an annual distributed from the Eastern Mediterranean to Iran, from Briza had 1177 been suggested already by previous morphological and molecular studies (Jirásek & Chrtek, 1178 1967; Tzvelev, 1968, 1976; Hoffmann & al., 2013; Persson & Rydin, 2016; Essi & al., 2017).

1179

Morphological characteristics. — The sequence of the following examples of morphological characteristics is character no., character state in brackets, whereby character states with an underline mean the occurrence of different character states in a single taxon. This instance appears in suppl. Fig. S2 as a pie chart. If more than one character was found within a lineage, the character states are given in alphabetical order. If character state (b) is more frequent than (a), it is mentioned first (for example, b, a).
1186	Several morphological characters listed in suppl. Appendix S2 displayed states that
1187	were almost consistently found in most lineages retrieved in the molecular phylogenetic
1188	analyses: 002 (a), 027 (d), 028 (a), 029 (a), 038 (d), 039 (a), 040 (b), 041 (b), 043 (b), 045 (a),
1189	046 (c), 047 (b), 053 (b), 054 (a), 055 (b), 058 (c), 060 (a), 061 (a), 062 (a), 063 (a), 064 (a),
1190	066 (a), 069 (e), 071 (a), 072 (a), 083 (a), 084 (a), 092 (a), 103 (c), 112 (a), 115 (a), 116 (a),
1191	117 (a), 118 (a), 122 (a, b), 123 (a, b), 124 (a), 126 (a, b), 127 (c), 139 (a), 140 (a), 142 (a),
1192	145 (a), 151 (a), 156 (b), 159 (b), 160 (b, a), 161 (a, a_b) and 164 (a), 169 (d), 176 (a), 181
1193	(c), 182 (b, a), 183 (b, a), 184 (a), 185 (a), 187 (a, b; see suppl. Fig. S2).
1194	Some lineages were characterized by particular character states such as
1195	Anthoxanthinae: 57 (b_c), 126 (a_b), 138 (d); Aveninae: 165 (a_e); Phalaridinae: 45 (f);
1196	Calothecinae 165 (f), 167 (f); Airinae: 146 (a_d); Dactylidinae: 36 (e); Cynosurinae: 27 (d_g),
1197	45 (b_c), Parapholiinae 28 (c), 57 (b_c), 59 (d), 73 (c), 74 (c), 102 (b_c); Coleanthinae 136
1198	(a_g); Miliinae 16 (c_d), 167 (g); Phleinae 31 (c), 115 (c), (136 (a_g), 127 (b_c); Poinae 119
1199	(b); Beckmanninae 28 (c) and Alopecurinae 50-52 (a), 119 (b_c), 122 (b). Antinoriinae
1200	differed from Airinae and Helictochloinae in characters 2, 20, and 119 but also 14 and 74
1201	through which they resembled rather Loliinae. Helictochloinae differed from Airinae and
1202	Antinoriinae in characters 41, 73, 125, 149 and 188. Agrostidinae differed from
1203	Hypseochloinae in characters 85, 102, 125, 138, 139, 171. Within the ABCV+A clade the
1204	placement of Rhizocephalus was not unambiguously ascertainable. Its inclusion within
1205	Beckmanniinae was supported by characters 17, 18, 24, 26, 48, 50, 52, 124 and possibly 56,
1206	whereas affinities to Brizochloinae were suggested by characters 28, 58, 70, 74, 89 and 122.
1207	Characters 29 and 30 underscored the unique inflorescence shape of Rhizocephalus.
1208	On a whole the number of clear-cut synapomorphic characters that could be used to

1209 characterize the retrieved clades in terms of phylogenetic systematics was rather low, which 1210 points to a high degree of homoplasy in most morphological characters that were scored. 1211 None of the major lineages such as tribes Aveneae and Poeae, supersubtribes Agrostidodinae, Loliodinae and Pooidinae (~PAM clade), the PPAM clade and also larger subtribes such as 1212 1213 Aveninae, Loliinae or Coleanthinae were morphologically reliably identifiable. Some 1214 characters revealed identifiable clades corresponding to subtribes but frequently the number 1215 of suitable characters was rather low: Agrostidinae: 50 (a), 52 (a), 74 (mostly c); Airinae: 148 1216 (d); Alopecurinae: 50 (a), 51 (a), 52 (a), 58 (b), 148 (d), 169 (b_d); Anthoxanthinae: 50 (a), 51 1217 (a), 52 (a), 115 (c), 138 (d), 139 (b); Calothecinae: 1 (b), 118 (b), 165 (f), 167 (f), 182 (a); 1218 Coleanthinae: 9 (a); Dactylidinae: 36 (e); Helictochloinae: 24 (c), 49 (b), 125 (c), 150 (c), 186

1219 (c); Holcinae: 96 (b); Phalaridinae: 45 (a_f), 59 (d), 84 (a_b), 101 (a_b), 115 (c), 165 (c), 169

- 1220 (a) and Scolochloinae: 72 (b).
- 1221 Smaller groups of genera sharing common characters could be discerned within
- 1222 several subtribes, for example, *Coleanthus* and *Phippsia* within Coleanthinae: 182 (a);
- 1223 Parvotrisetum and Ventenata: 148 (d), 150 (c), 155 (c) or Alopecurus and Cornucopiae within
- 1224 Alopecurinae: 137 (a_b, b), 181 (a).
- 1225 Single genera representing monogeneric subtribes were frequently identifiable based
- 1226 on (aut-)apomorphic attributes: Ammochloinae (*Ammochloa*): 31 (e), 59 (d), 84 (a_b), 136
- 1227 (a_f) and 184 (a_c); Antinoriinae (*Antinoria*): 2 (b), 24 (c), 186 (a); Cynosurinae (*Cynosurus*):
- 1228 45 (b_c); Hypseochloinae (*Hypseochloa*): 76 (d), 83 (b), 100 (b), 153 (b), 171 (b); Miliinae
- 1229 (*Milium*): 54 (c), 90 (b), 167 (g), 169 (a) and Phleinae (*Phleum*): 31 (c), 84 (a_b), 124 (b), 127
- 1230 (b_c), 136 (a_g), 175 (c).
- Macrobriza maxima shared a number of characters with Brizinae, the subtribe which provided one of its ancestors: 54 (a_b), 118 (a_b_c), 136 (a_f), 138 (a_c), 140 (a_b). In other characters *Macrobriza* deviated from Brizinae, for example, 24 (c), 142 (d_e), 171 (a_b), 175 (a_c), which supports its hybrid origin as disclosed by molecular phylogenetics.
- 1235
- Ancestral state reconstruction. Ancestral state reconstructions applied for 74 nonmolecular characters (described in suppl. Appendix S2) of the taxa of Poodae studied are
 visualised in suppl. Appendix S3 and, exemplarily for character 50, in Fig. 8. The ancestral
 character states of supertribe Poodae (tribes Aveneae and Poeae) were:
- 1240 perennial life form (character 1) with a conspicuous transition to annual life cycle
- 1241 within Aveneae especially in Agrostidinae and within Poeae in Parapholiinae, most
- 1242 Ventenatinae, some Airinae, Loliinae and Poinae;
- absence of rhizomes (character 4) with secondary development of rhizomatous speciesin many lineages;
- 1245 ligule an eciliate membrane (character 12);
- flat leaves (character 17) with secondary development of conduplicate, involute andconvolute vernation in many lineages;
- 1248 inflorescence an open panicle (characters 28 and 31) with a transition to contracted
- 1249 panicle or even more condensed, spike-like or glomerate inflorescence within Aveneae
- 1250 especially in Aveninae (prevalently the lineage of Koeleriinae), Phalaridinae and parts of
- 1251 Agrostidinae, within Poeae in Aristaveninae, Dactylidinae and Phleinae. Capitate

inflorescences originated within some Poeae, namely in Sesleriinae, Ammochloinae and somemembers of the ABCV+A clade;

panicles with many spikelets (character 35) and reduction to few spikelets in many
lineages, within Aveneae especially in some Aveninae and Agrostidinae, within Poeae in
some Loliinae, many Parapholiinae and Coleanthinae;

panicle branches at most moderately divided (character 38); flexible (character 41).
Stiff branches originated infrequently (e.g., in Parapholiinae), whereas capillary branches
were frequent in Airinae and Coleanthinae. In Airinae, such capillary branches were likely to
be the original character state, whereas in Coleanthinae flexible branches appeared to be
plesiomorphic;

panicle branches smooth (character 42), whereas scaberulous or scabrous branchesdeveloped multiple times in parallel;

spikelets pedicelled (characters 46 and 47), whereas sessile spikelets developed
multiple times and less frequently in Aveneae (some Aveninae, especially *Koeleria*, and
Phalaridinae) than within Poeae (in Loliinae two times in parallel, CP clade, parts of
Coleanthinae);

1268 spikelets with >3 fertile florets, which had higher probability for Poodae than spikelets 1269 with 2–3 florets or 1 floret (character 50; Fig. 8). Spikelets with 1 floret had the highest 1270 probability to be ancestral in Aveneae as a whole and were most likely ancestral within 1271 Agrostidodinae and Agrostidinae, whereas spikelets with 2–3 florets were seemingly ancestral 1272 in Aveninae. Within 1-flowered Agrostidodinae, Calothecinae have seemingly secondarily 1273 developed spikelets with >3 florets. In Poeae, spikelets with >3 florets, followed by spikelets 1274 with 2–3 spikelets appeared to be the most probable ancestral state. Spikelets with 1 floret 1275 have developed secondarily within parts of Parapholiinae but, significantly, seem to be 1276 plesiomorphic in the entire PPAM clade, in which a transition to 2-3 or 3-flowered spikelets 1277 occurred secondarily in Poinae and most parts of the ABCV+A clade, except for 1278 Alopecurinae, Cinninae and some others;

spikelets with a rhachilla extension bearing a sterile florets at the apex were slightly
more likely than a barren rhachilla extension or a missing rhachilla extension (character 51).
For Aveneae, a barren rhachilla extension was the most likely ancestral state, which applies
also for Aveninae and Agrostidinae but parts of Echinopogoninae and Agrostidinae and *Airopsis* of Brizinae showed an obviously secondary loss of the rhachilla extension, whereas
absence of a rhachilla extension was the plesiomorphic character state in the anyway strongly
modified spikelets of Anthoxanthinae and Phalaridinae. For Poeae, a rhachilla extension

bearing a sterile floret at the apex was the most likely ancestral state and was present also in

- 1287 most Loliinae, Poinae and the ABVC clade. The reconstruction was ambiguous for the large
- 1288 PPAM clade, because this character state was equally likely to be ancestral than the absence
- 1289 of a rhachilla extension as found in Antinoriinae, most Coleanthinae (except
- 1290 Puccinellia/Sclerochloa), Miliinae, Alopecurinae, most Beckmanniinae and Cinninae;
- 1291 spikelets with 2 or more fertile florets, which was likewise ancestral for both Aveneae 1292 and Poeae (character 52). Within Aveneae, spikelets with only 1 fertile floret originated in 1293 Anthoxanthinae and Phalaridinae and might be the plesiomorphic state in supersubtribe 1294 Agrostidodinae, which means that Brizinae and Calothecinae were characterized by a reversal to the ancestral state of Aveneae or Poodae as a whole with 2 or more fertile florets. Within 1295 1296 Poeae, the transition to spikelets with only 1 fertile floret occurred infrequently in some 1297 Loliinae, some Coleanthinae (especially *Colpodium* and the lineage of *Coleanthus/Phippsia*), 1298 Miliinae and Phleinae. The situation was less clear in the ABCV+A clade, in which 2 or more 1299 fertile florets versus 1 fertile floret were almost equally likely as ancestral states. In the former 1300 instance, the presence of only 1 fertile floret in Alopecurinae, Beckmanniinae, Cinninae and 1301 some Ventenatinae (Apera) would be a derived character state;
- 1302

the lowermost flower in the spikelet not male or barren (character 53);

- spikelets laterally and at most moderately compressed (characters 54 and 55); terete or
 dorsally compressed spikelets in only few lineages (Brizinae, *Holcus*, some Loliinae, *Colpodium* p.p., Miliinae);
- comparatively large spikelets of either 4–6 mm or >6 mm in length with almost equal
 probability. This applied also to be the ancestral state in Aveneae, whereas a length of 4–6
 mm is more likely in Poeae (character 57). For Aveninae, the larger size of >6mm was most
 likely ancestral, with a seemingly secondary diminution in the American lineage of *Limnodea/Peyritschia/Sphenopholis* and the supersubtribe Agrostidodinae, in which
 especially Agrostidinae underwent a reduction to <3 mm. Secondary downsizing was likely
- 1312 also for Airinae, Antinoriinae, a part of Coleanthinae (Coleanthus, Colpodium, Phippsia) and
- 1313 some representatives of the ABCV+A clade, namely within Cinninae and Ventenatinae
- 1314 (especially *Apera* and *Parvotrisetum*);
- 1315 spikelets breaking up at maturity (character 58). Spikelets falling entire appeared
- 1316 occasionally and in various lineages, namely Aveninae (Gaudinia, Limnodea, Sphenopholis),
- 1317 Holcinae (Holcus), Loliinae, Parapholiinae (Parapholis), and especially Cinninae,
- 1318 Beckmanniinae and Alopecurinae;

spikelets, which disarticulate below each floret (character 61), but with few exception
in Aveninae, Parapholiinae, Alopecurinae and Ventenatinae; rhachilla internodes that are not
thickened (character 63) but with sporadic exceptions in various groups; glumes persistent on
branch, if spikelet breaks up (character 71) but with sporadic exceptions in Aveninae,
Agrostidinae, Holcinae, Parapholiinae, Coleanthinae and the ABCV+A clade; similar glumes
but with sporadic exceptions in Aveninae and Agrostidinae and especially Scolochloinae
(character 72);

glumes shorter than spikelet, which applied also for tribes Aveneae and Poeae as a
whole, respectively, but not for Aveninae, in which the longer glumes reaches or exceeds the
length of the spikelet (character 73). The latter applied also to Agrostidinae, whereas
Torreyochloinae, most Brizinae and Calothecinae have kept the ancestral state of shorter
glumes. Within Poeae, there was a comparatively rare trend to longer glumes discernable,
namely in Airinae, some Parapholiinae and Coleanthinae, Miliinae and few members of the
ABCV+A clade (Alopecurinae, Cinninae);

