

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

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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  
48 spikelets and their components might be that they have little to do with pollination (always  
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 Pooideae 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, Hypseochoinae 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. trichopodium*, *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

62 **Keywords** ancestral state reconstruction; ASR; *Arctohyalopoa*; Aveneae; classification;  
63 *Hyalopodium*; phylogenetic character mapping; phylogeny; Poeae; taxonomy

64

65 **Supporting Information** may be found online in the Supporting Information section at the  
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<sub>3</sub> 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; Quintanar & 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  
91 (Torrecilla & Catalán, 2002, Catalán & al., 2004; Torrecilla & al., 2004; Catalán & al., 2007;  
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  
99 Poeae s.str. since molecular phylogenetic data did not corroborate their separation according  
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).

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

122 Secondly, we attempted to clarify the phylogenetic position of several genera  
123 previously not sampled in molecular phylogenetic investigations, to address questionable data  
124 in DNA sequence repositories and to correct a few problem cases we have created ourselves  
125 in previous publications from our lab.

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

131

## 132 MATERIAL AND METHODS

133 **Classification employed.** — We follow in this study, as far as possible, the  
134 classification of grass subfamily Pooideae displayed by Soreng & al. (2017). This  
135 classification utilizes a comparatively narrow delineation of subtribes and the rather  
136 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 Pooideae 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/](http://botany.si.edu/ing/)),  
147 *Tropicos* ([tropicos.org](http://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 257 species 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 Pooideae, 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  
169 **Molecular methods and sequence alignment.** — FastPrep FP120 cell disrupter  
170 (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*  
185 AACTGAGCATCCTGACCTTTTCTTG) were used in combination with the primers cited.  
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

205 plastid (including *matK* gene–3′*trnK* exon and *trnL–trnF*) DNA sequence datasets were first  
206 analysed separately using the phylogenetic approaches of Maximum Likelihood (ML),  
207 Maximum Parsimony (MP) and Bayesian Inference (BI) following Tkach & al. (2019). All  
208 trees were visualized with FigTree 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>). Support  
209 values are cited in the text in the following sequence: ML bootstrap support/MP bootstrap  
210 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).

233 We commonly used the genus data in the morphological character matrix. Exceptions  
234 were made when genus boundaries did not match our genus circumscriptions or when no data  
235 were available for a genus. Then we used species data and checked them for their  
236 applicability for the whole genus and eventually modified them accordingly. Character  
237 mapping on the molecular phylogenetic tree derived from the concatenated plastid and

238 nuclear DNA sequence dataset was conducted in R version 3.5.0 with the package Phytools  
239 (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-](http://blog.phytools.org/2016/10/stochastic-mapping-discrete-character.html)  
251 [mapping-discrete-character.html](http://blog.phytools.org/2016/10/stochastic-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

264 **Plastid DNA analysis.** — The plastid *matK* gene–3′*trnK* exon DNA sequence dataset  
265 for 208 taxa included 2,530, the *trnL–trnF* DNA dataset for 199 taxa included 1,414 aligned  
266 positions, respectively. The combined data matrix of the two plastid DNA markers for 214  
267 taxa included a total of 3,927 aligned positions, of which 1,470 were variable (*matK* gene–  
268 3′*trnK* exon: 984, *trnL–trnF*: 488) and 907 parsimony-informative (*matK* gene–3′*trnK* exon:  
269 622, *trnL–trnF*: 286).

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



272 100/99/1.00, respectively (Fig. 1). One of the lineages agreed with the “Poeae chloroplast  
273 group 1 (Aveneae type)” as termed by Soreng & al. (2007) or tribe Aveneae as suggested here  
274 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  
293 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).

300 The second main lineage of the plastid DNA tree was the “Poeae chloroplast group 2  
301 (Poeae type)” or tribe Poeae s.str. as suggested in this study. It had a major basal polytomy  
302 consisting of Airinae, which received maximum support (100/100/1.00), a large lineage with  
303 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).

359           The large clade with 85/-/1.00 support of the backbone polytomy showed a partly  
360 well-supported internal structure. It encompassed Holcinae (100/100/1.00) and Airinae  
361 (100/99/1.00) as supported sister clades (95/84/1.00), Anthoxanthinae, a lineage (95/-/1.00) of  
362 *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  
368 with low support along with Echinopogoninae, which encompassed also '*Deyeuxia contracta*  
369 (93/91/1.00).

370           Aveninae segregated into two different lineages similar to the ones encountered in the  
371 plastid DNA tree, except for the position of *Tricholemma* (Röser) Röser and *Lagurus* L. One  
372 of the lineages, Aveninae s.str. (76/56/1.00), assembled with non-monophyletic Sesleriinae in

373 a common lineage (85/58/1.00), whereas the other corresponded to the Koeleriinae lineage  
374 (96/53/1.00). It had *Lagurus* (Lagurinae) as early branching genus and encompassed  
375 ‘*Calamagrostis*’ *rigida*.

376

377 **Analysis of the combined DNA dataset.** — Following the rationale outlined in  
378 Material and Methods we analyzed also a concatenated dataset of plastid and nuclear DNA  
379 sequence data to evaluate which of the clades retrieved by the individual analyses kept stable  
380 or eventually became even better supported and which clades became less supported or  
381 collapsed.

382 The combined data matrix of all plastid and nuclear DNA sequences for 218 taxa  
383 included a total of 5,736 aligned positions of which 2,564 were variable and 1,770 parsimony-  
384 informative.

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).

397 Within the clade of Poeae (98/64/1.00), several highly supported lineages were  
398 resolved but were part of a polytomy: Scolochloinae, Aristaveninae, Helictochloinae  
399 (100/100/1.00 each), Sesleriinae (100/99/1.00), Holcinae (100/100/1.00) unified with Airinae  
400 (100/100/1.00) in a common clade (88/88/1.00), a low-support clade of Antinoriinae with  
401 supersubtribe Loliidinae (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 Loliidinae 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.

444 *Macrobriza* as member of monophyletic Brizinae in the plastid DNA tree was nested  
445 along with Sesleriinae and Aveninae in the nuclear tree. Furthermore, *Arctopoa* was placed in  
446 a clade along with Poinae in the plastid but within the ABCV+A clade in the nuclear tree  
447 (Gillespie & al., 2008, 2010; Nosov & al., 2015, 2019). Many further genera showed  
448 switching positions within their respective subtribes, for example, within Aveninae,  
449 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  
455 *Macrobriza*), the ADCP, AD and CP clades (Fig. 4, suppl. Fig. S1). Also many subtribes were  
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 Loliidinae, 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 these  
474 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

487 *Hybrid origin of major lineages or subtribes and genera derived from hybridization*  
488 *between them.* – The examples of discordant grouping are best explained by ‘chloroplast  
489 capture’, which means hybridization (Rieseberg & Soltis, 1991). Some lineages and genera  
490 have seemingly reticulate origin documented by the incongruent placement in the plastid and  
491 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).

504 (3) Scolochloinae had a maternal parent inheriting the plastid DNA from Poeae s.str.,  
505 most likely from outside the PPAM clade, namely from relatives of Loliinae and Sesleriinae  
506 (Figs. 1, 4). The paternal parent as indicated by the nuclear rDNA was distantly related and  
507 was close to supersubtribe Agrostidodinae such as seen in Phalaridinae and Torreyochloinae  
508 (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*).

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



543 between a maternal *Sesleriella*- and a paternal *Psilathera*-like ancestor. The monospecific  
544 genus *Echinaria* was unlikely to be involved in the origin of *Sesleria*, because it is a short-  
545 lived annual of the Mediterranean lowlands in contrast to the other genera in question, which  
546 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. [ $\equiv$  *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*  
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).

558 (4) The monospecific genus *Castellia* Tineo [*C. tuberculosa* (Moris) Bor] of subtribe  
559 Loliinae presumably originated from a *Festuca* Tourn. ex L.-like maternal ancestor providing  
560 the plastid and a paternal ancestor related to *Drymochloa* Holub (Figs. 1, 2; see below  
561 *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* [≡ *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*, Sub-Saharo-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  $\times$ *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*  
643 (Kunth) Finot studied by Wölk & Röser (2017) showing their monophyly], *Sphenopholis*  
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 ≡ *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  
663 clade with clade A genera (Figs. 1, 5) in the former analysis and sister to the Koeleriinae clade  
664 B (74/68/0.86) in the latter (Figs. 2, 5). Most likely due to the different taxon sampling, *S.*  
665 *sibiricum* stood in the study of Barberá & al. (2019) in a polytomy with clades A and B  
666 according to the nuclear DNA, whereas it was sister to clade B according to their plastid DNA  
667 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

679 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  
683 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  
685 ITS/GBSSI tree of their Fig. 2, whereas *B. media* clustered with taxa of *Chascolytrum*, which  
686 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  
691 (plastid donor) and Aveninae/Sesleriinae as discussed above suggests its exclusion from  
692 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 ‘*Deyeuxia*’  
701 *contracta*. A placement within Echinopogoninae was reported also for the species of  
702 ‘*Deyeuxia*’ 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 ‘*Deyeuxia*’ *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 ‘*Deyeuxia*’ is not applicable anyway (see following  
709 chapter).

710         Calothecinae (Mexico to South America) encompasses only *Chascolytrum* Desv. [type  
711 *C. subaristatum* (Lam.) Desv.] after inclusion of several segregate genera such as  
712 *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  
717 & al. (2008: fig. 2) although without support. As addressed above, this was possibly due to  
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).

741 The second supported lineage in the plastid DNA tree (96/81/1.00; Fig. 1) comprised  
742 *Agrostis alopecuroides* Lam. [= *Polypogon monspeliensis* (L.) Desf., type of *Polypogon*  
743 Desf.], *A. avenacea* J.F.Gmel. [= *Lachnagrostis filiformis* (G.Forst.) Trin., type of  
744 *Lachnagrostis* Trin.], *A. capillaris* L., *A. linkii* Banfi, Galasso & Bartolucci [= *Chaetopogon*  
745 *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  
752 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  
754 within *Agrostis* considering the ITS data investigated by Quintanar & al. (2007) and Saarela  
755 & 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).

760 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 (Hitcch.) Hultén. It was separate from *Agrostis* in both analyses, which supports to maintain  
764 *Podagrostis* as a distinct genus (Figs. 1, 2).

765 The holarctic, temperate species of *Calamagrostis* sampled in this study (Old and New  
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 *Deyeuxia* (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  
779 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. [= *×Calammophila baltica* (Flüggé ex Schrad.) Brand ≡ *×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

803 *Sesleriinae and Scolochloinae.* – The largely European subtribe Sesleriinae  
804 encompasses species with capitate or spiciform inflorescences, among them two small genera  
805 of short-lived annuals, *Mibora* with two species [type *M. minima* (L.) Desv.] and  
806 monospecific *Echinaria* [*E. capitata* (L.) Desf.]. *Mibora* and *Oreochloa* [type *O. disticha*  
807 (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, *Mibora/Oreochloa* 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



815 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, Torreychloinae 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  
838 Schneider & al. (2012), was included (Saarela & al., 2017). *Deschampsia* encompasses  
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).

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 Lolioidinae, 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

883 *Loliinae*. – The large and worldwide distributed subtribe *Loliinae* was represented in  
884 this study by a small sample of taxa. It has been investigated and shown to be monophyletic  
885 by several previous studies (see Introduction). Affiliation of former *Megalachne* Steud. and  
886 *Podophorus* Phil., endemics of the Juan Fernández Islands (Chile), with *Loliinae* was  
887 established by Schneider & al. (2011, 2012). Subtribe *Loliinae* was characterized in this study  
888 by two supported main lineages in the plastid and combined data analyses (Fig. 1, suppl. Fig.  
889 S1), one of which was formed by *Drymochloa sylvatica* (Pollich) Holub (= *Festuca altissima*  
890 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. [≡ *F. gigantea* (L.) Vill. ≡  
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).

904 The nuclear DNA results agreed widely with the trees of the plastid data analyses,  
905 however, *Castellia* was differently placed, namely together with *Drymochloa* (Fig. 2) and not  
906 with the lineage of *Festuca* s.str. as just mentioned. This points to a hybrid origin of this odd  
907 monotypic, Mediterranean to mid-East genus (see above *Reticulations within major lineages*).

