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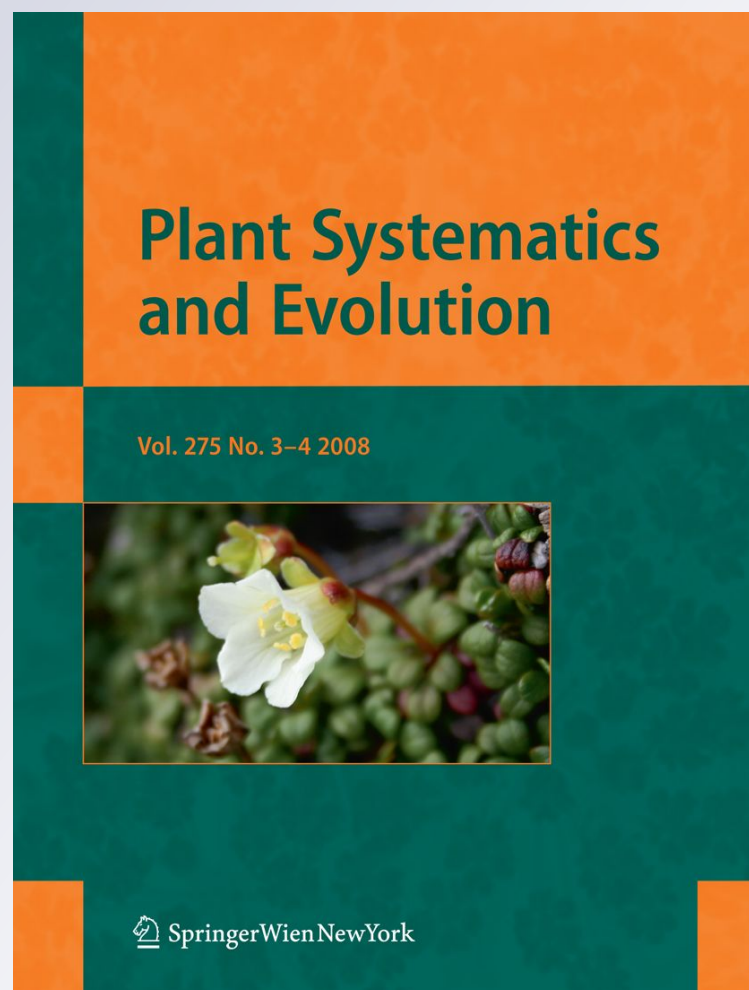
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Stipa (Poaceae) and allies in the Old World: molecular phylogenetics realigns genus circumscription and gives evidence on the origin of American and Australian lineages

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Abstract The tribe Stipeae with an estimated number of ca. 600 species is part of the grass subfamily Pooideae and has near worldwide distribution. Its species are often dominant constituents of steppe vegetation and other grasslands, especially in Eurasia, the Americas and Australia. The taxonomy of Old World Stipeae has been studied to date primarily on the basis of morphology and anatomy, while existing molecular phylogenetic investigations have mainly dealt with New World or Australian taxa. We studied 109 new ingroup taxa with a focus on Old World Stipeae (in addition with an extensive outgroup sampling) using chloroplast and nuclear ribosomal DNA sequences (*3'trnK* region, ITS1–5.8S gene–ITS2), and discuss taxonomic key characters. Five highly supported monophyletic lineages were identified, some of which were rather unexpected: (a) the narrowly defined *Stipa* core clade, which is primarily Eurasian but extends into Africa north of the Sahara Desert, (b) the majority of Old World *Piptatherum*, (c) a “Transcontinental Stipeae Clade” encompassing Eurasian, African,

American and Australian lineages, (d) a Himalayan to E Asian clade and (e) the single species *Achnatherum splendens*. The large “Transcontinental Stipeae Clade” contained several lineages of Eurasian Stipeae different from the *Stipa* core (a), i.e., genera *Aristella*, *Celtica*, *Oloptum* gen. nov., *Stipella* stat. et. gen. nov., species of *Achnatherum*, and the species-rich lineages of *Nassella*/*Jarava* in America and of *Austrostipa* in Australia. In our circumscription *Ptilagrostis* was nested in (d), a clade (which included some species of *Achnatherum* and poorly studied Himalayan species ascribed to either *Stipa* or *Orthoraphium*) and whose internal structure remained unclear. *Oloptum*, gen. nov., is described, and the following combinations are made: *Achnatherum pelliottii*, comb. nov., *Aristella keniensis*, comb. nov., *Oloptum miliaceum*, comb. nov., *Stipella*, stat. et. gen. nov., *S. capensis*, comb. nov., *S. nitens*, comb. nov., *S. parviflora*, comb. nov., *S. staintonii*, comb. nov., and *S. tigrensis*, comb. nov.