1333 glumes in consistency thinner than the lemma or similar (character 74). Both states 1334 were equally probable for Poodae, but thinner glumes were ancestral for Aveneae, whereas 1335 similarly firm glumes and lemmas are ancestral in Poeae. Within Agrostidodinae, there was a 1336 transition to firmer glumes in Calothecinae and especially Agrostidinae. Within Poeae, a 1337 similar consistency of glumes and lemmas prevailed by far, but there were firmer lemmas in 1338 Scolochloinae, Avenulinae and Miliinae, Helictochloa (Helictochloinae), a part of 1339 Parapholiinae, Poinae and Ventenatinae, whereas the opposite, i.e., glumes firmer than 1340 lemmas, also occurred, namely in Parapholis, some Loliinae and Beckmanniinae;

lower glume 3–6 mm long (character 78), with a sporadic trend to diminution, namely
within Aveneae in Aveninae (especially Koeleriinae clade A; Fig. 5) and Calothecinae, within
Poeae in *Molineriella* (Helictochloinae), Aristaveninae, parts of Airinae, Sesleriinae and
Ventenatinae (*Apera, Bellardiochloa* Chiov., *Nephelochloa*), in Antinoriinae and

1345 Coleanthinae. The opposite, namely enlargement of glumes, was infrequently found.

1346 Examples were some Aveninae and Agrostidinae (*Calamagrostis* s.str.), South American

1347 members of Loliinae and a few members of the ABCV+A clade;

lower glume 0.6-fold to as long as the upper, with shortening as well as enlargement
sporadically encountered in various groups (character 79); of similar consistency on margins
or margins much thinner in several groups (character 81); 1-keeled, with sporadic transition to
unkeeled shape in various groups (character 82); keeled all along, with sporadic transition to
keeled only above or below in various groups (character 83); 1-veined, with rare transition to

1353 either veinless (few Coleanthinae) and infrequent to \geq 3-veined, namely in some Aveninae, 1354 Phalaridinae, Brizinae, Calothecinae, Helictochloa (Helictochloinae), Antinoriinae, most 1355 Parapholiinae, Miliinae, Phleinae and the majority of Ventenatinae, in which this character 1356 state might have even been plesiomorphic (character 85); primary vein eciliate (character 87); 1357 without lateral veins and infrequent presence of distinct lateral veins in Anthoxanthinae, some 1358 Aveninae, Calothecinae, Helictochloa (Helictochloinae), some Loliinae and the majority of 1359 Ventenatinae, in which this character state might have been plesiomorphic (character 88), are 1360 the ancestral states, respectively;

1361 upper glume 3–6 mm long (character 95), with occasional diminution comparable to 1362 the lower glume (character 78) occurring within Aveneae in some Aveninae, Calothecinae 1363 and Agrostidinae, within Poeae in Molineriella (Helictochloinae), parts of Airinae, Sesleriinae 1364 and Ventenatinae (Apera, Bellardiochloa, Nephelochloa) as well as in Antinoriinae and 1365 Coleanthinae. Enlargement of glumes occurred in most Aveninae, in which this character 1366 appeared to be the plesiomorphic state, within Poeae in *Helictochloa* (Helictochloinae), South 1367 American members of Loliinae (Festuca berteroniana, F. floribunda, F. masatierrae) and 1368 some members of the ABCV+A clade (Arctopoa, Hookerochloa E.B.Alexeev, Pholiurus, 1369 etc.).

1370 uncertain considering the length relation of upper glume and adjacent lemma 1371 (character 96). The upper glume shorter than the lemma was the most likely ancestral state in 1372 Aveneae and Aveninae, in which most of the Koeleriinae lineage, few members of the 1373 Aveninae s.str. lineage, Calothecinae and some Echinopogoninae showed a secondary 1374 transition to shorter glumes. The upper glume shorter than the adjacent lemma was, by 1375 contrast, the most likely ancestral state in Poeae, with a secondary change to longer glumes in 1376 Holcinae, Airinae, Antinoriinae, Parapholis (Parapholiinae), Avenulinae, Miliinae, some 1377 Beckmanniinae and Ventenatinae:

1378 upper glume with undifferentiated margins (character 98) and sporadic transition to 1379 hyaline, membranous or scarious margins in various lineages of both Aveneae as well as 1380 Poeae; 1-keeled, with sporadic transition to unkeeled shape in various groups (character 99); 1381 keeled all along, with sporadic transition in various lineages to keeled only below (some 1382 Coleanthinae) or above (character 100); 3-veined, with transition to 1-veined within Aveneae 1383 in most Agrostidinae (probably plesiomorphic in this subtribe), within Poeae in Sesleriinae, 1384 Ammochloinae, some Coleanthinae; with transition to \geq 5-veined within Aveneae in some 1385 Aveninae, Phalaridinae, Brizinae, within Poeae in some Helictochloinae (partly in 1386 *Helictochloa*), Loliinae and sporadically within the ABCV+A clade (character 102); primary

1387 vein distinct (character 103); primary vein smooth but in several lineages transition to 1388 scaberulous or scabrous, especially within Aveneae in a part of Aveninae, namely Koeleriinae 1389 clade A (Fig. 5), in Phalaridinae, Brizinae, Hypseochloinae, Echinopogoninae, Agrostidinae, 1390 and within Poeae only in Antinoriinae, Ammochloinae, Poinae and most of the ABCV+A 1391 clade except for the DAD clade (character 104); lateral veins distinct but absent in some 1392 Echinopogoninae, Agrostidinae, Sesleriinae, sporadically in Loliinae and Coleanthinae 1393 (character 106); upper glume muticous (absence of awns), but seemingly secondarily 1394 mucronate or awned in several lineages, namely in Aveninae, Echinopogoninae 1395 (*Pentapogon*), Sesleriinae, some Loliinae, Parapholiinae and Phleinae (character 114); 1396

spikelets without basal sterile florets (character 115) but present in Anthoxanthinae
and Phalaridinae and, as a rare exception, in Aveninae (*Arrhenatherum*); fertile florets (if
more than 1) all alike, with occasional exceptions, especially Holcinae and *Ventenata*(character 116);

1400 lemma 1.6–4 mm, which was slightly more likely than >4mm long (character 119), 1401 which applied also for both Aveneae and Poeae. Nevertheless, the latter is the ancestral state 1402 in Aveninae (Figs. 9E,M,N, 10I, 11I,K,L) most likely also in Echinopogoninae (Fig. 11C; all 1403 Aveneae) and, within Poeae in Scolochloinae, probably in Helictochloinae (Fig. 10H), 1404 Aristaveninae (Fig. 9H), Loliinae (Fig. 11A), and some lineages within the ABCV+A clade 1405 (Arctopoa, HSAQN clade and Ventenata; Figs. 9K,11H). A diminution to 1.5 mm was found 1406 within Helictochloinae, in which it occurred apparently secondarily in *Molineriella* and within 1407 Coleanthinae, namely in *Coleanthus* and *Phippsia*;

1408 lemma without keel (character 122), which was the ancestral state also for both 1409 Aveneae and Poeae but transition to keeled occurred within Aveneae in Koeleriinae clade A 1410 (Figs. 5, 10G), Phalaridinae and Calothecinae, within Poeae in parts of Loliinae and 1411 Parapholiinae, in the PPAM and, even more, in the PAM clade (~supersubtribe Poodinae), in 1412 which keeled lemmas (Fig. 11B,F,L) were seemingly the ancestral state. This implies that the 1413 unkeeled lemmas in parts of Beckmanniinae and Ventenatinae (Figs. 9K,11H) were most 1414 likely a reversal within the PAM clade to the original character state of the whole Poeae and 1415 Poodae;

lemma with 4–5 veins (characters 125, 126), which was the ancestral state also of both
Aveneae and Poeae but transition to >5 veins occurred within Aveneae in Aveninae (in
Aveninae s.str. and parts of Koeleriinae), Hypseochloinae and parts of Brizinae, within Poeae
in Helictochloinae, Ammochloinae, Phleinae and parts of Loliinae. Diminution to 1–3 veins

such as found in some Aveninae (parts of Koeleriinae), Agrostidinae, Parapholiinae,

1421 Coleanthinae and the DAD clade was encountered more rarely;

1422 lemma surface generally rough (character 133) with sporadic exceptions, such as in Sesleriinae (Fig. 11M) and others (Figs. 9C,L, 10A, 11D,F,J,L); general extent of hairiness all 1423 1424 along (character 134; Figs. 9F,M, 11K) with occasional secondary restriction to hairiness 1425 above (Fig. 10E,L) or in the middle to below (frequent in many lineages); 1426 lemma apex erose or dentate (character 143). Entire lemma apices occurred 1427 occasionally in various groups but were frequent in Loliinae and especially in supersubtribe 1428 Poodinae (except for Avenula; Fig. 9J), in which it seemed to be the plesiomorphic state; 1429 lemma apex mucronate to awned (character 146), which was the ancestral state also of 1430 both Aveneae and Poeae. Within Aveneae, there were occasional transitions to muticous 1431 apices (for example, Anthoxanthinae, few Aveninae, Agrostidinae; Fig. 9A, 10G). Within 1432 Poeae, muticous apices seemed to be plesiomorphic for the PPAM clade (Fig. 11B) with a reversal to mucronate/awned lemma apices in some Poinae and members of the ABCV+A 1433 1434 clade such as Alopecurinae (Fig. 9I) and especially Ventenatinae (Figs. 9L, 11H); 1435 apical awns were the ancestral state of both Aveneae and Poeae (character 148). 1436 Within Aveneae, the characteristic dorsal awns of Aveninae (Figs. 9M, 10I, 11I,K,L) and 1437 Agrostidinae (Figs. 9A,C,O, 10D,F) as well as of Hypseochloinae (Hypseochloa) and 1438 Amphibromus (Torreyochloinae; Fig. 9E) seemingly were derived secondarily and in parallel, 1439 moreover, this seemed to be the plesiomorphic state of Aveninae and Agrostidinae. Within 1440 Poeae, the dorsal awns occurred secondarily in Helictochloinae (Fig. 10H), Aristaveninae 1441 (Fig. 9H), Holcinae (Fig. 10K), Airinae (Figs. 9D, 10C), Alopecurinae (Fig. 9I) and some 1442 Ventenatinae (Fig. 11H). Due to the unresolved relationships of the former four subtribes, it 1443 remains unclear, if this transition occurred only once in their putative common ancestor or 1444 multiple times in parallel. Considering Ventenatinae, the occurrence of the apical awns 1445 present in Apera (Fig. 9L), Bellardiochloa and Nephelochloa might have been a character 1446 reversal to the ancestral state in Poeae and Poodae, if dorsal awns had been the plesiomorphic 1447 character state for Ventenatinae; 1448 principal lemma awn (if present) straight, which was the ancestral state also for both 1449 Aveneae and Poeae (character 150), and secondary transition to geniculately bent shape 1450 within Aveneae in Aveninae (Figs. 9M, 10D,F,I, 11E,G,I,K,L; note a reversal to straight awns 1451 in parts of the Koeleriinae lineage), in Torreyochloinae (Amphibromus; Fig. 9E), 1452 Hypseochloinae, Echinopogoninae (Fig. 11C) and Agrostidinae (Fig. 9A,C,O), within Poeae

1453 in Helictochloinae (Fig. 10H), Airinae (Figs. 9D,H, 10C; with an apparent reversal in awned

specimens of *Periballia* Trin.), Avenulinae (Fig. 9J) and some members of Ventenatinae (Fig.
11H); geniculate awns mostly clearly exserted from spikelets, whereas straight awns were not
or scarcely exserted (character 154);

principal lemma awn not coloured, whereas coloured awns seemed to occur
sporadically and secondarily, namely within Aveneae in parts of Aveninae, Echinopogoninae
and Agrostidinae, within Poeae in Helictochloinae, Airinae, more rarely in Loliinae and
Poinae (character 156);

absence of a distinct column of the lemma awn, which was the ancestral state also for
Aveneae and Poeae; acquisition of distinct columns (character 155) was seemingly linked
with the origin of dorsal awns (as described before). Distinctness of columns was secondarily
lost especially in parts of the Aveninae, namely some members of the Koeleriinae lineage,
and Agrostidinae;

1466 column of lemma awn not twisted, which was the ancestral also for both Aveneae and1467 Poeae (character 160), whereas twisted columns originated within Aveneae in Aveninae (Figs.

1468 9M,O, 10D,F,I, 11E,G,I,K,L) for which they were seemingly plesiomorphic, including a

1469 reversal to untwisted columns in some members of the Koeleriinae lineage and some

1470 Agrostidinae, in which twisted columns (Figs. 9A,C) were most likely plesiomorphic.

1471 Twisted columns evolved within Poeae also repeatedly in parallel, namely within

1472 Helictochloinae (Fig. 10H), Aristaveninae, Airinae (Fig. 9D,H), Avenulinae (Fig. 9J), some

1473 Alopecurinae (Fig. 9L) and Ventenatinae (Ventenata, Parvotrisetum; Fig. 11H);

1474 column of lemma awn (if present) transversally not flattened (character 159), whereas

1475 flattened columns occurred sporadically, namely in some Aveninae, Agrostidinae (Fig. 9C),

1476 Helictochloinae (Helictochloa; Fig. 10H), Alopecurinae (Alopecurus; Fig. 9I) and

1477 Ventenatinae (Ventenata; Fig. 11H);

1478 lateral lemma awns absent (character 161). Lateral lemma awns originated

1479 occasionally but not consistently in various lineages, e.g., Aveninae (Figs. 10I, 11I),

1480 Echinopogoninae (Fig. 11C), Sesleriinae (Fig. 11M), Coleanthinae, Poinae and the ABCV+A1481 clade;

1482palea ≥0.7-fold longer than the lemma (character 166) and with smooth keels1483(character 172). Shorter or missing paleas as well as scaberulous or scabrous palea keels

1484 originated sporadically and inconsistently in many lineages;

1485 eciliate palea keels, which was the ancestral state also for both Aveneae and Poeae
1486 individually (character 173). Puberulous, pubescent, ciliolate or ciliate palea keels originated
1487 in many lineages, within Aveneae especially in Aveninae, in which this might be the

1488 plesiomorphic character state of Aveninae s.str., within Poeae especially in Sesleriinae,

1489 Poinae and some Coleanthinae;

1490 apical sterile florets (if present) resembling fertile though underdeveloped (character 1491 179). Sterile florets variously modified and distinct from fertile were characteristic of 1492 Anthoxanthinae, in which they represented the plesiomorphic state, but originated secondarily 1493 within various other lineages of Aveneae, namely sporadically in Aveninae, Agrostidinae and 1494 Echinopogoninae, within Poeae in Helictochloinae, Aristaveninae, Airinae, Coleanthinae, in 1495 which this character represented most likely the plesiomorphic state, and the ABCV+A clade; 1496 stamens 3, with reduction in number sporadically encountered in various lineages of both Aveneae and Poeae (character 182); anthers ≥ 1 mm with diminution of size likewise in 1497 1498 various lineages of both tribes and presumably frequently related with self-pollination 1499 (character 183);

1500 caryopsis \geq 1.6 mm long, which was the ancestral state also for both Aveneae and 1501 Poeae (character 187), whereas shorter caryopses originated within Aveneae especially in 1502 Agrostidinae, for which they were seemingly plesiomorphic, but also in some 1503 Torreyochloinae, Phalaridinae, Brizinae, Hypseochloinae and Calothecinae and thus might be 1504 plesiomorphic for the common lineage comprising the latter subtribes. Shorter caryopses 1505 originated more sporadically also in Aveninae. Within Poeae, they originated infrequently, 1506 especially in Sesleriinae, Coleanthinae, Phleinae, Poinae, and a part of the ABCV+A clade, 1507 but sporadically also in Loliinae, Parapholiinae, etc.

hilum linear and straight, which was the ancestral state for also for both Aveneae and
Poeae individually (character 188). A transition to short, elliptic or punctiform hila occurred
within Aveneae especially in the Koeleriinae lineage of Aveninae, in Calothecinae and some
Agrostidinae. Within Poeae it seemed to be quite characteristic of Airinae, Sesleriinae,
Ammochloinae, Coleanthinae but occurred more sporadically also in parts of Parapholiinae
and the ABCV+A clade.