908 The South American representatives sampled of *Festuca* s.str., namely *F. floribunda*  
909 from the Andes and the endemics of Chilean Juan Fernández Islands, *F. berteroniana* and *F.*  
910 *masatierrae*, formed a monophyletic cluster in the nuclear DNA analysis. *Festuca floribunda*  
911 belongs to the group “American II” of fine-leaved *Festuca* in the study on the historical  
912 biogeography of *Loliinae* by Minaya & al. (2017). Group “American II” has colonised South  
913 America in the Miocene, a time frame that makes sense also for the establishment of *F.*  
914 *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.) and  
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 et 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.) Burolet [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

950 *PPAM clade and Coleanthinae*. – The PPAM clade was resolved in all analyses of this  
951 study. It was more strongly supported in the nuclear than the plastid DNA analysis but  
952 obtained maximum support in the combined data tree (see above *Tree of the combined plastid*  
953 *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).

977 The nuclear tree revealed *Hyalopodium* (*H. araraticum*) as sister to the clade with the  
978 species of *Colpodium*, which was similarly encountered in the ITS studies of Rodionov & al.  
979 (2008) and Kim & al. (2008, 2009). However, the plastid tree supported a deviant relationship  
980 of *Hyalopodium* (Figs. 2, 7), namely to *Paracolpodium* and *Hyalopoa* (*H. pontica*). These  
981 differences between the plastid and nuclear DNA analyses suggest an origin of *Hyalopodium*  
982 as a hybrid between two different lineages of Coleanthinae (Fig. 7). *Hyalopodium araraticum*  
983 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 a 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/Phippisia* 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/Phippisia*-like rDNA from its paternal ancestor while its  
1017 maternal rDNA from *Catabrosa/Catabrosella* was lost.

1018 Monospecific holarctic annual *Coleanthus* [*C. subtilis* (Tratt.) Seidel ex Roem. &  
1019 Schult.] was clear sister to perennial Arctic (two species) and high Andean (one species)  
1020 *Phippsia* [type *P. algida* (Sol.) R.Br.]. Both genera share conspicuous morphological  
1021 characters such as missing or obsolescent, small glumes and a caryopsis protruding from the  
1022 floret at maturity (Nicora & Rúgolo de Agrasar, 1981; Clayton & Renvoize, 1986; Rúgolo,  
1023 2012b).

1024 The sister relation of the small genus *Sclerochloa* [2–3 species; type *S. dura* (L.)  
1025 P.Beauv.] and the large genus *Puccinellia* (110 species) was likewise firmly supported (Figs.  
1026 1, 2, 7), even after inclusion of more species of the latter genus (data not shown; Appendix 2;  
1027 Hoffmann & al., 2013; Soreng & al., 2015b).

1028

1029 *PAM clade, Avenulinae, Miliinae and Phleinae.* – The small subtribes Avenulinae  
1030 (*Avenula*), Miliinae (*Milium* L.) and Phleinae (*Phleum* L.) formed together with Poinae and  
1031 the elements of the ABCV(+A) clade the PAM clade (~supersubtribe Poodinae). It was  
1032 resolved in the plastid DNA and combined data analysis of this study and encompassed also  
1033 *Avenula pubescens* (Huds.) Dumort., type of the monospecific genus *Avenula* (Fig. 1, suppl.  
1034 Fig. S1). The PAM clade was unresolved in the nuclear DNA tree since its subtribes did not  
1035 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  
1048 and does not give evidence on hybrid origin of this taxon. In- or exclusion of this taxon did  
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).

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 *Poa* 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 weakly 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 *Nepheleochloa* 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 *Nepheleochloa*, which supports to maintain them as separate  
1093 genera.

1094 The HSAQN clade was well-supported only in the trees of the nuclear and combined  
1095 DNA data, such as the DAD clade (Fig. 2, suppl. Fig. S1). The former is biogeographically  
1096 characterized 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,  
1098 whereas the remaining taxa of the HSAQN clade occur in Australasia and southern South  
1099 America.

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  
1103 many other taxa in the large polytomy of the ABCV clade (Fig. 1). *Arctohyalopoa* comprises  
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). It should be noted that our previously published  
1116 sequence of *Hyalopoa lanatiflora* (Döring & al., 2007; Döring, 2009) is wrong such as  
1117 seemingly a sequence of Rodionov & al. (2008), which was also used by Hoffmann & al.  
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* [ $\equiv$  *Colpodium lanatiflorum* (Roshev.) Tzvelev] differs from both the other species  
1122 of *Colpodium* subg. *Hyalopoa* Tzvelev ( $\equiv$  *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, ...  
1125 paleas bare and smooth on keels...” (cited from Tzvelev, 1995a: 94–95). The epithet  
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 &  
1138 al., 2004) and the occurrence of hybrids between *D. fisheri* and *D. fulva* (Trin.) Röser &  
1139 Tkach, comb. nov. that were formerly regarded as intergeneric hybrid and treated under the  
1140 nothogenus  $\times$ *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.

1149 *Beckmannia* [type *B. eruciformis* (L.) Host] and monospecific *Pholiurus* [*P.*  
1150 *pannonicus* (Host) Trin.] were well-supported sister in the nuclear DNA tree in agreement  
1151 with Hoffmann & al. (2013) but less supported in the plastid DNA tree (Figs. 1, 2).  
1152 *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  
1160 supported sister in the nuclear and combined trees. Both share spikelets that are falling entire,  
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,  
1166 Beckmanniinae and Cinninae and the delineation of these tribes certainly warrant future work.

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 yet 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

1180 **Morphological characteristics.** — The sequence of the following examples of  
1181 morphological characteristics is character no., character state in brackets, whereby character  
1182 states with an underline mean the occurrence of different character states in a single taxon.  
1183 This instance appears in suppl. Fig. S2 as a pie chart. If more than one character was found  
1184 within a lineage, the character states are given in alphabetical order. If character state (b) is  
1185 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 Hypseochoinae 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,  
1212 Loliidinae and Poidinae (~PAM clade), the PPAM clade and also larger subtribes such as  
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).

1231 *Macrobriza maxima* shared a number of characters with Brizinae, the subtribe which  
1232 provided one of its ancestors: 54 (a\_b), 118 (a\_b\_c), 136 (a\_f), 138 (a\_c), 140 (a\_b). In other  
1233 characters *Macrobriza* deviated from Brizinae, for example, 24 (c), 142 (d\_e), 171 (a\_b), 175  
1234 (a\_c), which supports its hybrid origin as disclosed by molecular phylogenetics.

1235  
1236 **Ancestral state reconstruction.** — Ancestral state reconstructions applied for 74 non-  
1237 molecular characters (described in suppl. Appendix S2) of the taxa of Poodae studied are  
1238 visualised in suppl. Appendix S3 and, exemplarily for character 50, in Fig. 8. The ancestral  
1239 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;

1243 absence of rhizomes (character 4) with secondary development of rhizomatous species  
1244 in many lineages;

1245 ligule an eciliate membrane (character 12);

1246 flat leaves (character 17) with secondary development of conduplicate, involute and  
1247 convolute 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. Capitulate

1252 inflorescences originated within some Poeae, namely in Sesleriinae, Ammochloinae and some  
1253 members of the ABCV+A clade;

1254 panicles with many spikelets (character 35) and reduction to few spikelets in many  
1255 lineages, within Aveneae especially in some Aveninae and Agrostidinae, within Poeae in  
1256 some Loliinae, many Parapholiinae and Coleanthinae;

1257 panicle branches at most moderately divided (character 38); flexible (character 41).  
1258 Stiff branches originated infrequently (e.g., in Parapholiinae), whereas capillary branches  
1259 were frequent in Airinae and Coleanthinae. In Airinae, such capillary branches were likely to  
1260 be the original character state, whereas in Coleanthinae flexible branches appeared to be  
1261 plesiomorphic;

1262 panicle branches smooth (character 42), whereas scaberulous or scabrous branches  
1263 developed multiple times in parallel;

1264 spikelets pedicelled (characters 46 and 47), whereas sessile spikelets developed  
1265 multiple times and less frequently in Aveneae (some Aveninae, especially *Koeleria*, and  
1266 Phalaridinae) than within Poeae (in Loliinae two times in parallel, CP clade, parts of  
1267 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;

1279 spikelets with a rhachilla extension bearing a sterile florets at the apex were slightly  
1280 more likely than a barren rhachilla extension or a missing rhachilla extension (character 51).  
1281 For Aveneae, a barren rhachilla extension was the most likely ancestral state, which applies  
1282 also for Aveninae and Agrostidinae but parts of Echinopogoninae and Agrostidinae and  
1283 *Airopsis* of Brizinae showed an obviously secondary loss of the rhachilla extension, whereas  
1284 absence of a rhachilla extension was the plesiomorphic character state in the anyway strongly  
1285 modified spikelets of Anthoxanthinae and Phalaridinae. For Poeae, a rhachilla extension

1286 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  
1295 to the ancestral state of Aveneae or Poodae as a whole with 2 or more fertile florets. Within  
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/Phippisia*),  
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);  
1303 spikelets laterally and at most moderately compressed (characters 54 and 55); terete or  
1304 dorsally compressed spikelets in only few lineages (Brizinae, *Holcus*, some Loliinae,  
1305 *Colpodium* p.p., Miliinae);  
1306 comparatively large spikelets of either 4–6 mm or >6 mm in length with almost equal  
1307 probability. This applied also to be the ancestral state in Aveneae, whereas a length of 4–6  
1308 mm is more likely in Poeae (character 57). For Aveninae, the larger size of >6mm was most  
1309 likely ancestral, with a seemingly secondary diminution in the American lineage of  
1310 *Limnodea/Peyritschia/Sphenopholis* and the supersubtribe Agrostidodinae, in which  
1311 especially Agrostidinae underwent a reduction to <3 mm. Secondary downsizing was likely  
1312 also for Airinae, Antinoriinae, a part of Coleanthinae (*Coleanthus*, *Colpodium*, *Phippisia*) 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;

1319 spikelets, which disarticulate below each floret (character 61), but with few exception  
1320 in Aveninae, Parapholiinae, Alopecurinae and Ventenatinae; rhachilla internodes that are not  
1321 thickened (character 63) but with sporadic exceptions in various groups; glumes persistent on  
1322 branch, if spikelet breaks up (character 71) but with sporadic exceptions in Aveninae,  
1323 Agrostidinae, Holcinae, Parapholiinae, Coleanthinae and the ABCV+A clade; similar glumes  
1324 but with sporadic exceptions in Aveninae and Agrostidinae and especially Scolochloinae  
1325 (character 72);

1326 glumes shorter than spikelet, which applied also for tribes Aveneae and Poeae as a  
1327 whole, respectively, but not for Aveninae, in which the longer glumes reaches or exceeds the  
1328 length of the spikelet (character 73). The latter applied also to Agrostidinae, whereas  
1329 Torreyochloinae, most Brizinae and Calothecinae have kept the ancestral state of shorter  
1330 glumes. Within Poeae, there was a comparatively rare trend to longer glumes discernable,  
1331 namely in Airinae, some Parapholiinae and Coleanthinae, Miliinae and few members of the  
1332 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;

1341 lower glume 3–6 mm long (character 78), with a sporadic trend to diminution, namely  
1342 within Aveneae in Aveninae (especially Koeleriinae clade A; Fig. 5) and Calothecinae, within  
1343 Poeae in *Molineriella* (Helictochloinae), Aristaveninae, parts of Airinae, Sesleriinae and  
1344 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;

1348 lower glume 0.6-fold to as long as the upper, with shortening as well as enlargement  
1349 sporadically encountered in various groups (character 79); of similar consistency on margins  
1350 or margins much thinner in several groups (character 81); 1-keeled, with sporadic transition to  
1351 unkeeled shape in various groups (character 82); keeled all along, with sporadic transition to  
1352 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  
1397 and Phalaridinae and, as a rare exception, in Aveninae (*Arrhenatherum*); fertile florets (if  
1398 more than 1) all alike, with occasional exceptions, especially Holcinae and *Ventenata*  
1399 (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;  
1416 lemma with 4–5 veins (characters 125, 126), which was the ancestral state also of both  
1417 Aveneae and Poeae but transition to >5 veins occurred within Aveneae in Aveninae (in  
1418 Aveninae s.str. and parts of Koeleriinae), Hypseochloinae and parts of Brizinae, within Poeae  
1419 in Helictochloinae, Ammochloinae, Phleinae and parts of Loliinae. Diminution to 1–3 veins

1420 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  
1423 Sesleriinae (Fig. 11M) and others (Figs. 9C,L, 10A, 11D,F,J,L); general extent of hairiness all  
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  
1433 reversal to mucronate/awned lemma apices in some Poinae and members of the ABCV+A  
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 Hypseochoinae (*Hypseochoa*) 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 Hypseochoinae, 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