Keywords Feathergrasses · Grasses · Phylogenetics · Poaceae · Stipeae

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Introduction

The species of grass tribe Stipeae Dumort. are common or even dominant in open grasslands and steppe communities in temperate and warm temperate regions of Eurasia, Australia and America. The tribe's members are mostly perennial, tussock-forming plants with single-flowered spikelets. The apically awned lemmas are usually indurate, and the glumes reach or slightly exceed the base of the awns. Chromosomes are small, and the chromosome base number is $x = 10\text{--}12$ (cf. Barkworth et al. 2008; Romaschenko et al. 2008). The tribe is placed in the grass

subfamily Pooideae and belongs to the more early diverging phylogenetic lineages together with the tribes Brachyelytreae Ohwi, Nardeae Koch, Phaenospermateae Renvoize & Clayton, Meliceae Rchb. and Diarrheneae (Ohwi) C.S. Campb. (cf. Catalán et al. 1997; Soreng and Davis 2000; Grass Phylogeny Working Group 2001; Davis and Soreng 2007; Döring et al. 2007; Schneider et al. 2009).

Tribe Stipeae has long been considered a natural and more or less well-defined entity (e.g., Bentham 1883; Hackel 1887; Pilger 1954; Clayton and Renvoize 1986; Watson and Dallwitz 1992a, b; Barkworth and Everett 1987; Tzvelev 1989; Jacobs et al. 2007). Disagreement has prevailed on the inclusion of several small genera, e.g., *Ampelodesmos* Link, *Anisopogon* R. Br., *Diarrhena* P. Beauv., *Lygeum* L., *Milium* L. or *Nardus* L. (Clifford and Watson 1977; Wheeler et al. 1982; Dahlgren et al. 1985; Clayton and Renvoize 1986; Barkworth and Everett 1987; Watson and Dallwitz 1992a, b). The tribal affiliation of these genera has been tentatively clarified by molecular phylogenetic studies, which suggests abandoning the tribe Ampelodesmeae Tutin by including its only species in Stipeae (Schneider et al. 2009), treating *Diarrhena* as separate tribe, Diarrheneae (e.g., Soreng and Davis 2000; Grass Phylogeny Working Group 2001; Schneider et al. 2009), unifying *Lygeum* and *Nardus* in an expanded Nardeae (Döring et al. 2007; Schneider et al. 2009), and retaining *Milium* in the tribe Poeae (e.g., Macfarlane and Watson 1982; Soreng and Davis 2000; Davis and Soreng 2007; Schneider et al. 2009). *Anisopogon* seems firmly nested in the Phaenospermateae, an assemblage of morphologically non-uniform genera separate from Stipeae but related with it (cf. Soreng and Davis 2000; Grass Phylogeny Working Group 2001; Davis and Soreng 2007; Döring et al. 2007; Schneider et al. 2009).

The numbers of genera and the generic boundaries within narrowly defined Stipeae have been debated for a long time, and generic definitions substantially differ among authors (reviewed by Barkworth 1990; Jacobs et al. 2000 for the pre-molecular era taxonomy). We here concentrate on the Eurasian species of Stipeae that were first treated under a broad generic concept of *Stipa* by Linnaeus. Starting with Palisot de Beauvois (1812), *Stipa* s.lat. has been split into a number of additional genera, among them the Eurasian, or primarily Eurasian, *Achnatherum*, *Celtica*, *Macrochloa*, *Orthoraphium*, *Piptatherum*, *Psammochloa* Hitchc., *Ptilagrostis*, *Timouria* Roshev., *Trikeria* Bor and some others accepted only infrequently. Some of the diagnostic characters employed (e.g., the outline of the lemma, the shape of the callus and the hairiness of its awn) were regarded as rather weak or transient. In consequence, a comparatively broad, though varying delineation of the genus *Stipa* has been in use up to the present (e.g., Freitag 1975, 1985; Clayton and Renvoize 1986).