1514

1515 **Classification.** — Using the molecular phylogenetic data of both DNA analyses 1516 (plastid, nuclear) it can be concluded that the main bifurcation of the plastid DNA tree 1517 backbone is not reflected in the nuclear tree, which, however, does not provide a supported 1518 alternative topology. In this regard, the nuclear tree is un-informative and does not contribute 1519 to answer the question why classification should not use the supported plastid DNA lineages 1520 to re-instate tribes Aveneae and Poeae instead of acknowledging an enlarged Poeae (Poeae 1521 s.l.) as done in most recent classifications (Kellogg, 2015; Soreng & al., 2015, 2017; Saarela 1522 & al., 2017). All of these classifications actually make use of an informal arrangement of the

- subtribes in two groups within Poodae or Poeae s.l. according to the chloroplast DNA types
- 1524 (Soreng & Davis, 2000; Davis & Soreng, 2007; Döring & al., 2007; Quintanar & al., 2007;
- 1525 Soreng & al., 2007; Döring, 2009; Schneider & al., 2009, 2012; Saarela & al., 2010, 2017,
- 1526 2018; Pimentel & al., 2017; Orton & al. 2019).
- We suppose (1) that the consistent occurrence of two clearly differentiated chloroplastDNA lineages without intermediates reflects a major evolutionary differentiation.
- The absence (2) of equivalent differentiation in the nuclear DNA of these plants does make it impossible to use the plastid DNA results for classification. It should be noted in this context that supported backbone structure was absent also in several nuclear single copy gene trees we have studied (J. Schneider, unpub. data) and not only in the repetitive rDNA tree used in this study.
- 1534 The occurrence of hybridization (3) between the two different plastid DNA lineages as 1535 documented by several instances does not make a classificatory recognition of two tribes 1536 impossible. Morphologically, the two tribes are not clearly defined, which holds true, 1537 however, also for many of their subtribes. All in all, there is obviously a high degree of 1538 homoplasy in many morphological characters as seen, for example, in traditionally highly 1539 ranked characters for classification such as the presence of a dorsal lemma awn or long 1540 glumes in relation to the entire spikelet as presumably typical of Aveneae. Comparable 1541 difficulties in underlining classification by morphology are encountered also in many other 1542 grass groups. Examples would be the delineation of Stipeae within subfamily Pooideae, 1543 whether or not including Ampelodesmos Link as sole genus with several-flowered spikelets 1544 (see Schneider & al., 2011; Kellogg, 2015; Soreng & al., 2017), or the vague morphological
- 1545 circumscription of subfamily Micrairoideae (Sánchez-Ken & al., 2007; Kellogg, 2015).
- The proposed modified classification uses narrowly delineated and preferably
 monophyletic subtribes as applied in most recent treatments of the study group (e.g., Soreng
 & al. (2007, 2015, 2017); Kellogg, 2015; Saarela & al. 2017):
- Supertribe Poodae L.Liu: (1) tribe Aveneae Dumort.: subtribes Aveninae J.Presl,
 Anthoxanthinae A.Gray, Torreyochloinae Soreng & J.I.Davis, Phalaridinae Fr., Brizinae
 Tzvelev, Hypseochloinae Röser & Tkach, Echinopogoninae Soreng, Calothecinae Soreng,
 Agrostidinae Fr.; (2) tribe Poeae R.Br.: subtribes Scolochloinae Tzvelev, Aristaveninae
 F.Albers & Butzin, Helictochloinae Röser & Tkach, Holcinae Dumort., Airinae Fr.,
 Sesleriinae Parl., Antinoriinae Röser & Tkach, Loliinae Dumort., Ammochloinae Tzvelev,
 Dactylidinae Stapf, Cynosurinae Fr., Parapholiinae Caro, Coleanthinae Rouy, Avenulinae

1556 Röser & Tkach, Miliinae Dumort., Phleinae Dumort., Poinae Dumort., Brizochloinae Röser & 1557 Tkach, Cinninae Caruel, Beckmanniinae Nevski, Alopecurinae Dumort., Ventenatinae Holub 1558 ex L.J.Gillespie, Cabi & Soreng.

1559

1560 **NEW NAMES AND COMBINATIONS**

1561 Antinoriinae Röser & Tkach, subtribus nov. – Type: Antinoria Parl., Fl. Palerm. 1: 92. 1845.

1562

Description. - Annual or rarely (in A. agrostidea) perennial, caespitose or decumbent; 1563 1564 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 1565 1566 florets, disarticulating above the glumes and between the florets, with distinctly elongated 1567 rhachilla internode between the florets, glabrous, terminated by a female-fertile floret; glumes 1568 relatively large, more or less equal, exceeding the spikelets, awnless, carinate, 3-nerved; 1569 lemmas elliptic, widest near the tip, membranous, incised or blunt, awnless, glabrous, 5-1570 nerved; palea relatively long, tightly clasped by the lemma, 2-nerved, 2-keeled; anthers 0.5-1 1571 mm long; ovary glabrous; caryopsis pyriform, compressed dorsiventrally, smooth; hilum

- 1572 short; embryo less than 1/3 as long as fruit.
- 1573 Included genus. – Antinoria.
- 1574 Distribution. - Mediterranean.
- 1575
- Avenulinae Röser & Tkach, subtribus nov. Type: Avenula (Dumort.) Dumort., Bull. Soc. 1576 1577 Roy. Bot. Belgique 7: 68. 1868.

1578 Description. – Perennial, loosely caespitose, with creeping underground shoots; roots 1579 without sclerenchyma surrounding endodermis; culms with 1-3 visible nodes. Leaf sheaths 1580 closed over more than 1/2 their length from base; leaf blades flat or \pm conduplicate, not 1581 furrowed, relatively soft but rigid, with long hairs; bulliform cells forming a row each side of 1582 the adaxial midrib; with abaxial midrib and margins scarcely evident; secondary nerves few; 1583 well-developed subepidermal sclerenchyma forming O-shaped girders at lateral nerves; 1584 inflorescence lax panicle; spikelets 14-20 mm long, with 3-4 developed bisexual florets, two 1585 upper floret not or scarcely exceeding the upper glume, apical floret reduced; glumes unequal, 1586 keeled on the back, somewhat scabrid on the central nerve at the base, the lower glume 1-3-1587 nerved, the upper glume 3-nerved; rhachilla disarticulating above the glumes and between the 1588 florets; lemmas glabrous (except for the callus); dorsally awned, with a strongly twisted, 1589 rounded column, without pale margins; palea scarcely 2-keeled, with glabrous and smooth

1590	keels; lodicules as long or shorter than the ovary, ovate or obovate, 2–3-lobed or with a
1591	irregularly dentate apex; caryopsis furrowed; hilum linear; embryo with a truncated epiblast
1592	and obtuse scutellum.
1593	Included genus. – Avenula.
1594	Distribution Europe to eastern Siberia, Caucasus, northern Central Asia, Mongolia.
1595	
1596	Brizochloinae Röser & Tkach, subtribus nov. – Type: Brizochloa Jirás. & Chrtek, Novit.
1597	Bot. Delect. Seminum Horti Bot. Univ. Carol. Prag. (1966). 40. 1966.
1598	Diagnosis. – Differs from Brizinae and Macrobriza by upright pedicels of the
1599	spikelets, slightly scabrous rhachillas and non-cordate lemmas.
1600	Included genus. – Brizochloa.
1601	Distribution. – Eastern Mediterranean to Caucasus and Iran.
1602	
1603	Helictochloinae Röser & Tkach, subtribus nov. – Type: Helictochloa Romero Zarco,
1604	Candollea 66: 96. 2011.
1605	Description Perennial (Helictochloa) or annual (Molineriella); leaf sheaths split
1606	almost up to base, leaf blades flat, conduplicate or convolute; inflorescence lax panicle to
1607	(sometimes in <i>Helictochloa</i>) raceme-like; spikelets 10–36 mm (<i>Helictochloa</i>) or 1.5–2.5 mm
1608	(Molineriella), with (2–)3-9(–12) (Helictochloa) or 2 (Molineriella) developed, bisexual
1609	florets; glumes shorter than spikelets, the lower glume with (1-)3-5 (Helictochloa) or 1
1610	(Molineriella) nerves, the upper glume with 3-5(-7) (Helictochloa) or 3 (Molineriella) nerves;
1611	rhachilla disarticulating above the glumes and between the florets; lemmas glabrous or
1612	sericeous towards the base, awned dorsally in the half (Helictochloa) or in upper 1/3 of the
1613	lemma or awnless (Molineriella); awn with a loosely twisted column and a long subula
1614	(Helictochloa) or straight, extending by more than 10 mm (Helictochloa) or by 0.3-0.6 mm
1615	(Molineriella) beyond the lemma apex; palea 2-keeled, keels minutely ciliate (Helictochloa)
1616	or almost smooth (Molineriella); lodicules lanceolate, with a lateral lobe.
1617	Included genera. – Helictochloa, Molineriella.
1618	Distribution. – Mediterranean, Eurasia, North America.
1619	
1620	Hypseochloinae Röser & Tkach, subtribus nov. – Type: Hypseochloa C.E.Hubb., Bull.
1621	Misc. Inform. Kew 1936: 300, Fig. 1 (1936).

1622	Diagnosis Differs from Airinae by 1-flowered spikelets, 5-nerved glumes (the upper
1623	rarely 3-nerved), an apically deeply bifid lemma (about 1/3 incised), which is crustaceously
1624	indurated at maturity, the awn arising from the apical sinus.
1625	Included genus. – Hypseochloa.
1626	Distribution. – Cameroon Mt. and Tanzania.
1627	
1628	Anthoxanthum glabrum (Trin.) Veldkamp subsp. sibiricum (Tzvelev) Röser & Tkach,
1629	comb. nov. ≡ <i>Hierochloe odorata</i> (L.) P.Beauv. subsp. <i>sibirica</i> Tzvelev, Novosti Sist.
1630	Vyssh. Rast. 1968: 21. 1968.
1631	
1632	Anthoxanthum nitens (Weber) Y.Schouten & Veldkamp subsp. kolymensis (Prob.) Röser &
1633	Tkach, comb. nov. ≡ <i>Hierochloe odorata</i> (L.) P.Beauv. subsp. <i>kolymensis</i> Prob.,
1634	Novosti Sist. Vyssh. Rast. 15: 69. 1979.
1635	
1636	Arctohyalopoa Röser & Tkach, gen. nov. – Type: Poa lanatiflora Roshev., Izv. Bot. Sada
1637	Akad. Nauk S.S.S.R. 30: 303. 1932 ≡ Arctohyalopoa lanatiflora (Roshev.) Röser &
1638	Tkach
1639	Description: Differs from Hyalopoa by lemmas with copious and long hairs on the
1640	basal half and especially on nerves, calli copiously covered with long crinkly hairs and
1641	glabrous paleas with rarely a few hairs along keels.
1642	
1643	<i>Arctohyalopoa lanatiflora</i> (Roshev.) Röser & Tkach, comb. nov. ≡ <i>Poa lanatiflora</i> Roshev.,
1644	Izv. Bot. Sada Akad. Nauk S.S.S.R. 30: 303. 1932.
1645	
1646	<i>Arctohyalopoa lanatiflora</i> subsp. <i>ivanoviae</i> (Malyschev) Röser & Tkach, comb. nov. ≡
1647	Colpodium ivanoviae Malyschev, Novosti Sist. Vyssh. Rast. 7: 295. 1971 [1970 publ.
1648	1971].
1649	
1650	<i>Arctohyalopoa lanatiflora</i> subsp. <i>momica</i> (Tzvelev) Röser & Tkach, comb. nov. ≡
1651	Colpodium lanatiflorum Tzvelev subsp. momicum Tzvelev, Fl. Arct. URSS 2: 172.
1652	1964.
1653	
1654	<i>Colpodium biebersteinianum</i> (Claus) Röser & Tkach, comb. nov. ≡ <i>Agrostis biebersteiniana</i>
1655	Claus, Beitr. Pflanzenk. Russ. Reiches 8: 264. 1851 = Zingeria biebersteiniana (Claus)

1656	P.A.Smirn., Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 51: 67. 1946 = Zingeria
1657	trichopoda subsp. biebersteiniana (Claus) Doğan, Notes Roy. Bot. Gard. Edinburgh
1658	40: 86. 1982.
1659	
1660	<i>Colpodium kochii</i> (Mez) Röser & Tkach, comb. nov. ≡ <i>Milium kochii</i> Mez, Notes Roy. Bot.
1661	Gard. Edinburgh 17: 211. 1921 ≡ Zingeria kochii (Mez) Tzvelev, Bot. Zhurn.
1662	(Moscow & Leningrad) 50: 1318. 1965.
1663	
1664	<i>Colpodium pisidicum</i> (Boiss.) Röser & Tkach, comb. nov. ≡ <i>Agrostis pisidica</i> Boiss., Ann.
1665	Sci. Nat., Bot., sér. 4, 2: 255. 1854 ≡ Zingeria pisidica (Boiss.) Tutin, Bot. J. Linn.
1666	Soc. 76: 365. 1978.
1667	
1668	<i>Colpodium trichopodum</i> (Boiss.) Röser & Tkach, comb. nov. = <i>Zingeria trichopoda</i> (Boiss.)
1669	P.A.Smirn., Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 51: 67. 1946 ≡ Zingeria
1670	biebersteiniana subsp. trichopoda (Boiss.) R.R.Mill, Fl. Turkey 9: 365. 1985.
1671	
1672	<i>Colpodium verticillatum</i> (Boiss. & Balansa) Röser & Tkach, comb. nov. ≡ <i>Milium</i>
1673	verticillatum Boiss. & Balansa, Bull. Soc. Bot. France 5: 169. 1858 ≡ Zingeria
1674	verticillata (Boiss. & Balansa) Chrtek, Novit. Bot. Delect. Seminum Horti Bot. Univ.
1675	Carol. Prag. 1963: 3. 1963 ≡ Zingeriopsis verticillata (Boiss. & Balansa) Prob.,
1676	Novosti Sist. Vyssh. Rast. 14: 12. 1977.
1677	
1678	Deschampsia micrathera (É.Desv.) Röser & Tkach, comb. nov. ≡ Trisetum micratherum
1679	É.Desv., Flora Chilena [Gay] 6: 352. 1854 ≡ <i>Leptophyllochloa micrathera</i> (É.Desv.)
1680	C.E.Calderón ex Nicora, Fl. Patagonica 3: 70. 1978.
1681	
1682	<i>Dupontia fulva</i> (Trin.) Röser & Tkach, comb. nov. ≡ <i>Poa fulva</i> Trin., Mém. Acad. Imp. Sci.
1683	StPétersbourg, Sér. 6, Sci. Math. 1: 378. 1830.
1684	
1685	<i>Festuca masafuerana</i> (Skottsb. & Pilg. ex Pilg.) Röser & Tkach, comb. nov. ≡ <i>Bromus</i>
1686	masafueranus Skottsb. & Pilg. ex Pilg., Repert. Spec. Nov. Regni Veg. 16: 385. 1920
1687	<i>≡ Megalachne masafuerana</i> (Skottsb. & Pilg. ex Pilg.) Matthei
1688	
1689	Festuca masatierrae Röser & Tkach, nom. nov.