1454 specimens of *Periballia* Trin.), Avenulinae (Fig. 9J) and some members of Ventenatinae (Fig.  
1455 11H); geniculate awns mostly clearly exerted from spikelets, whereas straight awns were not  
1456 or scarcely exerted (character 154);

1457 principal lemma awn not coloured, whereas coloured awns seemed to occur  
1458 sporadically and secondarily, namely within Aveneae in parts of Aveninae, Echinopogoninae  
1459 and Agrostidinae, within Poeae in Helictochloinae, Airinae, more rarely in Loliinae and  
1460 Poinae (character 156);

1461 absence of a distinct column of the lemma awn, which was the ancestral state also for  
1462 Aveneae and Poeae; acquisition of distinct columns (character 155) was seemingly linked  
1463 with the origin of dorsal awns (as described before). Distinctness of columns was secondarily  
1464 lost especially in parts of the Aveninae, namely some members of the Koeleriinae lineage,  
1465 and Agrostidinae;

1466 column of lemma awn not twisted, which was the ancestral also for both Aveneae and  
1467 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+A  
1481 clade;

1482 palea  $\geq 0.7$ -fold longer than the lemma (character 166) and with smooth keels  
1483 (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  
1497 both Aveneae and Poeae (character 182); anthers  $\geq 1$  mm with diminution of size likewise in  
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.  
1508       hilum linear and straight, which was the ancestral state for also for both Aveneae and  
1509 Poeae individually (character 188). A transition to short, elliptic or punctiform hila occurred  
1510 within Aveneae especially in the Koeleriinae lineage of Aveninae, in Calothecinae and some  
1511 Agrostidinae. Within Poeae it seemed to be quite characteristic of Airinae, Sesleriinae,  
1512 Ammochloinae, Coleanthinae but occurred more sporadically also in parts of Parapholiinae  
1513 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  
1523 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).

1527 We suppose (1) that the consistent occurrence of two clearly differentiated chloroplast  
1528 DNA lineages without intermediates reflects a major evolutionary differentiation.

1529 The absence (2) of equivalent differentiation in the nuclear DNA of these plants does  
1530 make it impossible to use the plastid DNA results for classification. It should be noted in this  
1531 context that supported backbone structure was absent also in several nuclear single copy gene  
1532 trees we have studied (J. Schneider, unpub. data) and not only in the repetitive rDNA tree  
1533 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).

1546 The proposed modified classification uses narrowly delineated and preferably  
1547 monophyletic subtribes as applied in most recent treatments of the study group (e.g., Soreng  
1548 & al. (2007, 2015, 2017); Kellogg, 2015; Saarela & al. 2017):

1549 Supertribe Poodae L.Liu: (1) tribe Aveneae Dumort.: subtribes Aveninae J.Presl,  
1550 Anthoxanthinae A.Gray, Torreyochloinae Soreng & J.I.Davis, Phalaridinae Fr., Brizinae  
1551 Tzvelev, Hypseochloinae Röser & Tkach, Echinopogoninae Soreng, Calothecinae Soreng,  
1552 Agrostidinae Fr.; (2) tribe Poeae R.Br.: subtribes Scolochloinae Tzvelev, Aristaveninae  
1553 F.Albers & Butzin, Helictochloinae Röser & Tkach, Holcinae Dumort., Airinae Fr.,  
1554 Sesleriinae Parl., Antinoriinae Röser & Tkach, Loliinae Dumort., Ammochloinae Tzvelev,  
1555 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.

1562 1845.

1563 *Description.* – Annual or rarely (in *A. agrostidea*) perennial, caespitose or decumbent;  
1564 leaf sheath margins free, leaf blades flat; ligule an unfringed membrane, 1–3 mm long;  
1565 inflorescence paniculate; spikelets pedicellate, laterally compressed, 1–2 mm long, with 2  
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

1576 **Avenulinae** Röser & Tkach, **subtribus nov.** – Type: *Avenula* (Dumort.) Dumort., Bull. Soc.

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 ± 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 *Helictochloa*) raceme-like; spikelets 10–36 mm (*Helictochloa*) 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.** ≡ *Hierochloe odorata* (L.) P.Beauv. subsp. *sibirica* 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.** ≡ *Hierochloe odorata* (L.) P.Beauv. subsp. *kolymensis* 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    ***Arctohyalopoa lanatiflora*** (Roshev.) Röser & Tkach, **comb. nov.** ≡ *Poa lanatiflora* Roshev.,  
1644            Izv. Bot. Sada Akad. Nauk S.S.S.R. 30: 303. 1932.

1645

1646    ***Arctohyalopoa lanatiflora*** subsp. ***ivanoviae*** (Malyshev) Röser & Tkach, **comb. nov.** ≡  
1647            *Colpodium ivanoviae* Malyshev, Novosti Sist. Vyssh. Rast. 7: 295. 1971 [1970 publ.  
1648            1971].

1649

1650    ***Arctohyalopoa lanatiflora*** subsp. ***momic*** (Tzvelev) Röser & Tkach, **comb. nov.** ≡  
1651            *Colpodium lanatiflorum* Tzvelev subsp. *momicum* Tzvelev, Fl. Arct. URSS 2: 172.  
1652            1964.

1653

1654    ***Colpodium biebersteinianum*** (Claus) Röser & Tkach, **comb. nov.** ≡ *Agrostis biebersteiniana*  
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 ***Colpodium kochii*** (Mez) Röser & Tkach, **comb. nov.** ≡ *Milium kochii* Mez, Notes Roy. Bot.  
1661 Gard. Edinburgh 17: 211. 1921 ≡ *Zingeria kochii* (Mez) Tzvelev, Bot. Zhurn.  
1662 (Moscow & Leningrad) 50: 1318. 1965.
- 1663
- 1664 ***Colpodium pisidicum*** (Boiss.) Röser & Tkach, **comb. nov.** ≡ *Agrostis pisidica* 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 ***Colpodium trichopodum*** (Boiss.) Röser & Tkach, **comb. nov.** ≡ *Zingeria trichopoda* (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 ***Colpodium verticillatum*** (Boiss. & Balansa) Röser & Tkach, **comb. nov.** ≡ *Milium*  
1673 *verticillatum* Boiss. & Balansa, Bull. Soc. Bot. France 5: 169. 1858 ≡ *Zingeria*  
1674 *verticillata* (Boiss. & Balansa) Chrték, Novit. Bot. Delect. Seminum Horti Bot. Univ.  
1675 Carol. Prag. 1963: 3. 1963 ≡ *Zingeriopsis verticillata* (Boiss. & Balansa) Probst.,  
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 ≡ *Leptophyllochloa micrathera* (É.Desv.)  
1680 C.E.Calderón ex Nicora, Fl. Patagonica 3: 70. 1978.
- 1681
- 1682 ***Dupontia fulva*** (Trin.) Röser & Tkach, **comb. nov.** ≡ *Poa fulva* Trin., Mém. Acad. Imp. Sci.  
1683 St.-Pétersbourg, Sér. 6, Sci. Math. 1: 378. 1830.
- 1684
- 1685 ***Festuca masafuerana*** (Skotts. & Pilg. ex Pilg.) Röser & Tkach, **comb. nov.** ≡ *Bromus*  
1686 *masafueranus* Skotts. & Pilg. ex Pilg., Repert. Spec. Nov. Regni Veg. 16: 385. 1920  
1687 ≡ *Megalachne masafuerana* (Skotts. & 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 ≡ *Hyalopodium araraticum* (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 ***Hyalopodium araraticum*** (Lipsky) Röser & Tkach, **comb. nov.** ≡ *Catabrosa araratica*  
1716 Lipsky, Trudy Imp. S.-Peterburgsk. Bot. Sada 13: 358. 1894.  
1717
- 1718 ***Paracolpodium baltistanicum*** (Dickoré) Röser & Tkach, **comb. nov.** ≡ *Colpodium*  
1719 *baltistanicum* Dickoré, Stapfia 39: 114. 1995.  
1720
- 1721 ***Parapholis cylindrica*** (Willd.) Röser & Tkach, **comb. nov.** ≡ *Hainardia cylindrica* (Willd.)  
1722 Greuter, Boissiera 13: 177. 1967.  
1723

1724 *Parapholis* *×pauneroi* (Castrov.) Röser & Tkach, **comb. nov.**  $\equiv$  *×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  
1731 topology for most regions of the phylogenetic trees. Some major polytomies remain and  
1732 should be resolved in future studies. Notably, the nuclear and plastid DNA trees agree in wide  
1733 portions and show congruent branching patterns, making it likely that they reflect the actual  
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 Torreyochloinae, 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.

1746           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.

1751           The phylogenetically ancestral character states (suppl. Appendix S3) of Poodae  
1752 include perennial life form; absence of rhizomes; ligule an eciliate membrane; flat leaves;  
1753 inflorescence an open panicle with many spikelets; panicle branches at most moderately  
1754 divided, smooth; spikelets pedicelled, with >3 fertile florets, with a rhachilla extension  
1755 bearing a sterile floret; spikelets without basal sterile florets, fertile florets (if more than 1) all  
1756 alike, laterally and at most moderately compressed, comparatively large, >4 mm in length,  
1757 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,  
1761 muticous, 1-keeled, 3-veined, primary vein distinct, smooth, lateral veins distinct; lemma 1.6–  
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;  
1765 palea  $\geq 0.7$ -fold longer than the lemma, with smooth and eciliate keels; apical sterile florets (if  
1766 present) resembling fertile though underdeveloped; stamens 3; caryopsis  $\geq 1.6$  mm long; hilum  
1767 linear and straight.

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  
1777 grass subfamilies, in which similarly shaped twisted geniculate awns have originated at least  
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**

1791 MR, JS and NT designed the study. MR guided the sampling, contributed taxonomic  
1792 knowledge, contributed data for the ancestral state reconstructions and wrote the manuscript.  
1793 JS, NT, ED, AW, AH, GW, JG contributed lab work. NT and JS contributed data by  
1794 supervising students in the lab. NT and JS undertook the phylogenetic analyses. JN and MR  
1795 performed the ancestral state reconstructions. NT and MHH contributed to write the  
1796 manuscript. — GW, <https://orcid.org/0000-0002-9866-335X>; MR, <https://orcid.org/0000-0001-5111-0945>; NT, <https://orcid.org/0000-0002-4627-0706>.

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1814

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**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, HAL0140638); **N**, *Calamagrostis arenaria* (M. Röser 11291, 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**, *Grappophorum 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**, *Hookerchloa eriopoda* (R. Pullen 4003, AD96435171); **M**, *Lamarckia aurea* (M. Röser 311, HAL). **A, B, H, J, K, L, M**, Lateral 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 buechananii* (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.

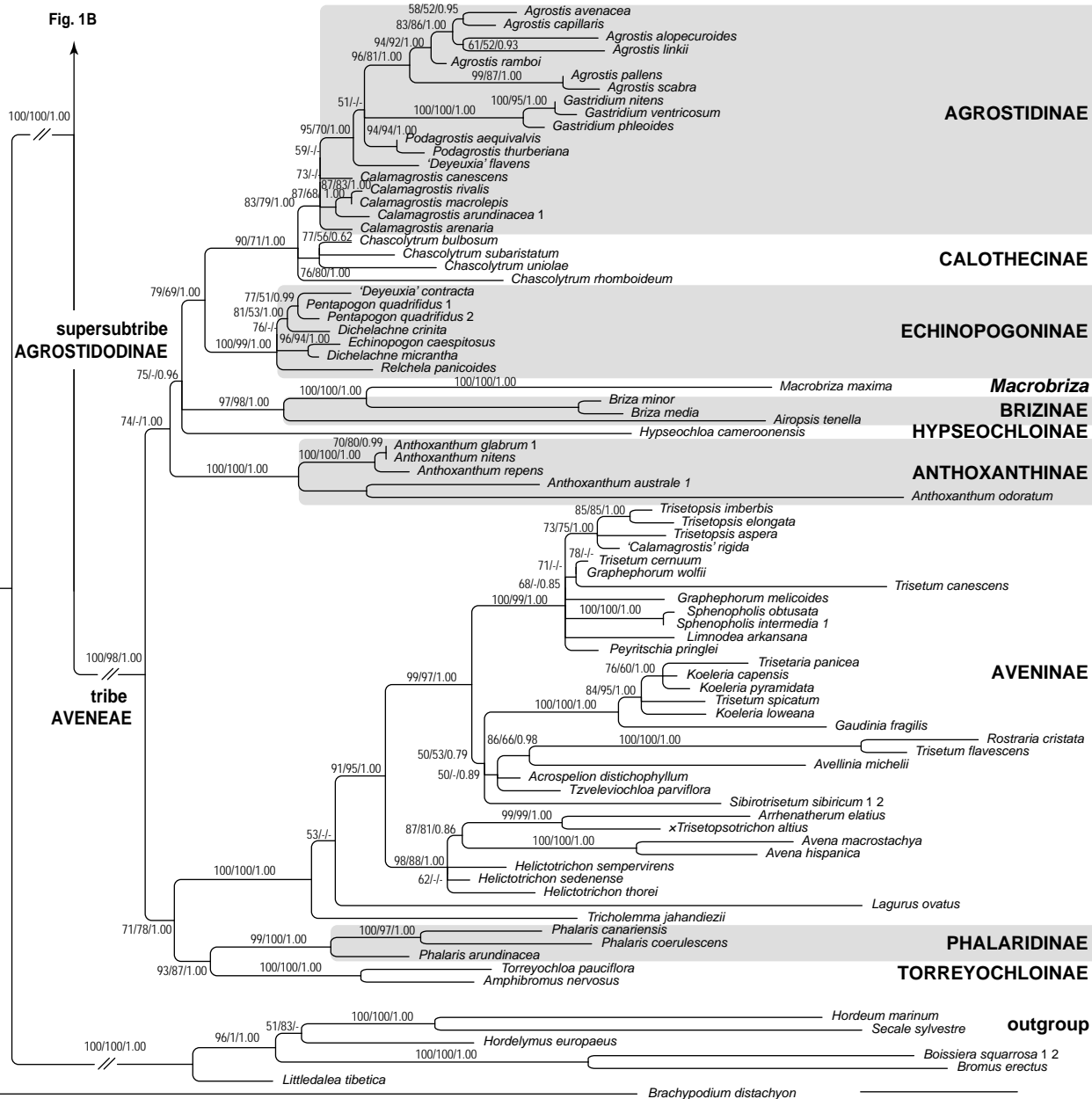
Maximum Likelihood phylogram of Poodae (Aveneae and Poeae) inferred from a concatenated matrix of plastid (*matK* gene–3’*trnK* exon, *trnL*–*trnF*) and nr (ITS, ETS) DNA sequences with species of Triticoideae and Brachypodieae as outgroup. Maximum Likelihood and Maximum Parsimony bootstrap support values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

Fig. 1B



0.006

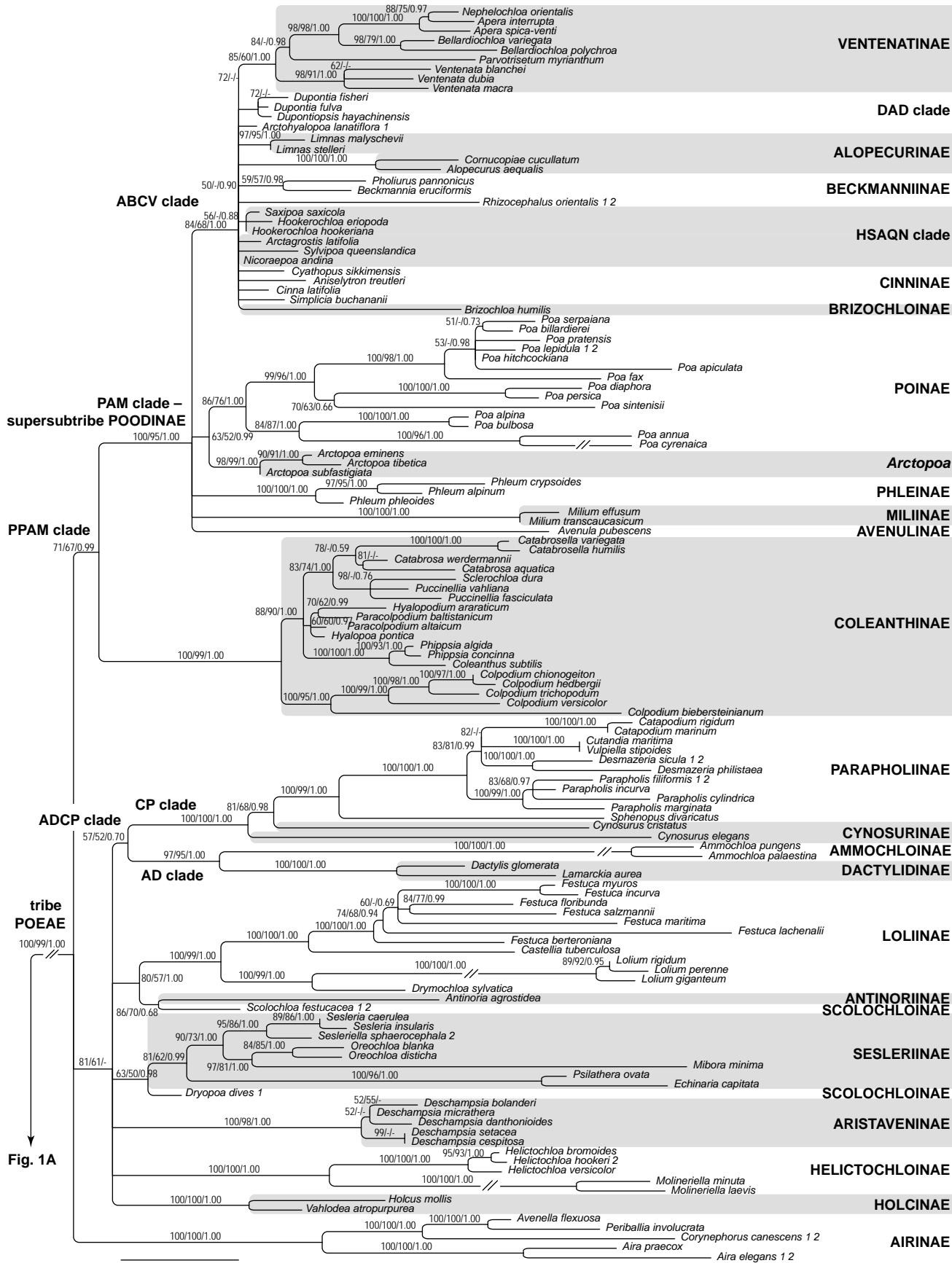
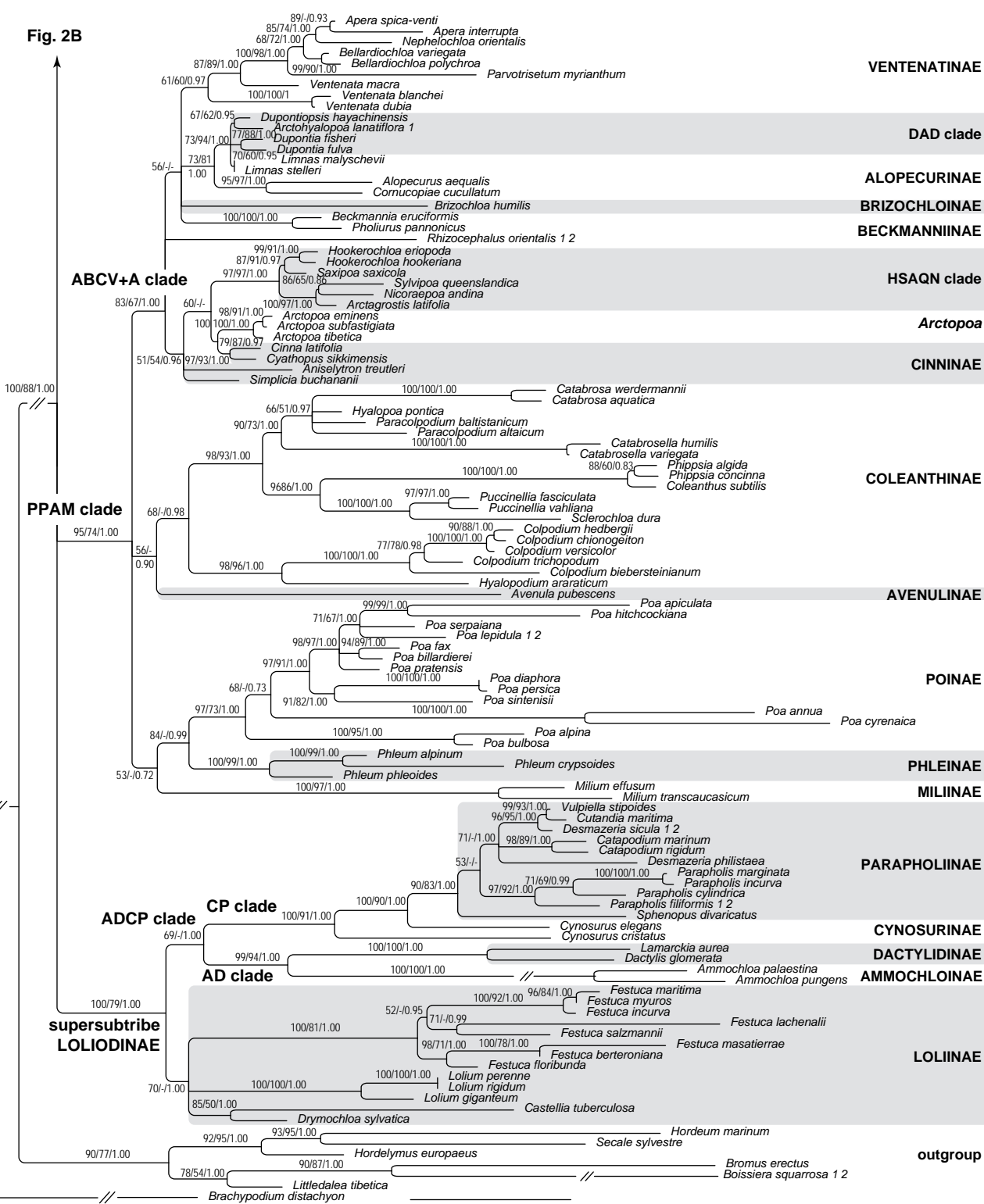
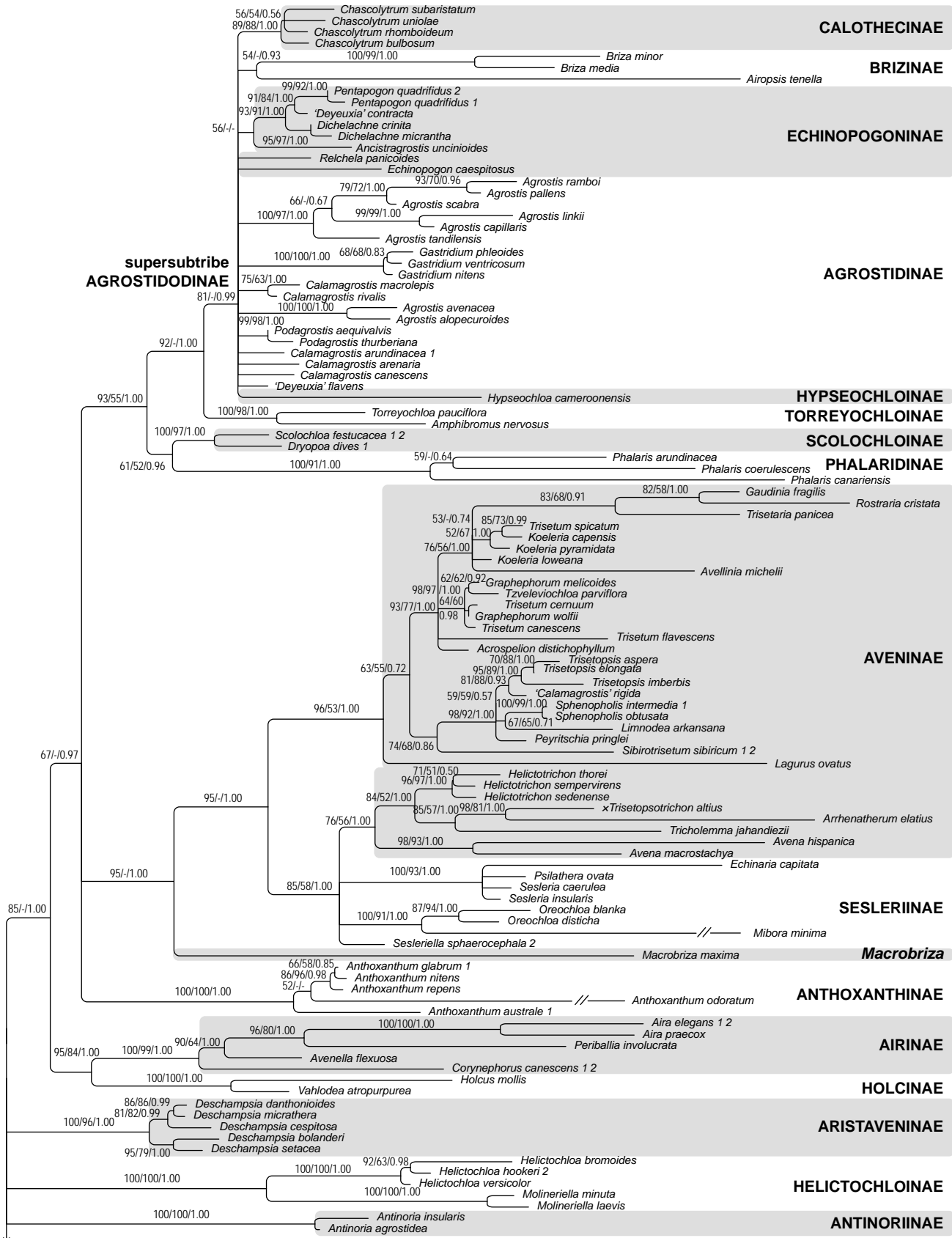