1690	Replaced synonym Podophorus bromoides Phil., Bot. Zeitung (Berlin) 14: 649.
1691	1856.
1692	Blocking name. – Festuca bromoides L., Sp. Pl. 1: 75. 1753.
1693	
1694	Hyalopodium Röser & Tkach, gen. nov. – Type: Catabrosa araratica Lipsky, Trudy Imp. S
1695	Peterburgsk. Bot. Sada 13: 358. 1894 ≡ <i>Hyalopodium araraticum</i> (Lipsky) Röser &
1696	Tkach
1697	Description: Perennial, caespitose, with creeping underground shoots; aerial shoots
1698	enclosed at the base by reticulately fibrous sheaths of dead leaves; culms erect, 20-55 cm
1699	long; ligule an eciliate membrane, 3–5 mm long, acute; leaf blades 4–11 cm long, 1–3 mm
1700	wide, midrib prominent beneath, surface glabrous, margins cartilaginous; inflorescence a
1701	panicle, contracted, linear, interrupted, 4–11 cm long, 0.5–1.5 cm wide; primary panicle
1702	branches short, 0.2–0.6 cm long; spikelets solitary, pedicelled, comprising 2(–3) fertile florets,
1703	without rhachilla extension, cuneate, laterally compressed, 6–7 mm long, disarticulating
1704	below each fertile floret; glumes persistent, similar, shorter than spikelet, similar to fertile
1705	lemma in texture, gaping; lower glume oblong, 4.5 mm long, 3/4 to as long as upper glume,
1706	membranous, much thinner above and on margins, purple, 1-keeled, 1-veined, lateral veins
1707	absent, apex acute; upper glume elliptic, 4.5–6 mm long, as long as adjacent fertile lemma,
1708	membranous, much thinner above, with hyaline margins, purple, 1-keeled, 3-veined, apex
1709	acute; lemma elliptic, 4–6 mm long, membranous, much thinner above, purple and yellow,
1710	tipped with yellow, keeled, 5-veined; lateral veins less than 2/3 length of lemma; lemma
1711	surface pubescent, hairy below; lemma apex erose, obtuse; callus very short, pilose; palea
1712	keels smooth, eciliate; anthers 3.3–4.5 mm long, yellow or purple; caryopsis about 3 mm
1713	long; hilum elliptic, 1/3–1/2 of the grain.
1714	
1715	<i>Hyalopodium araraticum</i> (Lipsky) Röser & Tkach, comb. nov. ≡ <i>Catabrosa araratica</i>
1716	Lipsky, Trudy Imp. SPeterburgsk. Bot. Sada 13: 358. 1894.
1717	
1718	<i>Paracolpodium baltistanicum</i> (Dickoré) Röser & Tkach, comb. nov. ≡ <i>Colpodium</i>
1719	baltistanicum Dickoré, Stapfia 39: 114. 1995.
1720	
1721	<i>Parapholis cylindrica</i> (Willd.) Röser & Tkach, comb. nov. ≡ <i>Hainardia cylindrica</i> (Willd.)
1722	Greuter, Boissiera 13: 177. 1967.
1723	

1724 *Parapholis ×pauneroi* (Castrov.) Röser & Tkach, comb. nov. ≡ ×*Hainardiopholis pauneroi*1725 Castrov., Anales Jard. Bot. Madrid 36: 238. 1980 [1979 publ. 1980].

1726

1727 CONCLUSIONS

1728 Our survey of the molecular phylogenetic differentiation of supertribe Poodae, 1729 including most of its genera and based on nuclear and plastid DNA sequence markers 1730 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 1731 1732 should be resolved in future studies. Notably, the nuclear and plastid DNA trees agree in wide portions and show congruent branching patterns, making it likely that they reflect the actual 1733 1734 phylogenetic relation of the taxa in these tree portions. Severe conflict between the trees, 1735 however, occurs but is confined to several clearly defined and localized, though sometimes 1736 larger stretches of the trees and is interpreted to be indicative of past hybridization (Figs. 1, 2, 1737 4). Taxonomic groups with hybrid origin are subtribes Scolochloinae, Sesleriinae, 1738 Torrevochloinae, Phalaridinae, Airinae, Holcinae and Phleinae. Major reticulation processes 1739 across subtribes include Macrobriza and Arctopoa. Well-identifiable infra-subtribe hybrid 1740 origins, which partly encompass lineages with several genera, were found, for example, 1741 within Aveninae, Coleanthinae, Loliinae, Puccinelliinae and Sesleriinae (Figs. 1, 2, 4, 5–7) 1742 but may be more frequent if denser sampling of taxa will be implemented and tree resolution 1743 will be improved by future studies. We found no evidence on a hybrid origin of Avenula and 1744 Helictochloa, whereas 'Calamagrostis' flavens is likely an intergeneric hybrid between 1745 Agrostis and Calamagrostis that warrants further study.

An analysis of morphological and other characteristics based on a final data matrix of 1747 188 mainly morphological characters and utilizing a phylogenetic tree based on all plastid and 1748 nuclear DNA markers studied was performed to reconstruct the evolutionary ancestral states 1749 of our study group Poodae and its major lineages. Altogether 74 characters could be analysed 1750 in detail this way.

The phylogenetically ancestral character states (suppl. Appendix S3) of Poodae include perennial life form; absence of rhizomes; ligule an eciliate membrane; flat leaves; inflorescence an open panicle with many spikelets; panicle branches at most moderately divided, smooth; spikelets pedicelled, with >3 fertile florets, with a rhachilla extension bearing a sterile floret; spikelets without basal sterile florets, fertile florets (if more than 1) all alike, laterally and at most moderately compressed, comparatively large, >4 mm in length, breaking up at maturity, disarticulating below each floret; glumes shorter than spikelet, in 1758 consistency thinner than the lemma or similar; lower glume 3–6 mm long, 0.6-fold to as long 1759 as the upper, of similar consistency on margins, 1-keeled, keeled all along, 1-veined, primary 1760 vein eciliate, without lateral veins; upper glume 3-6 mm long, with undifferentiated margins, muticous, 1-keeled, 3-veined, primary vein distinct, smooth, lateral veins distinct; lemma 1.6-1761 1762 4 mm, without keel, with 4–5 veins, surface generally rough, lemma apex erose or dentate, 1763 mucronate to awned, principal lemma awn straight, not coloured, without distinct column; 1764 column of lemma awn (if present) not twisted and not flattened, lateral lemma awns absent; palea ≥ 0.7 -fold longer than the lemma, with smooth and eciliate keels; apical sterile florets (if 1765 1766 present) resembling fertile though underdeveloped; stamens 3; caryopsis ≥ 1.6 mm long; hilum linear and straight. 1767

1768 Interestingly, the phylogenetically ancestral character states are sometimes different 1769 for Aveneae and Poeae, for example, the number of florets in the spikelets or spikelet size. A 1770 repeated switch of states during evolution including reversals is likely for many characters. 1771 The analysis revealed an overall high degree of homoplasy of spikelet characters. It includes, 1772 for example, the parallel, independent evolution of elaborate, geniculately bent awns multiple 1773 times in several evolutionarily separated lineages (Figs. 9-11). This character, once assumed 1774 by taxonomists to be characteristic of Aveneae, originated at least six times and also could 1775 become secondarily lost again (see above Ancestral state reconstruction: characters 146, 146, 1776 150; suppl. Fig. S2, suppl. Appendix S2). This parallels the findings in the PACMAD clade of grass subfamilies, in which similarly shaped twisted geniculate awns have originated at least 1777 1778 five times independently (Teisher & al., 2017).

1779 The overall high degree of homoplasy in many spikelet characters, we assume, relates 1780 to high degree of selective pressure acting on these structures. They have little to do with 1781 pollination as an important factor for the floral structures in many other angiosperms because 1782 all grass taxa in question are wind-pollinated. We suppose they have much more to do with 1783 efficient dispersal of diaspores, which is highly varied in grasses (Davidse, 1987). It can be 1784 supposed that the variety of dispersal mechanisms caused by spikelet structures (spikelet 1785 disarticulate or fall entire, different types of disarticulation, types of awns, animal dispersal, 1786 hygroscopic movement, bristles and hairs, lemma and palea structure, release of caryopses, 1787 etc.) are one of important evolutionary factors, which enabled Aveneae and Poeae to colonise 1788 successfully almost any habitat type in the temperate and cold zones of the world.

1789

1790 AUTHOR CONTRIBUTIONS

MR, JS and NT designed the study. MR guided the sampling, contributed taxonomic
knowledge, contributed data for the ancestral state reconstructions and wrote the manuscript.
JS, NT, ED, AW, AH, GW, JG contributed lab work. NT and JS contributed data by
supervising students in the lab. NT and JS undertook the phylogenetic analyses. JN and MR
performed the ancestral state reconstructions. NT and MHH contributed to write the
manuscript. — GW, https://orcid.org/0000-0002-9866-335X; MR, https://orcid.org/00000001-5111-0945; NT, https://orcid.org/0000-0002-4627-0706.

1798

1799 ACKNOWLEDGEMENTS

1800 We are grateful to Liliana Essi (Universidade Federal de Santa Maria, Santa Maria, 1801 RS), Božo Frajman (University of Innsbruck), Paola Gaiero (University of the Republic 1802 Uruguay, Montevideo), Caroline Mashau (South African National Biodiversity Institute, 1803 Pretoria), Mélica Muñoz-Schick (Museo Nacional de Historia Natural de Chile, Santiago de 1804 Chile), Carlos Romero Zarco (Departamento de Biología Vegetal y Ecología, Sevilla), Robert 1805 J. Soreng (Smithsonian Institution, Washington, D.C.), the late Nikolai N. Tzvelev (Komarov 1806 Botanical Institute, St. Petersburg) and the directors of the herbaria listed in Appendix 1 for 1807 supplying plant material for our study. Further we thank Bärbel Hildebrandt and Laura 1808 Freisleben (Halle) for technical support in our lab. Parts of this study were conducted by 1809 Antonia Lisker, Kerstin Schmidt, Peter Süssmann, Anne Weigelt within the framework of 1810 their university degree theses. Maria Vorontsova and Sarah Ficinski (both Royal Botanic 1811 Gardens, Kew) kindly provided the GrassBase data used for morphological analyses and ASR. A research grant of the German Research Foundation to MR (DFG RO 865/8) is 1812 1813 gratefully acknowledged.

1814

1815 **REFERENCES**

- Alonso, A., Bull, R.D., Acedo, C. & Gillespie, L.J. 2014. Design of plant-specific PCR
 primers for the ETS region with enhanced specificity for tribe Bromeae and their
 application to other grasses (Poaceae). *Botany* 92: 693–699.
- 1819 https://doi.org/10.1139/cjb-2014-0062
- 1820 Baker, W.J., Norup, M.V., Clarkson, J.J., Couvreur, T.L.P., Dowe, J.L., Lewis, C.E.,
- Pintaud, J.-C., Savolainen, V., Wilmot, T. & Chase, M.W. 2011. Phylogenetic
 relationships among arecoid palms (Arecaceae: Arecoideae). *Ann. Bot.* 108(8): 1417–
 1432. https://doi.org/10.1093/aob/mcr020
- 1824 Baldini, R.M. 1995. Revision of the genus *Phalaris* L. (Gramineae). *Webbia* 49: 265–329.