Fig. 1A

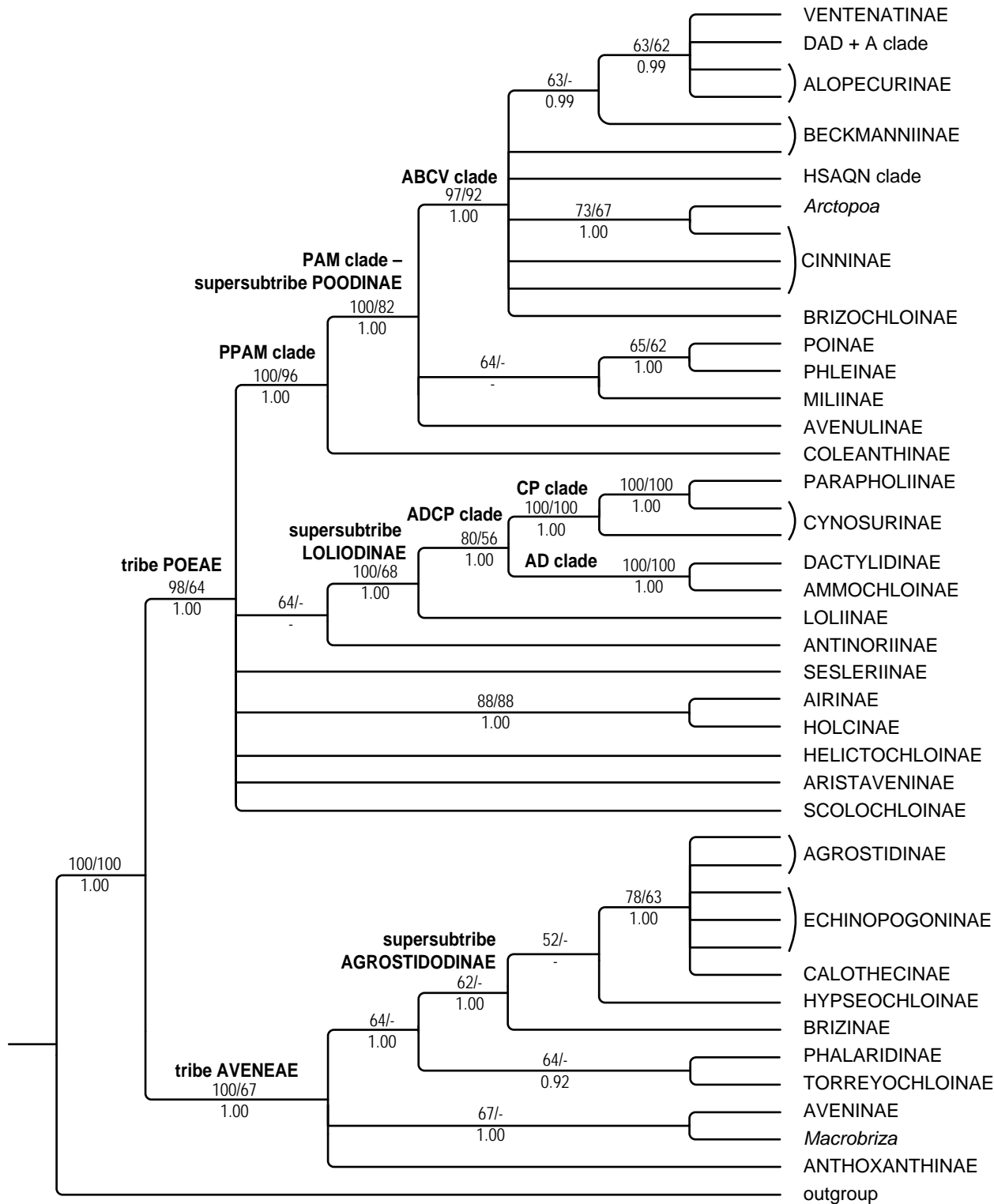
Fig. 2B



0.05

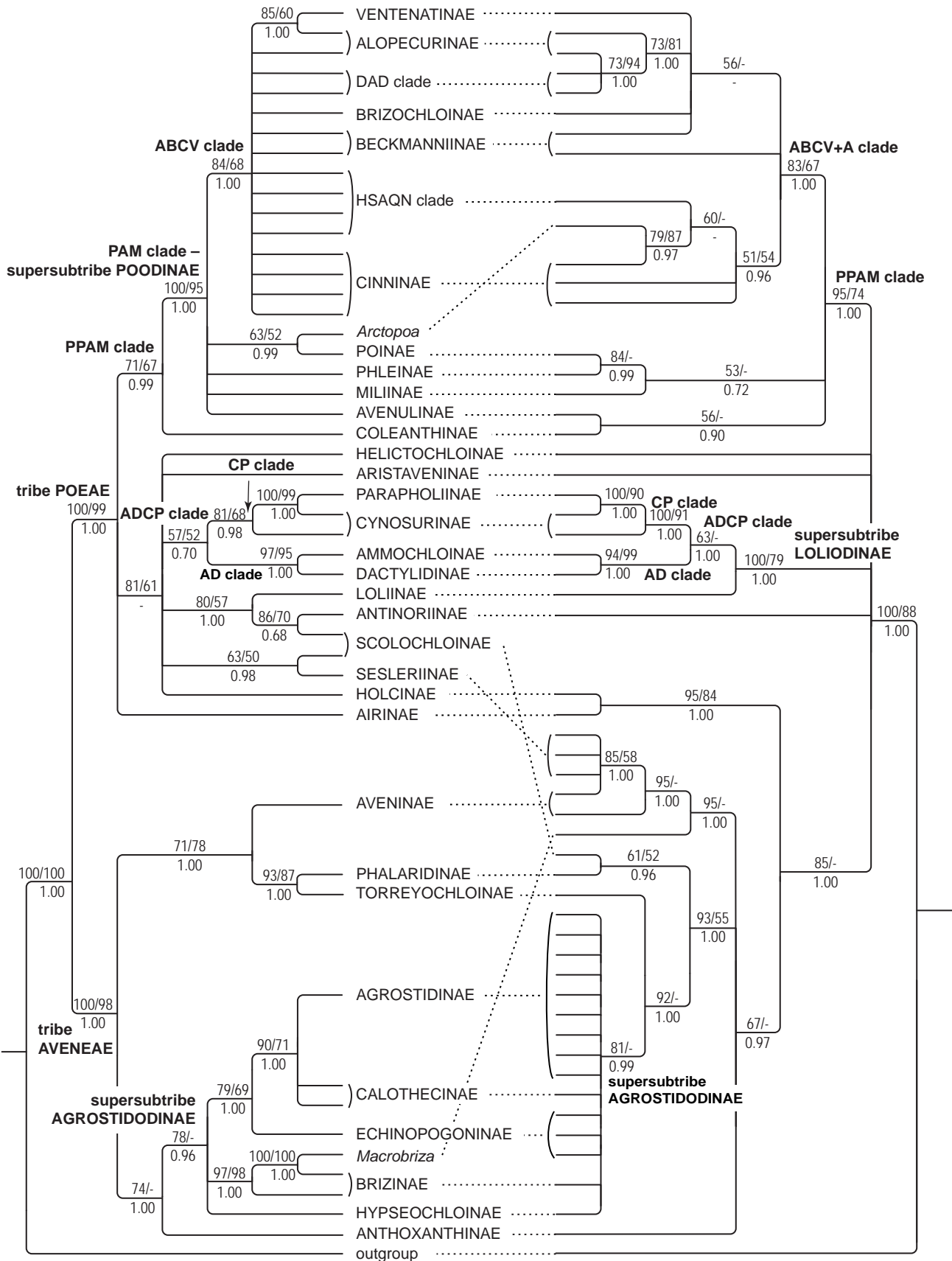


**Fig. 2A** 0.05



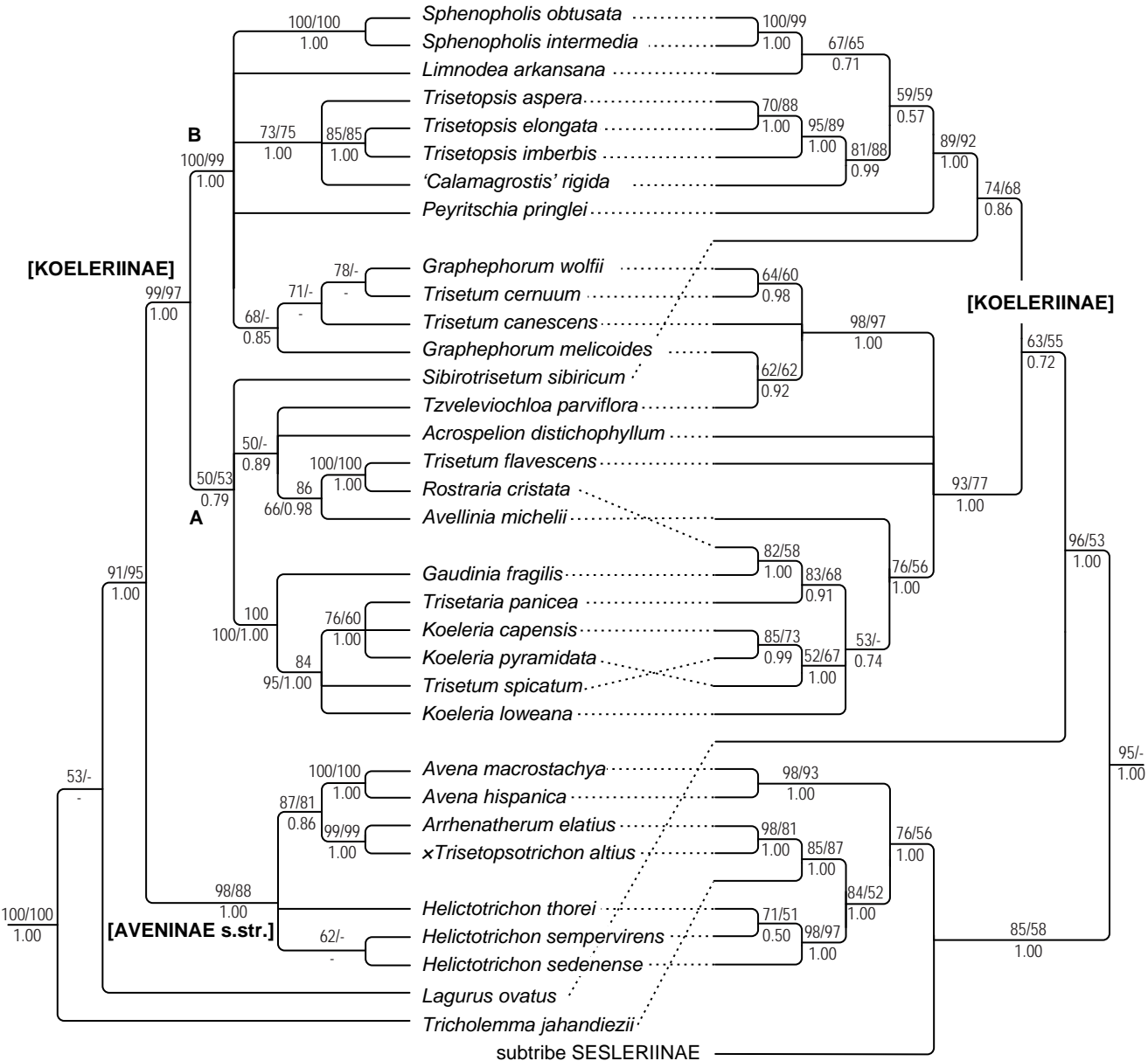
**Plastid DNA sequence data**

**Nuclear ribosomal DNA sequence data**

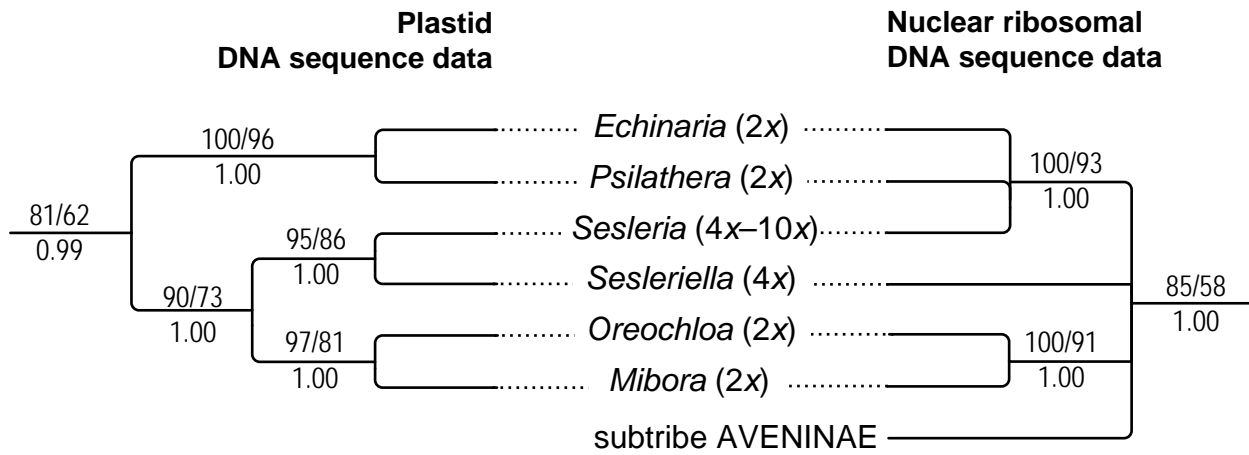


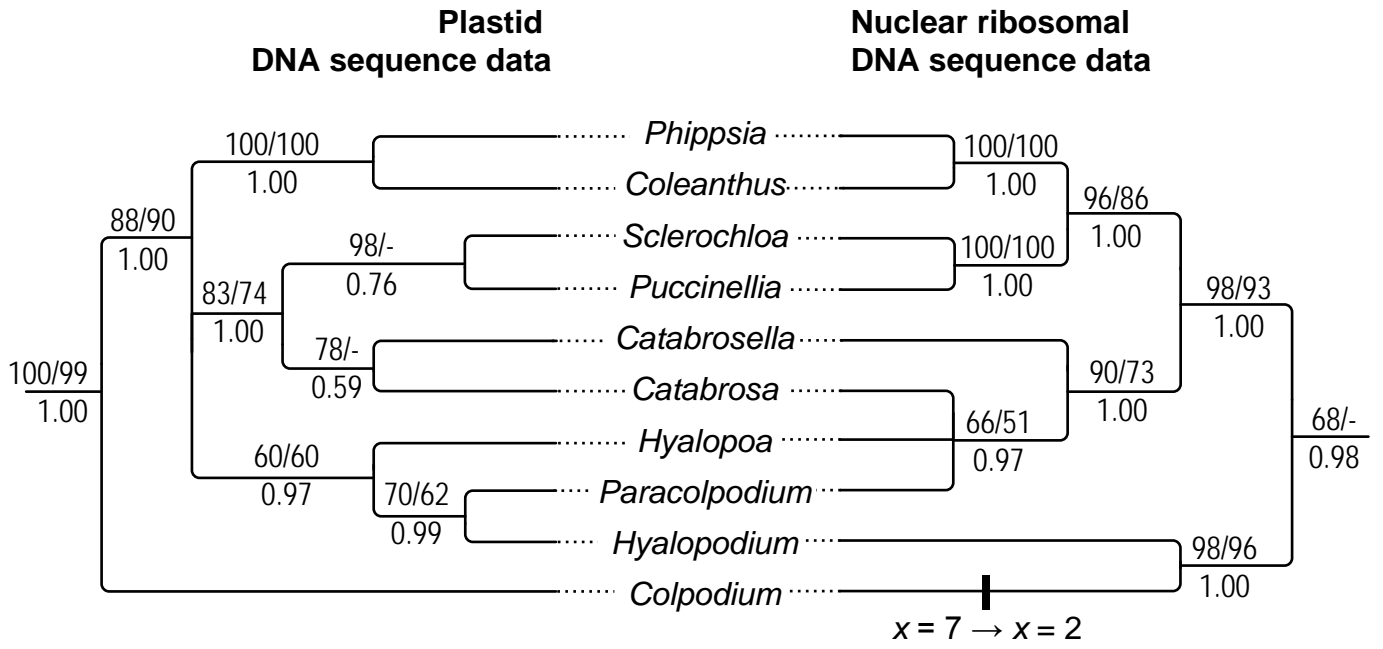
Plastid DNA sequence data

Nuclear ribosomal DNA sequence data



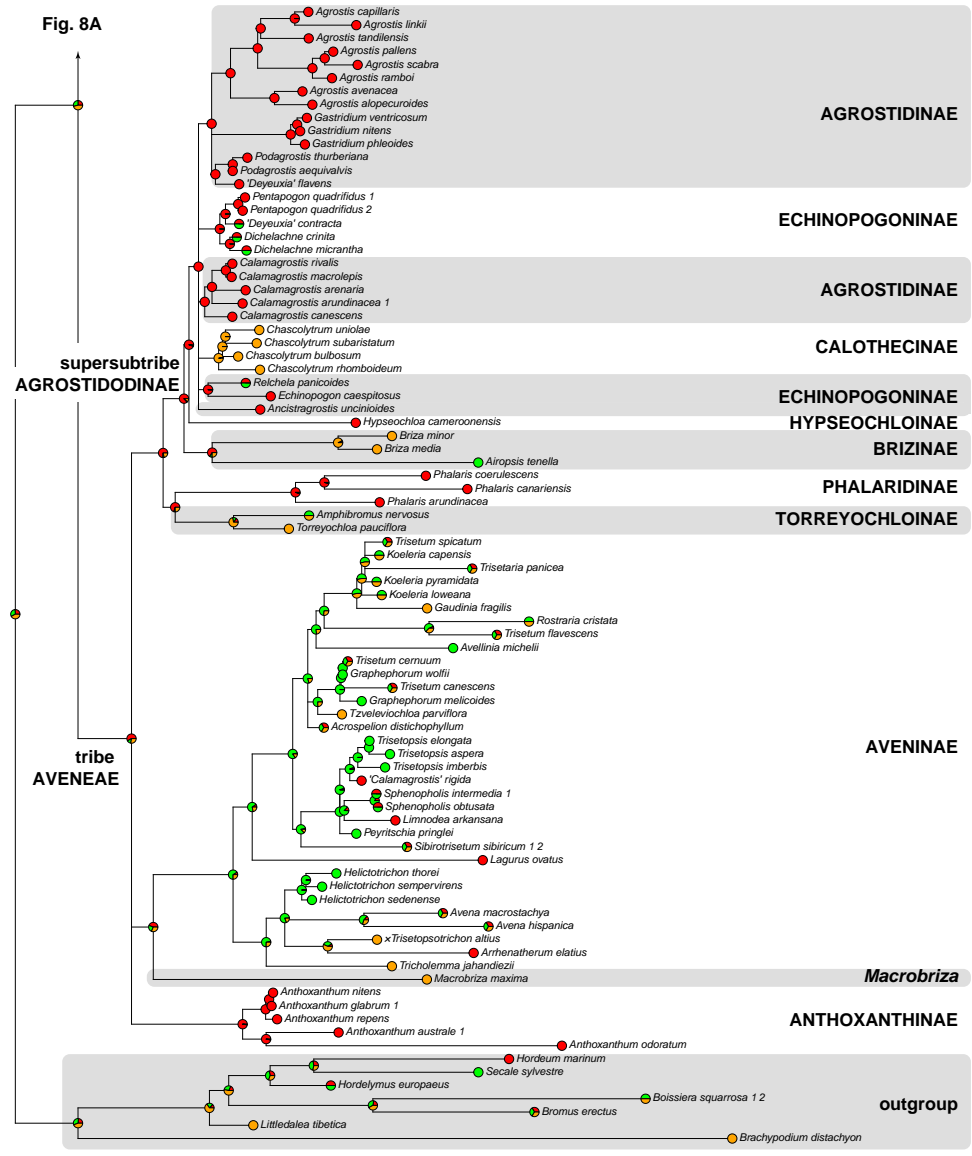






# (050) Spikelets comprising <number of fertile florets>

• a: 1 • b: 2–3 • c: >3



- a: 1
- b: 2–3
- c: >3

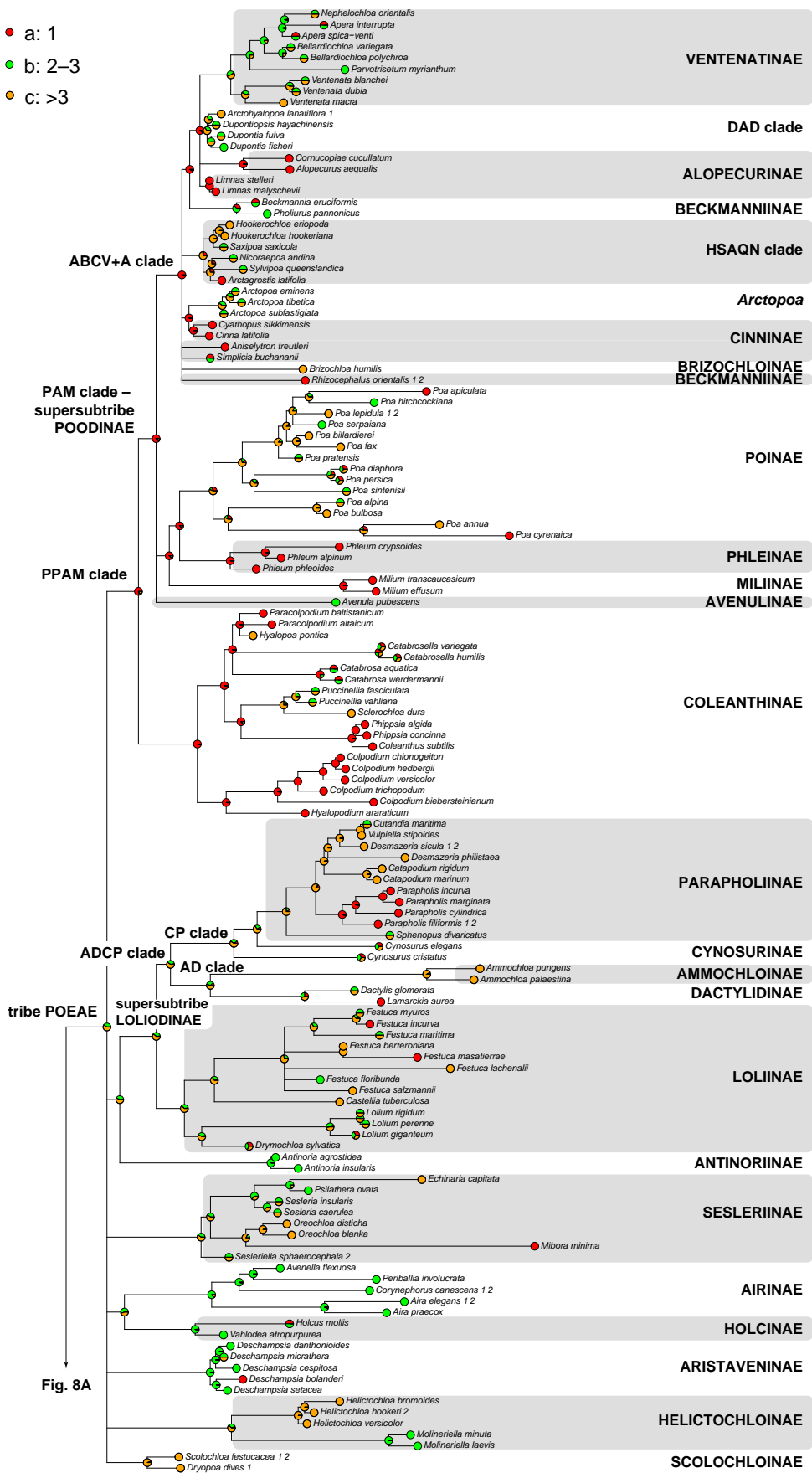
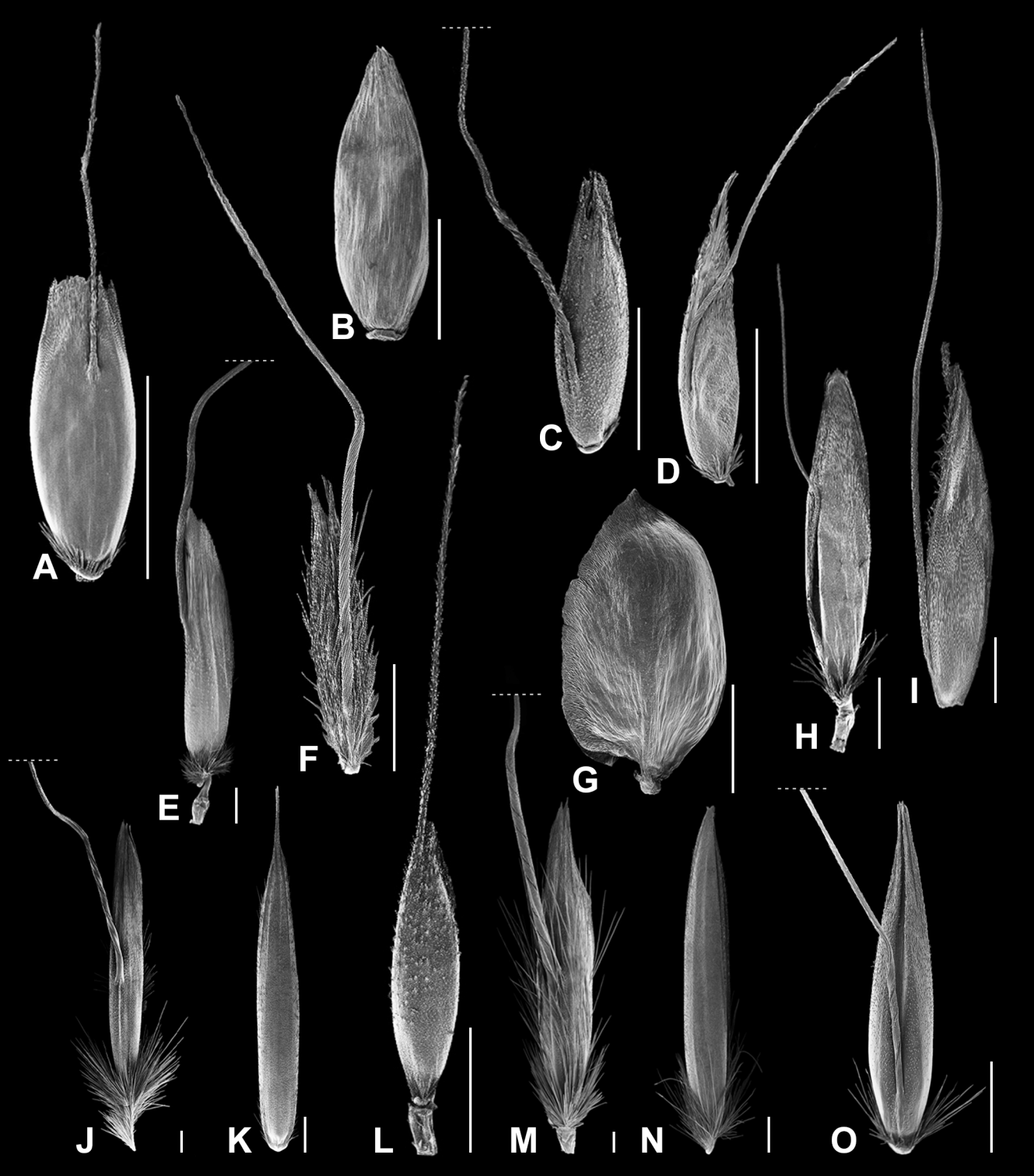
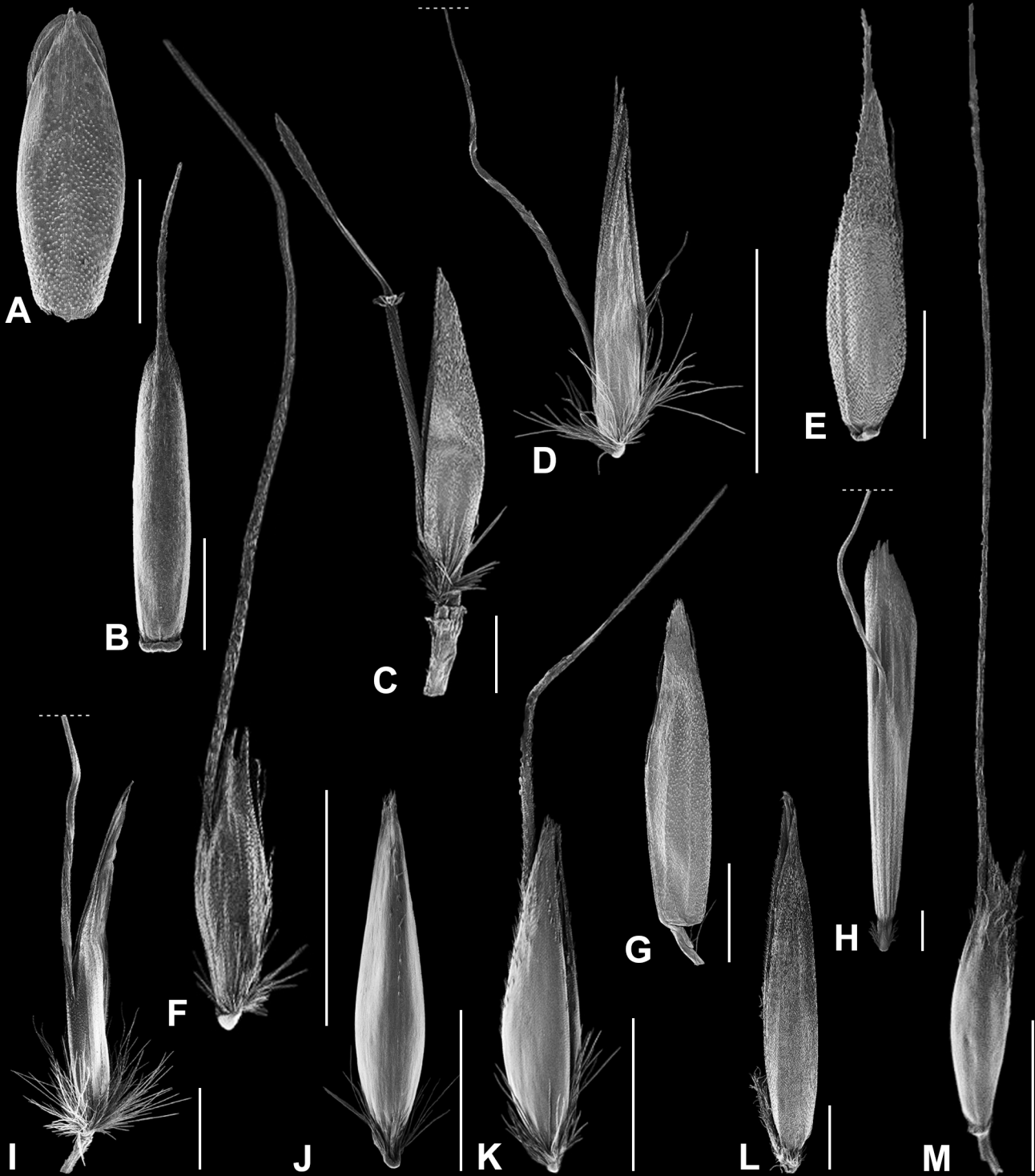
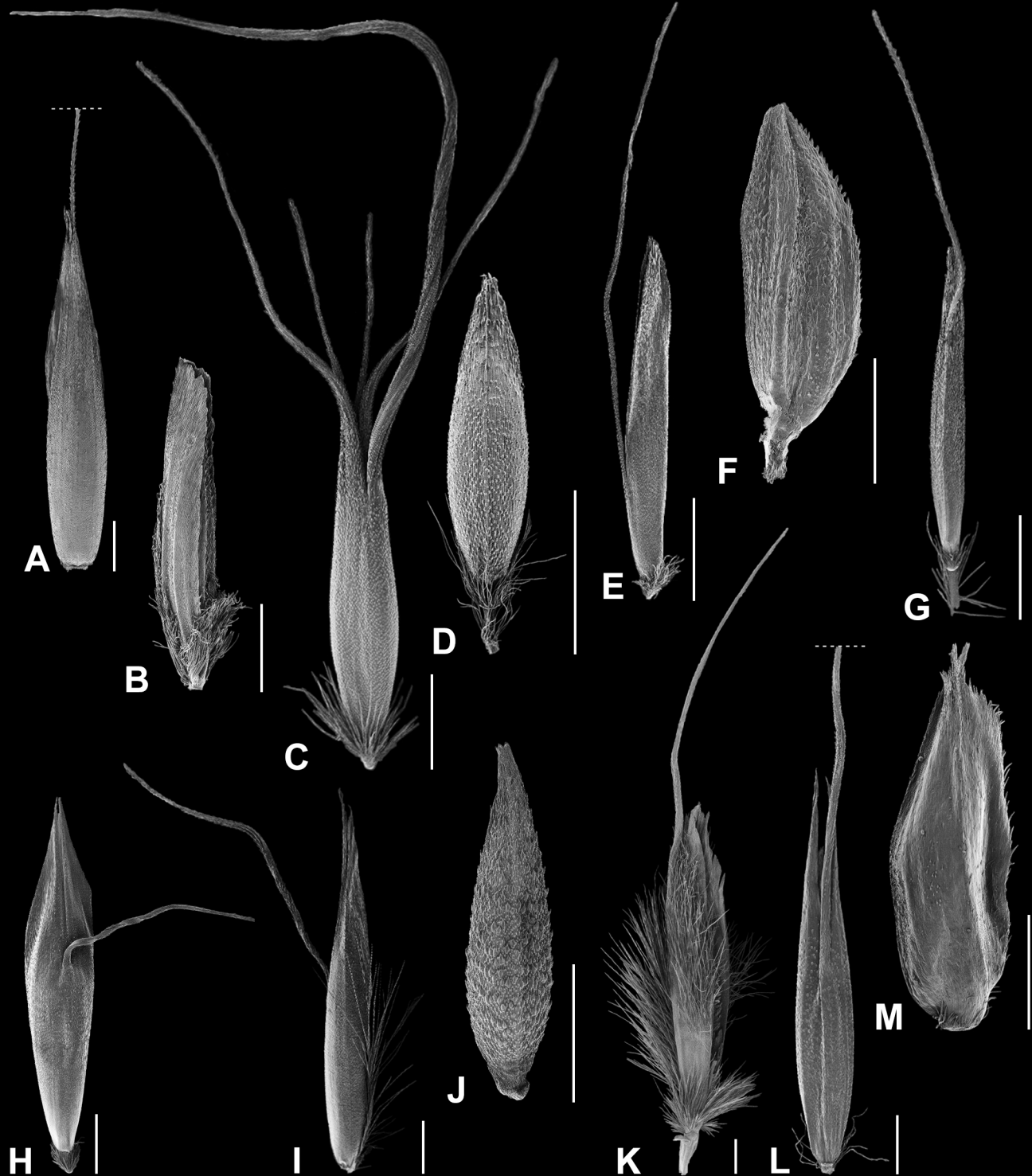


Fig. 8A







**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. Miede 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, Müritzer Lake, 28.05.2003, M. Röser 11009/1 (HAL); LR606813, AM234540; LR606615; FM179385; LR606324. *Airopsis tenella* (Cav.) Coss. & Durieu: France, Montpellier, Bellargues, 01.05.1956, R. Schubert (HAL0080969); LR606814; LR606616; LR606520; LR606325. *Alopecurus aequalis* Sobol.: Germany, Baden-