1825 Banfi, E., Galasso, G. & Bartolucci, F. 2018. Nomenclatural novelties for the Euro+Med 1826 flora. Nat. Hist. Sci. 5: 53-57. https://doi.org/10.4081/nhs.2018.365 1827 Barberá, P., Soreng, R.J., Peterson, P.M., Romaschenko, K., Quintanar, A. & Aedo, C. 1828 2019. Molecular phylogenetic analysis resolves *Trisetum* Pers. (Poaceae: Pooideae: 1829 Koeleriinae) polyphyletic: Evidence for a new genus, Sibirotrisetum, and resurrection 1830 of Acrospelion. J. Syst. Evol. (2019). https://doi.org/10.1111/jse.12523 1831 Birch, J.L., Cantrill, D.J., Walsh, N.G. & Murphy, D.J. 2014. Phylogenetic investigation and divergence dating of Poa (Poaceae, tribe Poeae) in the Australasian region. Bot. J. 1832 1833 Linn. Soc. 175: 523-552. https://doi.org/10.1111/boj.12185 1834 Birch, J.L., Walsh, N.G., Cantrill, D.J., Holmes, G.D. & Murphy, D.J. 2017. Testing efficacy of distance and tree-based methods for DNA barcoding of grasses (Poaceae 1835 1836 tribe Poeae) in Australia. PLoS ONE 12(10): e0186259. 1837 https://doi.org/10.1371/journal.pone.0186259 Blaner, A., Schneider, J. & Röser, M. 2014. Phylogenetic relationships in the grass family 1838 1839 (Poaceae) based on the nuclear single copy locus topoisomerase 6 compared to 1840 chloroplast DNA. Syst. Biodivers. 12: 111-124. 1841 https://doi.org/10.1080/14772000.2014.890137 1842 **Bor, N.L.** 1960. The grasses of Burma, Ceylon, India and Pakistan (excluding Bambuseae). 1843 Oxford, etc.: Pergamon Press. https://doi.org/10.1126/science.133.3459.1125 Bouchenak-Khelladi, Y., Salamin, N., Savolainen, V., Forest, V., Van der Bank, M., 1844 1845 Chase, M.W. & Hodkinson, T.R. 2008. Large multi-gene phylogenetic trees of the 1846 grasses (Poaceae): progress towards complete tribal and generic level sampling. 1847 Molec. Phylogen. Evol. 47: 488-505. https://doi.org/10.1016/j.ympev.2008.01.035 Brysting, A.K., Aiken, S.G., Lefkovitch, L.P. & Boles, R.L. 2003. Dupontia (Poaceae) in 1848 1849 North America. Canad. J. Bot. 81: 769-779. https://doi.org/10.1139/b03-067 1850 Brysting, A., Fay, M., Leitch, I. & Aiken, S. 2004. One or more species in the Arctic grass 1851 genus Dupontia? A contribution to the Panarctic Flora Project. Taxon 53(2): 365–382. 1852 https://doi.org/10.2307/4135615 1853 Catalán, P., Kellogg, E.A. & Olmstead, R.G. 1997. Phylogeny of Poaceae subfamily 1854 Pooideae based on chloroplast ndhF gene sequences. Molec. Phylogen. Evol. 8: 150-166. https://doi.org/10.1006/mpev.1997.0416 1855 1856 Catalán, P., Torrecilla, P., López-Rodríguez, J.A., & Olmstead, R.G. 2004. Phylogeny of 1857 the festucoid grasses of subtribe Loliinae and allies (Poeae, Pooideae) inferred from

1858	ITS and <i>trnL–F</i> sequences. <i>Molec. Phylogen. Evol.</i> 31: 517–541.
1859	https://doi.org/10.1016/j.ympev.2003.08.025
1860	Catalán, P., Torrecilla, P., López-Rodríguez, J.A., Müller, J. & Stace, C.A. 2007. A
1861	systematic approach to subtribe Loliinae (Poaceae: Pooideae) based on phylogenetic
1862	evidence. Aliso 23: 380-405. https://doi.org/10.5642/aliso.20072301.31
1863	Cayouette, J. & Darbyshire, S.J. 2007a. 14.15 Dupontia R. Br. Pp. 602-604 in: Barkworth,
1864	M.E., Capels, K.M., Long, S., Anderton, L.K. & Piep, M.B. (eds.), Flora of North
1865	America north of Mexico, vol. 24, Magnoliophyta: Commelinidae (in part): Poaceae,
1866	part 1. New York: Oxford University Press.
1867	Cayouette, J. & Darbyshire, S.J. 2007b. 14.17, Arctophila (Rupr.) Andersson. Pp. 605–607
1868	in: Barkworth, M.E., Capels, K.M., Long, S., Anderton, L.K. & Piep, M.B. (eds.),
1869	Flora of North America north of Mexico, vol. 24, Magnoliophyta: Commelinidae (in
1870	part): Poaceae, part 1. New York: Oxford University Press.
1871	CCDB (Chromosome Counts Database), version 1.46. 2019. http://ccdb.tau.ac.il/ (accessed
1872	1 June 2019).
1873	Cebrino Cruz, J. & Romero Zarco, C. 2017. Revisión taxonómica del género Molineriella
1874	Rouy (Gramineae: Poeae: Airinae) en la Península Ibérica. Acta Bot. Malac. 42: 203-
1875	214. https://doi.org/10.24310/abm.v42i2.3064
1876	Cheng, Y., Zhou, K., Humphreys, M.W., Harper, J.A., Ma, X., Zhang, X., Yan, H. &
1877	Huang, L. 2016. Phylogenetic relationships in the Festuca-Lolium complex (Loliinae;
1878	Poaceae): New insights from chloroplast sequences. Front. Ecol. Evol. 4: 89.
1879	https://doi.org/10.3389/fevo.2016.00089
1880	Clayton, W.D. & Renvoize, S.A. 1986. Genera graminum. Grasses of the world. Kew
1881	Bulletin Additional Series 13. London: HMSO.
1882	Clayton, W.D., Vorontsova, M.S., Harman, K.T. & Williamson, H. 2002 onwards. [World
1883	grass species: Synonymy] http://www.kew.org/data/grasses-syn.html (accessed 29 Apr
1884	2019)
1885	Clayton, W.D., Vorontsova, M.S., Harman, K.T. & Williamson, H. 2006 onwards.
1886	[GrassBase – The online world grass flora] http://www.kew.org/data/grasses-db.html
1887	(accessed 29 Apr 2019)
1888	Conert, H.J. 1979–1998. Poaceae (Echte Gräser oder Süßgräser), Pp. 1–898. in: H.J. Conert,
1889	E.J. Jäger, W. Schultze-Motel, G. Wagenitz & Weber, H.E. (eds.): Illustrierte Flora
1890	von Mitteleuropa. Ed. 3. vol. 1, part 3, Berlin: Parey Buchverlag.

- 1891 Conert, H.J. 2000. Pareys Gräserbuch. Die Gräser Deutschlands erkennen und bestimmen.
 1892 Berlin: Parey Buchverlag.
- 1893 Connor, H.E. 2012. Flowers and floral biology of the holy grasses (*Hierochloe* and
- 1894 *Anthoxanthum*: Aveneae, Gramineae). *Flora* 207: 323–333.
- 1895 https://doi.org/10.1016/j.flora.2012.01.010
- 1896 Cope, T.A. 1982. Poaceae. Pp. 1–678 in: Nasir, E. & Ali, S.I. (eds.), *Flora of Pakistan*, vol.
 143. Karachi: University of Karachi.
- 1898 Darbyshire, S.J. & Cayouette, J. 2007. 14.16 × Arctodupontia Tzvelev. Pp. 604–605 in:
- Barkworth, M.E., Capels, K.M., Long, S., Anderton, L.K. & Piep, M.B. (eds.), *Flora of North America north of Mexico*, vol. 24, *Magnoliophyta: Commelinidae (in part): Poaceae, part 1.* New York: Oxford University Press.
- 1902 Davidse, G. 1987. Fruit dispersal in the Poaceae. Pp. 143–155 in: Soderstrom, T.R., Hilu,
- K.W., Campbell, C.S. & Barkworth, M.E. (eds.), *Grass systematics and evolution*.
 Washington, D.C.: Smithsonian Institution Press.
- 1905 Davis, J.I. & Soreng, R.J. 1993. Phylogenetic structure in the grass family (Poaceae) as
 1906 inferred from chloroplast DNA restriction site variation. *Amer. J. Bot.* 80: 1444–1454.
- 1907 Davis, J.I. & Soreng, R.J. 2007. A preliminary phylogenetic analysis of the grass subfamily
 1908 Pooideae subfamily Pooideae (Poaceae), with attention to structural features of the
 1909 plastid and nuclear genomes, including an intron loss in GBSSI. *Aliso* 23: 335–348.
- 1910 **Dickoré, W.B.** 1995. Systematische Revision und chorologische Analyse der
- 1911 Monocotyledoneae des Karakorum (Zentralasien, West-Tibet) Flora Karakorumensis
 1912 I. Angiospermae, Monocotyledoneae. *Stapfia* 39: 1–298.
- 1913 **Döring, E.** 2009. *Molekulare Phylogenie der Hafer-Gräser (Poaceae: Pooideae: Aveneae)*.
- 1914Dissertation. Halle/Saale: Martin Luther University Halle-Wittenberg. Available at1915http://digital.bibliothek.uni-halle.de/hs/content/titleinfo/177571
- Döring, E., Schneider, J., Hilu, K.W. & Röser, M. 2007. Phylogenetic relationships in the
 Aveneae/Poeae complex (Pooideae, Poaceae). *Kew Bull.* 62: 407–424.
- 1918 Edgar, E. 1995. New Zealand species of *Deyeuxia* P. Beauv. and *Lachnagrostis* Trin.
- 1919 (Gramineae: Aveneae). *New Zealand J. Bot.* 33: 1–33.
- 1920 https://doi.org/10.1080/0028825X.1995.10412940
- 1921 Edgar, E. & Connor, H.E. 2000. *Flora of New Zealand*. vol. 5, *Gramineae*. 650 pp. Lincoln,
 1922 New Zealand: Manaaki Whenua Press.

1923	Essi, L., Longhi-Wagner, H.M. & Souza-Chies, T.T. 2008. Phylogenetic analysis of the
1924	Briza complex (Poaceae). Molec. Phylogen. Evol. 47: 1018–1029.
1925	https://doi.org/10.1016/j.ympev.2008.03.007
1926	Essi, L., Longhi-Wagner, H.M. & de Souza Chies, T.T. 2017. A synopsis of Briza,
1927	Brizochloa, and Chascolytrum (Poaceae, Pooideae, Poeae). Ann. Missouri Bot. Gard.
1928	102(3): 466–519. https://doi.org/10.3417/2012069
1929	Gabriel, J., Tkach, N. & Röser, M. 2019. Recovery of the type specimen of Avena
1930	breviaristata, an endemic Algerian grass species collected only once (1882):
1931	morphology, taxonomy and botanical history. doi: http://dx.doi.org/10.1101/691717
1932	[preprint]
1933	Gillespie, L.J. & Soreng, R.J. 2005. A phylogenetic analysis of the bluegrass genus Poa L.
1934	(Poaceae) based on cpDNA restriction site data. Syst. Bot. 30: 84–105.
1935	Gillespie, L.J., Archambault, A. & Soreng, R.J. 2007. Phylogeny of Poa (Poaceae) based
1936	on <i>trnT–trnF</i> sequence data: major clades and basal relationships. <i>Aliso</i> 23: 420–434.
1937	https://doi.org/10.5642/aliso.20072301.33
1938	Gillespie, L., Soreng, R., Bull, R., Jacobs, S. & Refulio Rodríguez, N. 2008. Phylogenetic
1939	relationships in subtribe Poinae (Poaceae, Poeae) based on nuclear ITS and plastid
1940	trnT-trnL-trnF sequences. Botany 86: 938-967. https://doi.org/10.1139/B08-076
1941	Gillespie, L.J., Soreng, R.J. & Jacobs, S.W.L. 2009. Phylogenetic relationships of
1942	Australian Poa (Poaceae: Poinae), including molecular evidence for two new genera,
1943	Saxipoa and Sylvipoa. Newslett. Austral. Syst. Bot. Soc. 22: 413-436.
1944	https://doi.org/10.1071/SB09016
1945	Gillespie, L.J., Soreng, R.J., Paradis, M. & Bull, R.D. 2010. Phylogeny and reticulation in
1946	subtribe Poinae and related subtribes (Poaceae) based on nrITS, ETS, and <i>trnTLF</i> data.
1947	Pp. 589-618 in: Seberg, O., Petersen, G., Barfod, A.S. & Davids, J.I. (eds.), Diversity,
1948	phylogeny, and evolution in the monocotyledons. Aarhus: Aarhus University Press.
1949	Gillespie, L.J., Soreng, R.J., Cabi, E. & Amiri, N. 2018. Phylogeny and taxonomic
1950	synopsis of Poa subgenus Pseudopoa (including Eremopoa and Lindbergella)
1951	(Poaceae, Poeae, Poinae). PhytoKeys 111: 69-101.
1952	https://doi.org/10.3897/phytokeys.111.28081
1953	Grebenstein, B., Röser, M., Sauer, W. & Hemleben, V. 1998. Molecular phylogenetic
1954	relationships in Aveneae (Poaceae) species and other grasses as inferred from ITS1
1955	and ITS2 rDNA sequences. Pl. Syst. Evol. 213: 233-250.

- GPWG (Grass Phylogeny Working Group) II. 2012. New grass phylogeny resolves deep
 evolutionary relationships and discovers C₄ origins. *New Phytol.* 193: 304–312.
 https://doi.org/10.1111/j.1469-8137.2011.03972.x
- Hilu, K.W., Alice, L.A. & Liang, H. 1999. Phylogeny of Poaceae inferred from *matK*sequences. *Ann. Missouri Bot. Gard.* 86: 835–851. https://doi.org/10.2307/2666171
- Hitchcock, A.S. 1920. The genera of grasses of the United States. *Bull. U.S.D.A.* 772: 1–307.
 Washington, D.C.: U.S. Dept. of Agriculture. https://doi.org/10.5962/bhl.title.64674
- Hochbach, A., Schneider, J. & Röser, M. 2015. A multi-locus analysis of phylogenetic
 relationships within grass subfamily Pooideae (Poaceae) inferred from sequences of
 nuclear single copy gene regions compared with plastid DNA. *Molec. Phylogen. Evol.*87: 14–27. https://doi.org/10.1016/j.ympev.2015.03.010.
- Hoffmann, M.H., Schneider, J., Hase, P. & Röser, M. 2013. Rapid and recent world-wide
 diversification of bluegrasses (*Poa*, Poaceae) and related genera. *PLoS ONE* 8(3): 1–9.
 https://doi.org/10.1371/journal.pone.0060061
- 1970 Hubbard, C.E. 1936. A new genus from the Cameroon Mountain. *Kew Bull.* 1936: 299–301.
- 1971 Hubbard, C.E. 1981. A new species of *Hypseochloa* from Tanzania. *Kew Bull.* 36: 62.
- Huelsenbeck, J.P., Nielsen, R. & Bollback, J.P. 2003. Stochastic mapping of morphological
 characters. *Syst. Biol.* 52: 131–158. https://doi.org/10.1080/10635150390192780
- 1974 Hunter, A.M., Orlovich, D.A., Lloyd, K.M., Lee, W.G. & Murphy, D.J. 2004. The generic
- 1975 position of *Austrofestuca littoralis* and the reinstatement of *Hookerochloa* and
- 1976 *Festucella* (Poaceae) based on evidence from nuclear (ITS) and chloroplast (*trnL*-
- 1977 *trnF*) DNA sequences. *New Zealand J. Bot.* 42: 253–262.
- 1978 https://doi.org/10.1080/0028825X.2004.9512902
- Hunziker, J.H. & Stebbins, G.L. 1987. Chromosomal evolution in the Gramineae. Pp. 179–
 187 in: Soderstrom, T. R., Hilu, K. W., Campbell, C. S. & Barkworth, M. E. (eds.) *Grass systematics and evolution*. Washington, D.C.: Smithsonian Institution Press.
- 1982 Inda, L.A., Segarra-Moragues, J.G., Müller, J., Peterson, P.M. & Catalán, P. 2008.
- 1983 Dated historical biogeography of the temperate Loliinae (Poaceae, Pooideae) grasses
- in the northern and southern hemispheres. *Molec. Phylogen. Evol.* 46: 932–957.
- 1985 https://doi.org/10.1016/j.ympev.2007.11.022
- Jacobs, S.W.L. & Brown, A.J. 2009. *Lachnagrostis*. Pp. 174–190 in: Wilson, A. (ed.), *Flora of Australia*, vol. 44A, *Poaceae* 2. Melbourne: ABRS/CSIRO
- Jirásek, V. & Chrtek, J. 1967. *Brizochloa*, eine neue Grasgattung. *Novit. Bot. Delect.*Seminum Horti Bot. Univ. Carol. Prag. 1966: 39–41.