Württemberg, near Tübingen, 28.06.1984, *M. Röser 1892* (HAL); LR606815; LR606617; LR606521; LR606326. *Ammochloa palaestina* Boiss.: Spain, Andalucía, Province Almería, Tabernas, 13.04.1965, *F. Bellot & S. Rivas Goday* (C); LR606816; LR606618; LR606522; LR606327. *A. pungens* Boiss.: Algeria, between Djelfa and Bou-Saâda, 06.04.1965, *V.P. Bochantsev 1238* (LE); LR606817; LR606619; LR606523; LR606328. *Amphibromus nervosus* (Hook.f.) Baill.: Australia, New South Wales, Great Dividing Range, 23.05.2002, *M. Röser 10770* (HAL); LR606818; LR606620; LR606524; LR606329. *Ancistragrostis uncinoides* 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. Zanolka 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, Müritzer 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.) Kerguelen 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, Freiburger 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 Paraguari, 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. trichopodium* (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, Viera, 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, Vronodus 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 Fernández, 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. salzmännii* (Boiss.) Boiss. ex Coss.: Spain, Andalucía, Province Malaga, Sierra de Mijas, Alhaurín el Grande, 08.05.1989, *S. Rivas-Martínez 17742* (BASBG); LR606897, HE646583; LR606695; HE646608; LR606405. *Gastridium nitens* (Guss.) Coss. & Durieu: Greece, Crete, Agios Nikolaos, 01.05.1983, *G. van Buggenhout* (ROM); LR606898; LR606696; LR606568; LR606406. *G.*

*phleoides* (Nees & Meyen) C.E.Hubb.: Lebanon, North Lebanon; cultivated in BG Halle, Germany from seed obtained from Kew's Millennium Seed Bank, UK (no. 241421), 28.07.2004, *M. van Slageren & Khairallah, S.* (HAL); LR606899; LR606697; LR606569; LR606407. *G. ventricosum* (Gouan) Schinz & Thell.: France, Corsica, 30.06.1987, *M. Röser 5491* (HAL); LR606900; LR606698; LR606570; LR606408. *Gaudinia fragilis* (L.) P.Beauv.: Spain, Andalucía, Province Cádiz, NW Gibraltar, 20.06.1985, *M. Röser 11070* (HAL); LN554436; LR606699; LT159737; –. *Grapphephorum 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. parlatoresi* (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. xkrischae* 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 & Castro.: 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. transcausicum* 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. Nicolás 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, *Royle 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; -. *Phippisia algida* (Sol.) R.Br.: Russia, E Taymyr, Nyunkarakutari River, Poymennoe Lake, 05.08.1998, *I.N. Pospelov 98-158* (NS); LR606952, AM234603; -, FM179424; LR606456. *P. concinna* (Th.Fr.) Lindeb.: Russia, Taymyr, Syndasko River, 23.07.1979, *N. Vodopyanova, R. Krogulevich, N. Frisen, V. Nikolayeva & N. Shumik 224* (NS); LR606953, AM234582; LR606750; FM179425; LR606457. *Phleum alpinum* L.: Austria, Styria, near St. Oswald, 31.07.2001, *M. Röser 11023* (HAL);

LN554448; LR606751; LR606589; LR606458. *P. crypsoides* (d'Urv.) Hack.: Cyprus, Cape Greco, 15.04.1992, *F. Skovgaard* (C); LR606954; –; HE802187; LR606459. *P. phleoides* (L.) Karsten: Norway, Oslo; cultivated in BG Halle, Germany from seed obtained from BG Oslo, Norway (no. 2003-669), 31.07.2003, *s.coll.* (HAL); LR606955, AM234552; LR606752; FM179426; LR606460. *Pholiurus pannonicus* (Host) Trin.: Hungary, Great Hungarian Plane (Alföld), Hortobágy Puszta, 13.06.1967, *W. Hilbig* (HAL0067272); LR606956, HE646586; LR606753; HE646616–HE646625 (clones consensus); LR606461. *Poa annua* L.: Germany, Saxony-Anhalt, 18.01.2005, *M. Röser 11065* (HAL); LR606957, AM234593; LR606754; FM179428; LR606462. *P. bulbosa* L.: Austria, Lower Austria, near Eggenburg, 28.04.1991, *M. Röser 7419* (HAL); LR606959, AM234594; LR606756; FM179429; LR606464. *P. cyrenaica* E.A.Durand & Barratte: Libya, Bengasi, 29.01.1924, *F. Lavara & L. Grande* (FI); LR606960; –; HE802196; LR606465. *P. diaphora* Trin.: Mongolia, Bajan Ölgii 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 Columbia, 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 Pusztá, 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 Pusztá, 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, Edelweiss Spitze, 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. *Torreyochloa 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); LR606992; LR606791; LR606602; LR606497. *T. elongata* (Hochst. ex A.Rich.) Röser & A.Wölk: Uganda, Mount Elgon, 23.02.2004, *K. Wesche* (HAL); LR606993, HG797469; LR606792; HG797566; LR606498. *T. imberbis* (Nees) Röser, A.Wölk & Veldkamp: South Africa, Western Cape, Betty's Bay, corner Kreupel hout street and Lipkin road, 25.10.2010, *A.C. Mudau & L. Smook 452* (PRE); LR606994, HG797483; LR606793; HG797631; LR606499. *T. longa* (Stapf) Röser & A.Wölk: South Africa, Western Cape, Table Mountain National Park, Jonkersdam, 23.10.2010, *A.C. Mudau & L. Smook 450* (PRE); LR606995, HG797475; LR606794; HG797597; LR606500. *T. turgidula* (Stapf) Röser & A.Wölk: Lesotho, Ligholong, Mine, 02.01.1900, *T. Edwards 7141* (NU4-2005/15), –; –; –; LR606501. *T. virescens* (Nees ex Steud.) Röser & A.Wölk: Pakistan, Hazara, Himalaya foothills, Indus Kohistan, 28.08.1995,

*B. Dickoré 12063* (MSB); –; LR606795; LT159791; LR606502. ×*Trisetopsotrichon altius* (Hitchc.) Röser & A.Wölk: China, Sechuan, Nereku River, 26.07.1885, *G.N. Potanin* (LE); LR606996; LR606796; LT159792; LR606503. *Trisetum 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; DQ353977; –; GQ324247, GQ324248, GQ324249. *A. subfastigiata* (Trin.) Prob.: KM523849\*; EU792449\*; EU792372\*; GQ324250\*. *A. tibetica* (Munro ex Stapf) Prob.: KM523850\*; EU792444\*; GQ324471\*; GQ324252\*. *Arrhenatherum elatius* (L.) P.Beauv. ex J.Presl & C.Presl: EU434292, EF137486, KJ529335; JF904748; –; –. *Avellinia michelii* (Savi) Parl.: KJ529340; DQ631465; –; –. *Avena hispanica* Ard.: GU367287, GU367288, EU833849; EU833874; –; –. *A. macrostachya* Balansa ex Coss. & Durieu: EU833852; EU833877; –; –. *Avenella flexuosa* (L.) Drejer: DQ786887; AY237913; –; –. *Avenula pubescens* (Huds.) Dumort.: EF137502; DQ631460; –; –. *Bellardiochloa polychroa* (Trautv.) Roshev.: –; –; –; GQ324256. *B. variegata* (Lam.) Kerguélen: DQ786890, KM523852; –; –; GQ324257. *Boissiera squarrosa* (Sol.) Nevski: EF137488; –; –; KJ632438, KP996869, KP996870. *Brachypodium distachyon* (L.) P.Beauv.: –; KU163229; AF303399; –. *Briza media* L.: –;

EU395902\*; –; –. *B. minor* L.: KJ599228, DQ786892; –; –; KJ599006. *Bromus erectus* Huds.: –; JX985261; –; –. *Calamagrostis arenaria* (L.) Roth subsp. *arundinacea* (Husn.) Banfi, Galasso & Bartolucci: KJ529326; DQ631456; –; JX438118. *C. arundinacea* (L.) Roth: DQ786895; KX372396; GQ266675; –. *C. canadensis* (Michx.) P.Beauv.: –; –; FJ377628\*; –. *C. purpurascens* R.Br.: –; FJ394570, FJ394568; –; –. *Castellia tuberculosa* (Moris) Bor: EF137492\*; EF137596\*; AF532954\*; –. *Catabrosa aquatica* (L.) P.Beauv.: DQ786898, KM523853; DQ353958\*; –; KM523697, GQ324258. *C. werdermannii* (Pilg.) Nicora & Rúgolo: –; EU792431\*; EU792333\*; GQ324259\*. *Catabrosella variegata* (Boiss.) Tzvelev: KM523854; –; –; KM523698\*. *Catopodium 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; –; –; –. *Dryochloa 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. salzmännii* (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\*. *Hookerchloa 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, GQ324273. *Molineriella laevis* (Brot.) Rouy: DQ786929; KJ529413; –; –. *Nephelochloa orientalis* Boiss.: KM523873; KM524075\*; –; KM523714. *Nicoraepoa andina* (Trin.) Soreng & L.J.Gillespie: DQ786934\*, KM523874; DQ353971\*; EU792354\*; GQ324275\*. *Oreochloa disticha* (Wulfen) Link: –; DQ631452\*; –; –. *Paracolpodium altaicum* (Trin.) Tzvelev: KM523878; KM524076; –; KM523715. *Parapholis cylindrica* (Willd.) Röser & Tkach: EF137501, KJ599283, KJ529366; KJ599395; –; KJ599056\*. *P. filiformis* (Roth) C.E.Hubb.: KJ529365; KJ529415; –; –. *P. incurva* (L.) C.E.Hubb.: DQ786931, EF137508, KJ599281; –; –; KJ599054. *Periballia involucrata* (Cav.) Janka: KJ529353; DQ631438; –; –. *Peyritschia pringlei* (Scribn.) S.D.Koch: –; FJ394581; –; –. *Phalaris arundinacea* L.: AF164396; JF951096; –; –. *P. canariensis* L.: –; DQ631443; –; –. *P. coerulescens* Desf.: KJ529325; JF951116; –; –. *Phippsia algida* (Sol.) R.Br.: KM523879, KM523880; KM524078\*; –; KM523716, KM523717, GQ283228, GQ283229. *Phleum*

*alpinum* L.: KM523881; KM524079; –; KM523718. *P. phleoides* (L.) Karsten: KM523884; KM524082; –; KM523718. *Poa alpina* L.: DQ786933\*, KM523888; DQ353986\*; EU792390\*; –. *P. annua* L.: KJ599339, KJ599340; 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* (Hitc.) 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* Hitc.: –; –; GQ283123 –. *P. perlaxa* (N.G.Walsh) N.G.Walsh & A.R.Williams: –; –; KJ598986 –. *P. phryganodes* (Trin.) Scribn. & Merr.: –; –; GQ283157 –. *P. pumila* (Macoun ex Vasey) Hitc.: –; –; GQ283158 –. *P. stricta* (Hook.f.) C.H.Blom: –; –; EU792339 –. *P. tenella* (Lange) Holmb.: –; –; GQ283110 –. *P. tenuiflora* (Griseb.) Scribn. & Merr.: –; –; KP711084 –. *P. vahliana* (Liebm.) Scribn. & Merr.: KM523915; –; –; GQ283185, GQ283186, GQ283187, GQ283188, GQ324285. *P. vassica* A.R.Williams: –; –; KJ598963 –. *P. walkeri* (Kirk) Allan subsp. *chathamica* (Cheeseman) Edgar: –; –; EU331103 –. *Relchela panicoides* Steud.: –; JF904801; –; –. *Rostraria cristata* (L.) Tzvelev: –; DQ336853, GQ324465; –; –. *Saxipoa saxicola* (R.Br.) Soreng, L.J.Gillespie & S.W.L.Jacobs: KJ599265, KM523917\*; GQ324465\*; GQ324558\*; GQ324392\*. *Sclerochloa dura* (L.) P.Beauv.: DQ786941, KJ599275, KM523918; KM524102; –; KM523745, KJ599049, KJ632435. *Scolochloa festucea* (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 sequences FJ196303 (Rodionov & al., 2008) and EU792365 (Gillespie & al., 2008), all of which are nested within Coleanthinae. A deviant ITS sequence reported for *H. pontica* (FJ196302; see Rodionov & al., 2008, Nosov & al., 2015, 2019) clusters among the sequences of *Poa*. The presumed occurrence of different ITS copies in *H. pontica* was discussed to rest on genetic introgression of *Poa* into *Hyalopoa* or allopolyploidy with subsequent loss of one

of the parental *Hyalopoa* 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*.