1990 Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., 1991 Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentjies, P. & 1992 Drummond, A. 2012. Geneious Basic: an integrated and extendable desktop software 1993 platform for the organization and analysis of sequence data. *Bioinformatics* 28(12): 1994 1647–1649. https://doi.org/10.1093/bioinformatics/bts199 1995 Kellogg, E.A. 2015. The families and genera of vascular plants, vol. 13, Flowering plants: 1996 Monocots; Poaceae. Cham: Springer. 1997 Kellogg, E.A. & Watson, L. 1993. Phylogenetic studies of a large data set. I. Bambusoideae, 1998 Andropogonodae, and Pooideae. Bot. Rev. (Lancaster) 59: 273-343. 1999 Kim, E.S., Bolsheva, N.L., Samatadze, T.E., Nosov, N.N., Nosova, I.V., Zelenin, A.V., Punina, E.E., Muravenko, O.V. & Rodionov, A.V. 2009. The unique genome of 2000 2001 two-chromosome grasses Zingeria and Colpodium, its origin, and evolution. Russ. J. 2002 Genet. 45: 1329-1337. Kim, E.S., Nosov, N.N., Dobroradova, M.A., Punina, N.B. Tyupa & Rodionov, A.V. 2003 2004 2008. Blizost *Catabrosella araratica* (2n = 6x = 42) k zlakam s dyukhromosomnymy 2005 genomami Zingeria biebersteiniana i Colpodium versicolor (2n = 2x = 4) - rod2006 Nevskia Tzvel. deystvitelno sushchestvuet? [Resemblance of Catabrosella araratica 2007 (2n = 6x = 42) to grasses with two-chromosome genomes of Zingeria biebersteiniana 2008 and Colpodium versicolor (2n = 2x = 4) – Does genus Nevskia Tzvel. really exist?]. 2009 Pp. 58-59 in: Rodionov, A.V. & Shneer, V.S. (eds.), 'Khromosomy i evolyutsiya' 2010 Simposium pamyati G.A. Levitskogo (1878–1942), Sankt Petersburg. 2011 Kotseruba, V., Pistrick, K., Gernand, D., Meister, A., Ghukasyan, A., Gabrielyan, I. & 2012 Houben, A. 2005. Characterisation of the low-chromosome number grass Colpodium 2013 *versicolor* (Stev.) Schmalh. (2n = 4) by molecular cytogenetics. *Caryologia* 58: 241– 2014 245. https://doi.org/10.1080/00087114.2005.10589457 Kotseruba, V., Pistrick, K., Blattner, F.R., Kumke, K., Weiss, O., Rutten, T., Fuchs, J., 2015 2016 Endo, T., Nasuda, S., Ghukasyan, A. & Houben, A. 2010. The evolution of the 2017 hexaploid grass Zingeria kochii (Mez.) Tzvel. (2n = 12) was accompanied by complex 2018 hybridization and uniparental loss of ribosomal DNA. Molec. Phylogen. Evol. 56: 2019 146–155. https://doi.org/10.1016/j.ympev.2010.01.003 2020 Kuzmanović, N., Lakušić, D., Frajman, B., Alegro, A. & Schönswetter, P. 2017. 2021 Phylogenetic relationships in Seslerieae (Poaceae) including resurrection of Psilathera 2022 and Sesleriella, two monotypic genera endemic to the Alps. Taxon 66: 1349–1370. 2023 https://doi.org/10.12705/666.5

2024	Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGettigan, P.A., McWilliam,
2025	H., Valentin, F., Wallace, I.M., Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J.
2026	& Higgins, D.G. 2007. ClustalW and ClustalX version 2.0. Bioinformatics 23: 2947–
2027	2948. https://doi.org/10.1093/bioinformatics/btm404
2028	Lu, S. 1999. 30. Calamagrostis Adans, 31. Deyeuxia Clarion. Pp. 130–138 in: Liu, S.W. (ed.)
2029	Flora qinghaiica, vol. 4. Xining: Qinghai People's Publishing House.
2030	Lu, S. & Phillips, S.M. 2006. 88. Calamagrostis Adanson. Pp. 359–361 in: Wu, Z.Y., Raven,
2031	P.H. & Hong, D.Y. (eds.), Flora of China, vol. 22. Beijing: Science Press; St. Louis:
2032	Missouri Botanical Garden Press.
2033	Lu, S., Chen, W. & Phillips, S.M. 2006. 87. Deyeuxia Clarion ex P. Beauvois. Pp. 348–359
2034	in: Wu, Z.Y., Raven, P.H. & Hong, D.Y. (eds.), Flora of China, vol. 22. Beijing:
2035	Science Press; St. Louis: Missouri Botanical Garden Press.
2036	Marr, K.L., Hebda, R.J. & Greene, C.W. 2007. 14.19 Calamagrostis Adans. Pp. 706–732
2037	in: Barkworth, M.E., Capels, K.M., Long, S., Anderton, L.K. & Piep, M.B. (eds.),
2038	Flora of North America north of Mexico, vol. 24, Magnoliophyta: Commelinidae (in
2039	part): Poaceae, part 1. New York: Oxford University Press.
2040	Minaya, M., Hackel, J., Namaganda, M., Brochmann, C., Vorontsova, M.S., Besnard, G.
2041	& Catalán, P. 2017. Contrasting dispersal histories of broad- and fine-leaved
2042	temperate Loliinae grasses: Range expansion, founder events, and the roles of distance
2043	and barriers. J. Biogeogr. 44: 1980–1993. https://doi.org/10.1111/jbi.13012
2044	Mill, R.R. 1985. Hyalopoa (Tzvelev) Tzvelev. Pp. 497–498 in: Davis, P.H. (ed.), Flora of
2045	Turkey and the East Aegean Islands vol. 9. Edinburgh: Edinburgh University Press.
2046	Nicora, E.G. 1978. Gramineae. Pp. 1–563 in Correa, M.N. (ed.), Flora patagonica, Parte 3.
2047	Buenos Aires: INTA.
2048	Nicora, E.A. & Rúgolo de Agrasar, Z.E. 1981. Catabrosa Pal. de Beauv. y Phippsia R.
2049	Brown (Gramineae) en América del Sur. Darwiniana 23: 179–188.
2050	Nicora, E.G. & Rúgolo de Agrasar, Z.E. 1987. Los géneros de gramíneas de América
2051	austral: Argentina, Chile, Uruguay y áreas limítrofes de Bolivia, Paraguay y Brasil.
2052	Buenos Aires: Editorial Hemisferio Sur.
2053	Nosov, N.N., Punina, E.O., Machs, E.M. & Rodionov, A.V. 2015. Interspecies
2054	hybridization in the origin of plant species: cases in the genus Poa sensu lato. Biol.
2055	Bull. Rev. 5: 366-382. https://doi.org/10.1134/S2079086415040088

2056	Orton, L.M., Burke, S.V., Duvall, M.R. 2019. Plastome phylogenomics and characterization
2057	of rare genomic change as taxonomic markers in plastome groups 1 and 2 Poeae
2058	(Pooideae; Poaceae). PeerJ 7: e6959. http://doi.org/10.7717/peerj.6959
2059	Nosov, N.N., Tikhomirov, V.N., Machs, E.M. & Rodionov, A.V. 2019. On polyphyly of the
2060	former section Ochlopoa and the hybridogenic section Acroleucae (Poa, Poaceae):
2061	insights from molecular phylogenetic analyses. Nordic J. Bot. 37:
2062	https://doi.org/10.1111/njb.02015
2063	Persson, N.L. & Rydin, C. 2016. Phylogenetic relationships of the 'Briza complex' to other
2064	members of the subfamily Pooideae (Poaceae). Pl. Ecol. Evol. 149: 216-227.
2065	https://doi.org/10.5091/plecevo.2016.1194
2066	Phillips, S.M. & Chen, W. 2003. Notes on grasses (Poaceae) for the Flora of China, I:
2067	Deyeuxia. Novon 13: 318-321. https://doi.org/10.2307/3393381
2068	Pirie, M.D. 2015. Phylogenies from concatenated data: Is the end nigh? Taxon 64: 421–423.
2069	https://doi.org/10.12705/643.1
2070	Pimentel, M., Sahuquillo, E., Torrecilla, Z., Popp, M., Catalán, P. & Brochmann, C.
2071	2013. Hybridization and long-distance colonization at different time scales: towards
2072	resolution of long-term controversies in the sweet vernal grasses (Anthoxanthum).
2073	Ann. Bot. 112: 1015-1130. https://doi.org/10.1093/aob/mct170
2074	Pimentel, M., Escudero, M., Sahuquillo, E., Minaya, M.Á. & Catalán, P. 2017. Are
2075	diversification rates and chromosome evolution in the temperate grasses (Pooideae)
2076	associated with major environmental changes in the Oligocene-Miocene? PeerJ 5:
2077	e3815. https://doi.org/10.7717/peerj.3815
2078	Quintanar, A., Castroviejo, S. & Catalán, P. 2007. Phylogeny of the tribe Aveneae
2079	(Pooideae, Poaceae) inferred from plastid <i>trnT</i> – <i>F</i> and nuclear ITS sequences. <i>Amer. J.</i>
2080	Bot. 94: 1554–1569. https://doi.org/10.3732/ajb.94.9.1554
2081	Quintanar, A., Catalán, P. & Castroviejo, S. 2010. A review of the systematics and
2082	phylogenetics of the Koeleriinae (Poaceae: Poeae). Pp. 539-556 in: Seberg, O.,
2083	Petersen, G., Barfod, A.S. & Davis, J.I. (eds.) Diversity, phylogeny, and evolution in
2084	the monocotyledons. Aarhus, Denmark: Aarhus University Press.
2085	Refulio-Rodríguez, N.F., Columbus, J.T., Gillespie, L.J., Peterson, P.M. & Soreng, R.J.
2086	2012. Molecular phylogeny of Dissanthelium (Poaceae: Pooideae) and its taxonomic
2087	implications. Syst. Bot. 37: 122-133. https://doi.org/10.1600/036364412X616701
2088	Renvoize, A.S. 1998. Gramíneas de Bolivia. Kew: The Royal Botanic Gardens.

2089	Revell, L.J. 2012. phytools: An R package for phylogenetic comparative biology (and other
2090	things). Meth. Ecol. Evol. 3: 217-223. https://doi.org/10.1111/j.2041-
2091	210X.2011.00169.x
2092	Revell, L.J. 2013. Two new graphical methods for mapping trait evolution on phylogenies.
2093	Meth. Ecol. Evol. 4: 754-759. https://doi.org/10.1111/2041-210X.12066
2094	Rieseberg, L.H. & Soltis, D.E. 1991. Phylogenetic consequences of cytoplasmic gene flow
2095	in plants. Evol. Trends Pl. 5: 65–84.
2096	Rodionov, A.V., Kim, E.S., Nosov, N.N., Rajko, M.P., Machs, E.M. & Punina, E.O. 2008.
2097	Molecular phylogenetic study of the genus Colpodium sensu lato (Poaceae: Poeae).
2098	Ekolog. Genet. 6: 34-46. [In Russian] https://doi.org/10.17816/ecogen6434-46
2099	Rodionov, A.V., Gnutikov, A.A., Kotsinyan, A.R., Kotseruba, V.V., Nosov, N.N., Punina,
2100	E.O., Rayko, M.P., Tyupa, N.B., Kim, E.S. 2017. ITS1–5.8S rDNA–ITS2 sequence
2101	in 35S rRNA genes as marker for reconstruction of phylogeny of grasses (Poaceae
2102	family). Biol. Bull. Rev. 7: 85-102. https://doi.org/10.1134/S2079086417020062
2103	Röser, M. 1989. Karyologische, systematische und chorologische Untersuchungen an der
2104	Gattung Helictotrichon Besser ex Schultes & Schultes im westlichen
2105	Mittelmeergebiet. Diss. Bot. 145: 1-250.
2106	Röser, M. 1996. Ecogeography of the grass genus Helictotrichon (Pooideae: Aveneae) in the
2107	Mediterranean and adjacent regions. Pl. Syst. Evol. 203: 181-281.
2108	https://doi.org/10.1007/BF00983512
2109	Röser, M., Döring, E., Winterfeld, G. & Schneider, J. 2009. Generic realignments in the
2110	grass tribe Aveneae (Poaceae). Schlechtendalia 19: 27-38.
2111	Rúgolo, Z.E. 2012a. Deyeuxia Clarion ex DC. Pp. 180–219 in: Zuloaga, F.O., Rúgolo, Z.E.
2112	& Anton, A.M.R. (eds.), Flora vascular de la Republica Argentina, vol. 3, II.
2113	Córdoba: Graficamente Ediciones.
2114	Rúgolo, Z.E. 2012b. Leptophyllochloa C.E. Calderón ex Nicora. Pp. 264–265 in: Zuloaga,
2115	F.O., Rúgolo, Z.E. & Anton, A.M.R. (eds.), Flora vascular de la Republica Argentina,
2116	vol. 3, II. Córdoba: Graficamente Ediciones.
2117	Rúgolo, Z.E. 2012c. Phippsia (Trin.) R.Br. Pp. 282–283 in: Zuloaga, F.O., Rúgolo, Z.E. &
2118	Anton, A.M.R. (eds.), Flora vascular de la Republica Argentina, vol. 3, II. Córdoba:
2119	Graficamente Ediciones.
2120	Rúgolo de Agrasar, Z.E. 1978. Las especies australes del género Deyeuxia Clar.
2121	(Gramineae) de la Argentina y de Chile. Darwiniana 21: 417–453.

2122 Rúgolo de Agrasar, Z.E. 1982. Revalidación del género Bromidium Nees et Meyen emend. 2123 Pilger (Gramineae). Darwiniana 24: 187-216. 2124 Rúgolo de Agrasar, Z.E. 2006. The species of the genus Deyeuxia (Poaceae, Pooideae) from 2125 Argentina and nomenclatural notes. Darwiniana 44: 131-293. 2126 Saarela, J.M., Liu, Q., Peterson, P.M., Soreng, R.J. & Paszko, B. 2010. Phylogenetics of 2127 the grass 'Aveneae-type plastid DNA clade' (Poaceae: Pooideae, Poeae) based on 2128 plastid and nuclear ribosomal DNA sequence data. Pp. 557–587 in: O. Seberg, G. 2129 Petersen, A. S. Barford, & J. I. Davis (Eds.), Diversity, phylogeny, and evolution in the 2130 monocotyledons. Aarhus: Aarhus University Press. 2131 Saarela, J.M., Wysocki, W.P., Barrett, C.F., Soreng, R.J., Davis, J.I., Clark, L.G., 2132 Kelchner, S.A., Pires, J.C., Edger, P.P., Mayfield, D.R. & Duvall, M.R. 2015. 2133 Plastid phylogenomics of the cool-season grass subfamily: clarification of relationships among early-diverging tribes. AoB Plants 7: plv046. 2134 2135 https://doi.org/10.1093/aobpla/plv046 2136 Saarela, J.M., Bull, R.D., Paradis, M.J., Ebata, S.N., Peterson, P.M., Soreng, R.J. & 2137 Paszko, B. 2017. Molecular phylogenetics of cool-season grasses in the subtribes 2138 Agrostidinae, Anthoxanthinae, Aveninae, Brizinae, Calothecinae, Koeleriinae and 2139 Phalaridinae (Poaceae: Pooideae: Poeae chloroplast group 1). PhytoKeys 87: 1-2140 139. https://doi.org/10.3897/phytokeys.87.12774 2141 Saarela, J.M., Burke, S.V., Wysocki, W.P., Barrett, M.D., Clark, L.G., Craine, J.M., 2142 Peterson, P.M., Soreng, R.J., Vorontsova, M.S. & Duvall, M.R. 2018. A 250 plastome phylogeny of the grass family (Poaceae): topological support under different 2143 2144 data partitions. PeerJ 6: e4299. https://doi.org/10.7717/peerj.4299 2145 Sánchez-Ken, J.G., Clark, L.G., Kellogg, E.A. & Kay, E.E. 2007. Reinstatement and 2146 emendation of subfamily Micrairoideae (Poaceae). Syst. Bot. 32: 71-80. 2147 https://doi.org/10.1600/036364407780360102 2148 Schneider, J., Döring, E., Hilu, K.W. & Röser, M. 2009. Phylogenetic structure of the grass subfamily Pooideae based on comparison of plastid matK gene-3'trnK exon and 2149 2150 nuclear ITS sequences. Taxon 58: 405-424. https://doi.org/10.1002/tax.582008 2151 Schneider, J., Winterfeld, G., Hoffmann, M.H. & Röser, M. 2011. Duthieeae, a new tribe 2152 of grasses (Poaceae) identified among the early diverging lineages of subfamily 2153 Pooideae: molecular phylogenetics, morphological delineation, cytogenetics and 2154 biogeography. Syst. Biodivers. 9: 27-44. 2155 https://doi.org/10.1080/14772000.2010.544339

2156	Schneider, J., Winterfeld, G. & Röser, M. 2012. Polyphyly of the grass tribe Hainardieae
2157	(Poaceae: Pooideae): identification of its different lineages based on molecular
2158	phylogenetics, including morphological and cytogenetic characteristics. Organisms
2159	<i>Diversity Evol.</i> 12: 113–132.
2160	Schouten, Y. & Veldkamp, J.F. 1985. A revision of Anthoxanthum including Hierochloe
2161	(Gramineae) in Malesia and Thailand. Blumea 30: 319–351.
2162	Sharp, D. & Simon, B.K. 2002. AusGrass: Grasses of Australia, Version 1.0. Australian
2163	Biological Resources Study: Canberra, and Environmental Protection Agency:
2164	Queensland. [CD-ROM].
2165	Soreng, R.J. & Davis, J.I. 2000. Phylogenetic structure in Poaceae subfamily Pooideae as
2166	inferred from molecular and morphological characters: misclassification vs.
2167	reticulation. Pp. 61-74 in: Jacobs, S.W.L. & Everett, J.E. (eds.), Grasses: systematics
2168	and evolution. Collingwood, Victoria, Australia: CSIRO Publishing.
2169	Soreng, R.J., Davidse, G., Peterson, P.M., Zuloaga, F.O., Judziewicz, E.J., Filgueiras,
2170	T.S. & Morrone, O. 2000 onwards. [Catalogue of New World grasses]
2171	http://www.tropicos.org/Project/CNWG (accessed 26 Apr 2019)
2172	Soreng, R.J., Peterson, P.M., Davidse, G., Judziewicz, E.J., Zuloaga, F.O., Filgueras,
2173	T.S. & Morrone, O. 2003. Catalogue of New World grasses (Poaceae): IV. subfamily
2174	Pooideae. Contr. U.S. Natl. Herb. 48: 1-730.
2175	Soreng, R.J., Davis, J.I. & Voionmaa, M.A. 2007. A phylogenetic analysis of Poaceae tribe
2176	Poeae sensu lato based on morphological characters and sequence data from three
2177	plastid-encoded genes: evidence for reticulation, and a new classification of the tribe.
2178	Kew Bull. 62: 425–454.
2179	Soreng, R.J., Bull, R.D. & Gillespie, L.J. 2010. Phylogeny and reticulation in Poa based on
2180	plastid <i>trnTLF</i> and nrITS sequences with attention to diploids. Pp. 619–643 in: Seberg,
2181	O., Petersen, G., Barfod, A.S. & Davis, J.I. (eds.), Diversity, phylogeny and evolution
2182	in the monocotyledons. Aarhus: Aarhus University Press.
2183	Soreng, R.J., Gillespie, L.J., Koba, H., Boudko, E. & Bull, R.D. 2015a. Molecular and
2184	morphological evidence for a new grass genus, Dupontiopsis (Poaceae tribe Poeae
2185	subtribe Poinae s.l.), endemic to alpine Japan, and implications for the reticulate origin
2186	of Dupontia and Arctophila within Poinae s.l. J. Syst. Evol. 53(2): 138–162.
2187	https://doi.org/10.1111/jse.12146
2188	Soreng, R.J., Peterson, P.M., Romaschenko, K., Davidse, G., Zuloaga, F.O., Judziewicz,
2189	E.J., Filgueiras, T.S., Davis, J.I. & Morrone, O. 2015b. A worldwide phylogenetic

bioRxiv preprint doi: https://doi.org/10.1101/707588; this version posted July 18, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

2190	classification of the Poaceae (Gramineae). J. Syst. Evol. 53: 117-137.
2191	https://doi.org/10.1111/jse.12150
2192	Soreng, R.J., Peterson, P.M., Romaschenko, K., Davidse, G., Teisher, J.K., Clark, L.G.,
2193	Barberá, P., Gillespie, L.J. & Zuloaga, F.O. 2017. A worldwide phylogenetic
2194	classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015
2195	classifications. J. Syst. Evol. 55(4): 259-290. https://doi.org/10.1111/jse.12262
2196	Starr, J.R., Harris, S.A., Simpson, D.A. 2003. Potential of the 5' and 3' ends of the
2197	intergenic spacer (IGS) of rDNA in the Cyperaceae: new sequences for lower-level
2198	phylogenies in sedges with an example from Uncinia Pers. Int. J. Plant Sci. 164: 213-
2199	227. https://doi.org/10.1086/346168
2200	Stuessy, T.F., Foland, K.A., Sutter, J.F., Sanders, R.W. & Silva, O.M. 1984. Botanical
2201	and geological significance of potassium-argon dates from the Juan Fernández Islands.
2202	Science 225: 49-51 https://doi.org/10.1126/science.225.4657.49
2203	Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. 1991. Universal primers for amplification
2204	of three non-coding regions of chloroplast DNA. Pl. Molec. Biol. 17: 1105–1109.
2205	Teisher, J.K., McKain, M.R., Schaal, B.A. & Kellogg, E.A. 2017. Polyphyly of
2206	Arundinoideae (Poaceae) and evolution of the twisted geniculate lemma awn. Ann.
2207	Bot. (Oxford) 120: 725-738. https://doi.org/10.1093/aob/mcx058
2208	Tkach, N.V., Hoffmann, M.H., Röser, M. & von Hagen, K.B. 2008. Temporal patterns of
2209	evolution in the Arctic explored in Artemisia L. (Asteraceae). Pl. Ecol. & Divers. 1:
2210	161-169. https://doi.org/10.1080/17550870802331912
2211	Tkach, N.V., Hoffmann, M.H., Röser, M., Korobkov, A.A. & von Hagen, K.B. 2008.
2212	Parallel evolutionary patterns in multiple lineages of arctic Artemisia L. (Asteraceae).
2213	Evolution 62: 184–198. https://doi.org/10.1111/j.1558-5646.2007.00270.x
2214	Tkach, N., Röser, M., Miehe, G., Muellner-Riehl, A.N., Ebersbach, J., Favre, A. &
2215	Hoffmann, M.H. 2015. Molecular phylogenetics, morphology and a revised
2216	classification of the complex genus Saxifraga (Saxifragaceae). Taxon 64: 1159–1187.
2217	https://doi.org/10.12705/646.4
2218	Tkach, N., Röser, M., Suchan, T., Cieślak, E., Schönswetter, P. & Ronikier, M. 2019.
2219	Contrasting evolutionary origins of two mountain endemics: Saxifraga wahlenbergii
2220	(Western Carpathians) and S. styriaca (Eastern Alps). B. M. C. Evol. Biol. 19: 18.
2221	https://doi.org/10.1186/s12862-019-1355-x

2222	Torrecilla, P. & Catalán, P. 2002. Phylogeny of broad-leaved and fine-leaved Festuca
2223	lineages (Poaceae) based on nuclear ITS sequences. Syst. Bot. 27: 241-251.
2224	https://doi.org/10.1043/0363-6445-27.2.241
2225	Torrecilla, P., López-Rodriguez, J.A. & Catalán, P. 2004. Phylogenetic relationships of
2226	Vulpia and related genera (Poeae, Poaceae) based on analysis of ITS and trnL-F
2227	sequences. Ann. Missouri Bot. Gard. 91: 124-158.
2228	Tucker, G.C. 1996. The genera of Pooideae (Gramineae) in the southeastern United States.
2229	Harvard Pap. Bot. 9: 11–90.
2230	Tutin, T.G. 1980. 90. Ammophila Host; 91. ×Ammocalamagrostis P. Fourn. Pp. 296 in:
2231	Tutin, T.G., V.H. Heywood, N.A. Burges, D.M. Moore, D H. Valentine, S.M. Walters
2232	& Webb, D.A. (eds.), Flora europaea, vol. 5. Cambridge: Cambridge University
2233	Press.
2234	Tzvelev, N.N. 1964a. O rode Colpodium Trin. [De genere Colpodium Trin.] Novosti Sist.
2235	Vyssh. Rast. 1: 5–30.
2236	Tzvelev, N.N. 1964b. Tablitza dlya opredeleniya rodov [Key to the genera]. Pp: 8–17 in:
2237	Tolmachev, A.I. (ed.), Arkticheskaya Flora SSSR, vol. 2, Gramineae. Moscow,
2238	Leningrad: Nauka.
2239	Tzvelev, N.N. 1964c. Rod 25. Colpodium Trin. Pp: 171–173 in: Tolmachev, A.I. (ed.),
2240	Arkticheskaya Flora SSSR, vol. 2, Gramineae. Moscow, Leningrad: Nauka.
2241	Tzvelev, N.N. 1968. Sistema zlakov (Poaceae) flory SSSR. [The system of the grasses
2242	(Poaceae) indigenous to the U.S.S.R.]. Bot. Zhurn. (Moscow & Leningrad) 53 (3):
2243	301–312.
2244	Tzvelev, N.N. 1970. Novye sektsii zlakov (Poaceae) flory SSSR. Poacearum sectiones novae
2245	florae URSS. Novosti Sist. Vyssh. Rast. 6 (1969): 19-22.
2246	Tzvelev, N.N. 1973. Zametki o zlakakh flory SSSR, 7. Notae de gramineis florae URSS, 7.
2247	Novosti Sist. Vyssh. Rast.10: 79–98.
2248	Tzvelev, N.N. 1976. Zlaki SSSR. Leningrad: Nauka. Tzvelev, N.N. 1993. Zametki o zlakakh
2249	(Poaceae) Kavkaza [Some notes on the grasses (Poaceae) of the Caucasus]. Bot.
2250	Zhurn. (Moscow & Leningrad) 78(10): 83–95
2251	Tzvelev, N.N. 1995a. Key to the genera. Pp. 88–97 in Tolmachev, A.I., Packer, J.G. &
2252	Griffiths, G.C.G. (eds.), Flora of the Russian Arctic, vol. 1, Polypodiaceae-
2253	Gramineae. Edmonton, Alberta: University of Alberta Press.

2254	Tzvelev, N.N. 1995b. Genus 25. Colpodium Trin. Pp. 231–233 in Tolmachev, A.I., Packer,
2255	J.G. & Griffiths, G.C.G. (eds.), Flora of the Russian Arctic, vol. 1, Polypodiaceae-
2256	Gramineae. Edmonton, Alberta: University of Alberta Press.
2257	Tzvelev, N.N. & Bolkhovskikh, Z.V. 1965. O rode tsingeria (Zingeria P.Smirn.) i blizkikh k
2258	nemu rodakh semeistva zlakov (Gramineae) (Kario-sistematicheskoe issledovanie).
2259	[On the genus Zingeria P. Smirn. and the closely allied genera of Gramineae (a caryo-
2260	systematic investigation)], Bot. Zhurn. (Moscow & Leningrad) 50: 1317-1320.
2261	Vickery, J.W. 1940. A revision of Australian species of Deyeuxia, with notes on the status of
2262	the genera Calamagrostis and Deyeuxia. Contr. New South Wales Natl. Herb. 1: 43-
2263	82.
2264	Villavicencio, X. 1995. Revision der Gattung Deyeuxia in Bolivien. Eine taxonomisch-
2265	anatomische Studie der in Bolivien auftretenden Arten der Gattung Deyeuxia.
2266	Dissertation. Freie Universität Berlin: Berlin.
2267	Watson, L. & Dallwitz, M.J. 1994. The grass genera of the world, 2nd ed. Wallingford:
2268	CAB International.
2269	Watson, L., Macfarlane, T.D. & Dallwitz, M.J. 1992 onwards. [The grass genera of the
2270	world: descriptions, illustrations, identification, and information retrieval; including
2271	synonyms, morphology, anatomy, physiology, phytochemistry, cytology,
2272	classification, pathogens, world and local distribution, and references.] Version: 4th
2273	April 2019. https://www.delta-intkey.com/ (accessed 29 Apr 2019)
2274	Weiller, C.M., Walsh, N.G. & Thompson, I.R. 2009. Deyeuxia. Pp. 190–213 in: Wilson, A.
2275	(ed.), Flora of Australia, vol. 44A, Poaceae 2. Canberra: ABRS; Melbourne: CSIRO.
2276	Wiens, J.J. 1998. Combining data sets with different phylogenetic histories. Syst. Biol. 47:
2277	568-581. https://doi.org/10.1080/106351598260581
2278	Winterfeld, G., Schneider, J. & Röser, M. 2009. Allopolyploid origin of Mediterranean
2279	species in Helictotrichon (Poaceae) and its consequences for karyotype repatterning
2280	and homogenisation of rDNA repeat units. Syst. Biodivers. 7: 277–295.
2281	https://doi.org/10.1017/S1477200009003041
2282	Winterfeld, G., Schneider, J., Perner, K. & Röser, M. 2012. Origin of highly polyploids:
2283	different pathways of auto- and allopolyploidy in 12-18x species of Avenula
2284	(Poaceae). Int. J. Pl. Sci. 173: 1-14. https://doi.org/10.1086/664710
2285	Wölk, A. & Röser, M. 2014. Polyploid evolution, intercontinental biogeographical
2286	relationships and morphology of the recently described African oat genus Trisetopsis
2287	(Poaceae). Taxon 63: 773-788. https://doi.org/10.12705/634.1

2288	Wölk, A. & Röser, M. 2017. Hybridization and long-distance colonization in oat-like grasses
2289	of South and East Asia, including an amended circumscription of Helictotrichon and
2290	the description of the new genus Tzveleviochloa (Poaceae). Taxon 66: 20-43.
2291	https://doi.org/10.12705/661.2
2292	Wölk, A., Winterfeld, G. & Röser, M. 2015. Genome evolution in a Mediterranean species
2293	complex: phylogeny and cytogenetics of Helictotrichon (Poaceae) allopolyploids
2294	based on nuclear DNA sequences (rDNA, topoisomerase gene) and FISH. Syst.
2295	Biodivers. 13: 326-345. https://doi.org/10.1080/14772000.2015.1023867
2296	Zuloaga, F.O., Nicora, E.G., Rúgolo de Agrasar, Z.E., Morrone, O., Pensiero, J. &
2297	Cialdella, A.M. 1994. Catálogo de la familia Poaceae en la República Argentina.
2298	Monogr. Syst. Bot. Missouri Bot. Gard. 47: 1–178.

2299

Fig. 1. Maximum Likelihood phylogram of Poodae (Aveneae and Poeae) inferred from plastid DNA sequences (*matK* gene–3'*trnK* exon, *trnL–trnF*) with species of Triticodae and Brachypodieae used as outgroup. 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. 2. Maximum Likelihood phylogram of Poodae (Aveneae and Poeae) inferred from nr (ITS, ETS) DNA sequences with species of Triticodae and Brachypodieae as outgroup. 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. 3. Overview of the Maximum Likelihood cladogram of Poodae (Aveneae and Poeae) inferred from the concatenated matrix of plastid (*matK* gene–3'*trnK* exon, *trnL–trnF*) and nr (ITS, ETS) DNA sequences with species of Triticodae and Brachypodieae as outgroup. 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 tree is displayed in Supplementary Fig. S1.

Fig. 4. Comparison of simplified Maximum Likelihood cladograms of Poodae (Aveneae and Poeae) inferred from plastid (*matK* gene–3'*trnK* exon, *trnL–trnF*) and nr (ITS, ETS) DNA sequences with species of Triticodae and Brachypodieae as outgroup. 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. 1 and 2, respectively.

Fig. 5. Comparison of Maximum Likelihood cladograms for the genera of subtribe Aveninae inferred from plastid (*matK* gene–3'*trnK* exon, *trnL–trnF*) and nuclear (ITS, ETS) DNA sequences. 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).

Fig. 6. Comparison of Maximum Likelihood cladograms for the genera of subtribe Sesleriinae inferred from plastid (*matK* gene–3'*trnK* exon, *trnL–trnF*) and nr (ITS, ETS) DNA sequences. 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. 7. Comparison of Maximum Likelihood cladograms for the genera of subtribe Coleanthinae inferred from plastid (*matK* gene–3'*trnK* exon, *trnL–trnF*) and nr (ITS, ETS) DNA sequences. Maximum Likelihood and Maximum Parsimony bootstrap support values >50% Bayesian posterior probabilities >0.5 are indicated on the branches. Clades with Maximum Likelihood support <50% are collapsed.

Fig. 8. Example of an ancestral state reconstruction (ASR) in Poodae (Aveneae and Poeae) for the number of florets in the spikelets (character 50). See text (Discussion – *Ancestral state reconstruction*) and Appendix 5 for further explanation. See suppl. Appendix S3 for all ASRs conducted for 74 characters.

Fig. 9. Lemmas and awns (partly trimmed) in species of Aveneae and Poeae. Scanning electron microphotographs: A, Agrostis avenacea (M. Röser 10762, HAL); B, A. capillaris (M. Röser 11296 & N. Tkach, HAL0140613); C, A. rupestris (M. Röser 11312 & N. Tkach, HAL0144916); D, Aira praecox (M. Röser 11041, HAL); E, Amphibromus nervosus (M. Röser 10770, HAL); F, Anthoxanthum odoratum (M. Röser 11006, HAL); G, Briza media (M. Röser 11072, HAL); H, Avenella flexuosa (M. Röser 11202 & N. Tkach, HAL0141248);
I, Alopecurus pratensis (M. Röser 11222 & N. Tkach, HAL0141246); J, Avenula pubescens (M. Röser 6528, HAL); K, Beckmannia eruciformis (s.coll. R382, HAL); L, Apera spica-venti (M. Röser 10699, HAL0140288); M, Avena fatua (N. Röser 11267 & N. Tkach, HAL0144749); O, Calamagrostis arundinacea (M. Röser 11274 & N. Tkach, HAL0141306). A, B, F, G, J, K, L, M & O, Dorsal view; C, D, E, H, I, N, Lateral view. — Scale bars = 1 mm.
Fig. 10. Lemmas and awns (partly trimmed) in species of Aveneae and Poeae. Scanning electron microphotographs: A, *Catapodium marinum (M. Röser 4352*, HAL); B, *Festuca lachenalii (M. Röser 5470*, HAL); C, *Corynephorus canescens (E. Willing 25.870D*, HAL0108617); D, '*Calamagrostis' flavens (I. Hensen*, HAL); E, *Cynosurus cristatus (M. Röser 622*, HAL); F, *Gastridium nitens (G. van Buggenhout 11991*, ROM); G, *Graphephorum wolfii (R.J. Soreng*, NY); H, *Helictochloa bromoides* subsp. *bromoides (M. Röser 10519*; HAL); I, *Helictotrichon petzense* subsp. *petzense (M. Röser 10646*, HAL); J & K, *Holcus mollis (M. Röser 10658*, HAL) with lower (J) and upper lemma (K); L, *Hookerochloa eriopoda (R. Pullen 4003*, AD96435171); M, *Lamarckia aurea (M. Röser 311*, HAL). A, B, H, J, Dorsal view; C, D, E, F, G, I, K, L, M, Lateral view. — Scale bars = 1 mm.

Fig. 11. Lemmas and awns (partly trimmed) in species of Aveneae and Poeae. Scanning electron microphotographs: A, *Lolium giganteum (M. Röser 11275 & N. Tkach*, HAL0141305); B, *Poa fax (D.E. Murfet 1278*, AD99151120); C, *Pentapogon quadrifidus (A. Moscal 11543*, HO 95925); D, *Periballia involucrata (s. coll., R58/R319*, HAL); E, *Peyritschia pringlei (P. Tenorio 15095*, MEXU542571); F, *Phleum crypsoides (F. Skovgaard*, C); G, *Trisetum flavescens (M. Röser 11245 & N. Tkach*, HAL0141270); H, *Ventenata macra (M. Röser 10688*, HAL); I, *Tzveleviochloa parviflora (S. & G. Miehe & K. Koch 01-073-24*, Institute of Geography, University Marburg, Germany); J, *Simplicia buchananii (A.P. Druce*, CHR 394262); K, *Tricholemma jahandiezii (M. Röser 10297*, HAL); L, *Trisetopsis elongata (S. Wagner R118b*, HAL0144713); M, *Sesleria caerulea (M. Röser 11239 & N. Tkach*, HAL0141254). A, D, G, H, J, L, M, Dorsal view; B, C, E, F, I, K, Lateral view. — Scale bars = 1 mm.

Supplementary Figure S1.

Maximum Likelihood phylogram of Poodae (Aveneae and Poeae) inferred from a concatenated matrix of plastid (*matK* gene–3'*trnK* exon, *trnL–trnF*) and nr (ITS, ETS) DNA sequences with species of Triticodae and Brachypodieae as outgroup. 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.

Supplementary Figure S2.

States of the scored 188 mainly morphological characters mapped on the tips of an ultrametric phylogenetic tree. The characters are listed in suppl. Appendix S2. The tree is based on the Maximum Likelihood analysis of the concatenated plastid and nuclear DNA sequence matrix as detailed in suppl. Fig. S1. Differently colored wedges indicate the presence of different character states.











Plastid DNA sequence data

Nuclear ribosomal DNA sequence data



Plastid DNA sequence data

Nuclear ribosomal DNA sequence data



bioRxiv preprint doi: https://doi.org/10.1101/707588; this version posted July 18, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.



bioRxiv preprint doi: https://doi.org/10.1101/707588; this version posted July 18, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.



(050) Spikelets comprising <number of fertile florets>











Appendix 1. Taxa studied in our lab for DNA sequences with 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.: USA, 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.: USA, 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 aegualis Sobol.: Germany, BadenWürttemberg, 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. kolymensis (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, Vil 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. 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: USA, Alaska, Barrow, Gas Well Road, 01.08.2000, R.J. Soreng 6204 (US); -; LR606652; LR606547; LR606361. C. nutkaensis (J.Presl) Steud.: USA, 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.' rigida (Kunth) Trin. ex Steud.: Bolivia, Department La Paz, Province Murillo, 12.02.1989, S.G. Beck 14738 (B 10 0448895); LR606851, HG797422; LR606656; HG797492; LR606364. 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. 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: USA, 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: USA, California, Siskiyou, Klamath River, 03.06.2000, R.J. Soreng 5965 (US); LR606877; LR606675; LR606558; LR606388. D. micrathera (É.Desv.) Röser & Tkach: Argentina, Neuquén Province, Los Lagos, Correntoso, 27.01.1990, Zulma Rúgolo 1245 (B 10 0448863); LR606878, LT159689; -; LT159754; LR606389. Desmazeria philistaea (Boiss.) H.Scholz: Israel, Philistean Plain, 21.03.1989, A. Danin et 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. 'D.' flavens Keng: China, Qinghai, surroundings of Maqen, 06.08.2004, I. Hensen (HAL); LR606882; LR606680; LR606561; LR606393. 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, Andalucíia, Province Cádiz, NW Gibraltar, 20.06.1985, M. Röser 11070 (HAL); LN554436; LR606699; LT159737; -. Graphephorum 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.: USA, 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 A.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. 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: USA, Texas, Washington County, 01.05.1976, T. F. Daniel 69 (NY); LR606926, LN554440; LR606728; LR606578; -. Littledalea tibetica Hemsl.: 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 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. Nikolaveva & 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: USA, 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): USA, 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.: USA, 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. Torrevochloa pauciflora (J.Presl) Church: USA, 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); LR6066992; 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 canescens Buckley: USA, Oregon, Josephine, Cave Creek, 02.06.2000, R.J. Soreng 5956 (US); LR606997, AM234611; LR606797; LR606603; LR606504. T. cernuum Trin.: USA, Montana, Glacier County, Alon Continental Divide, 19.07.2003, P. Lesica 8714 (NY1819808); LR606998, LT159703; LR606798; LT159797; LR606505. T. flavescens (L.) P.Beauv.: Germany, Baden-Württemberg, near Tübingen, 26.06.1984, M. Röser 1871 (HAL); LR606999; LR606799; LR606604; LR606506. T. spicatum (L.) K.Richt.: USA, Alaska, Dalton Hwy, Chandler Shelf, 05.08.2000, R.J. Soreng 6221 (US Catalog No.: 3682816, Barcode: 01259847), LR607000, LT159707; LR606800; LT159801; LR606507. 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. Vahlodea atropurpurea (Wahlenb.) Fr. ex Hartm.: Canada, British 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. Sequences included in the final alignments (suppl. Appendix S1) for the phylogenetic reconstructions are marked by an asterisk (see Material and Methods). 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.

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; -; -; -. 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; DO353977; -: GO324247, GQ324248, GQ324249. A. subfastigiata (Trin.) Prob.: KM523849*; EU792449*; EU792372*; GO324250*. 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 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; -; -. Lagurus ovatus L.: -; DQ631464; -; -. Lamarckia aurea (L.) Moench: KJ599279; KJ599392; -; KJ599052*. Limnas stelleri Trin.: -; -; -; KM523710*. Littledalea tibetica Hemsl.: 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, GO324273. Molineriella laevis (Brot.) Rouy: DO786929; 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; 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; -; -; GO283185, GO283186, GO283187, GO283188, GO324285. 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 canescens* Buckley: DQ786946; -; -; -, *T. cernuum* Trin.: DQ786946; -; -; -, *T. flavescens* (L.) P.Beauv.: -; JQ041860; -; -. *T. spicatum* (L.) K.Richt.: -; FJ394585; -; -. *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 repositories 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:

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).

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*.

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:

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. – The ITS sequence of *H*. correspond to sequencesFJ196303 (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* rDNAs (Nosov & al., 2015; Rodionov & al. 2017). The issue warrants further investigation.

Ammochloa palaestina Boiss. – The ITS sequence DQ539587 (Quintanar & al., 2005: Fig. 5) belongs to a species of the genus *Helictochloa* and not to *Ammochloa*.

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