Stipeae are distributed almost worldwide and have centers of species diversity in Central Asia, the Mediterranean region of Europe, the Americas and Australia. The generic names *Stipa*, *Achnatherum* and *Piptatherum* are originally based on Eurasian species but have also been used to encompass some of the New World taxa (reviewed by Barkworth 1993). This turned out to be unsatisfactory, mainly because even the few characters seemingly stable and diagnostic for Eurasian lineages were unstable and encountered in deviant combinations in the New World. In consequence, the taxonomic situation there is even more problematic with genera having been recognized by different taxonomists, e.g., *Aciachne* Benth., *Amelichloa* Arriaga & Barkworth, *Anatherostipa* (Hack. ex Kuntze) Peñailillo, *Hesperostipa* (M.K. Elias) Barkworth, *Jarava*, *Nassella*, *Pappostipa*, *Ptilostipa* Speg. and *Piptochaetium* (cf. Peñailillo 1996; Torres 1997; Matthei et al. 1998; Soreng et al. 2003; Arriaga and Barkworth 2006; Barkworth 2007; Romaschenko et al. 2008, 2010; Barber et al. 2009). Especially for the two major taxa, *Jarava* and *Nassella*, a generally accepted circumscription has not yet been achieved (Barkworth 1990; Barkworth and Torres 2001; Arriaga and Barkworth 2006; Peñailillo 1996, 2002, 2003; Cialdella et al. 2007; Barkworth et al. 2008; Romaschenko et al. 2008). The ca. 62 Australian members of the tribe are included in yet another genus, *Austrostipa* (Jacobs and Everett 1996). Finally, there is the monotypic genus *Anemanthele* Veldkamp from New Zealand with a single stamen and a special caryopsis structure (Veldkamp 1985). After segregation of all American and Australian species from *Stipa* and its division into many different genera also within Eurasia, the remainder of the genus still comprises an estimated number of more than 100 species.

Recent molecular phylogenetic studies in mainly American Stipeae confirmed that several taxa were highly poly- or paraphyletic (Jacobs et al. 2000, 2007; Cialdella et al. 2007; Barkworth et al. 2008; Romaschenko et al. 2007, 2008, 2010), which means that the diagnostic characters, e.g., the shape of the florets, induration and apex of lemmas, shape of callus and hairiness of the awns have evolved repeatedly. The Eurasian taxa that have been analyzed so far with molecular markers were placed in two different tree regions in the most comprehensive studies of Stipeae available (combined nuclear ITS and chloroplast DNA data; Barkworth et al. 2008; Romaschenko et al. 2010). One group of Eurasian taxa, e.g., *Macrochloa tenacissima* and species of *Stipa*, *Piptatherum*, or *Ptilagrostis*, was close to the base of the tree for Stipeae. Other Eurasian lineages, e.g., *S. parviflora*, *Celtica gigantea* [syn. *S. gigantea* Link, *Macrochloa gigantea* (Link) Hack.], *Piptatherum miliaceum* (L.) Coss., *Achnatherum calamagrostis* or *Ptilagrostis pelliottii* (Danguy) Grubov, were branching off between South American and other lineages from mainly the southern hemisphere in a

rather distal tree position. None of the Eurasian groups was found to be monophyletic, which confirmed the finding of Jacobs et al. (2007). The American members of *Achnatherum* were part of two or three probably unrelated clades among the mainly South American genera *Nassella*, *Jarava* and *Amelichloa*.

Few of the many American taxa were resolved as monophyletic, with the exception of *Pappostipa* (Romaschenko et al. 2008, 2010), *Piptochaetium* and *Hesperostipa* (Barkworth et al. 2008). The 34 Australian species analyzed to date and *Anemanthele* were almost monophyletic with very few exceptions (Jacobs et al. 2007).

In summary, most molecular work has been done on American and Australian taxa, but few of the ca. 160 Stipeae species from Eurasia have been evaluated yet. The main objective of this article, therefore, was to present a phylogenetic hypothesis for Eurasian lineages based on nuclear ribosomal (nr) and chloroplast (cp) DNA sequence data. This is used to discuss taxonomic boundaries and to resolve biogeographical questions.

Materials and methods

Plant material and classification

Our sampling comprised 109 species and subspecies. For several taxa two or more individuals (a total of 35 repetitions) were included. Most samples were taken from herbarium material, but others were from wild collections or from plants raised in Halle Botanical Garden from seed material with known origin (see Table 1). Vouchers were identified with standard floras. These were also employed to determine the geographic distribution of species. Sequence information for 26 species was additionally added from the EMBL database, 17 of which were outgroups. We included only a few of the many South American and Australian species analyzed to date as placeholders, because the relationships of these lineages have been discussed elsewhere (Cialdella et al. 2007; Barkworth et al. 2008; Romaschenko et al. 2008, 2010). The ITS data for *Austrostipa drummondii*, *A. setacea*, *A. velutina* and *Nassella trichotoma* were kindly provided by S.W.L. Jacobs and M.E. Barkworth. The generic treatment of most Eurasian Stipeae, e.g., the delineation of *Stipa* against *Achnatherum*, is still problematic (see "Introduction"). Thus, we kept the generic names used in major revisions or floras (Freitag 1975, 1985; Tzvelev 1976; Wu and Phillips 2006) unless transfers seemed essential in view of our results. For *Stipa* this implied a narrower generic delineation relative to previous treatments (e.g., Freitag 1985; Clayton and Renvoize 1986). For the American and Australian species we followed Jacobs and Everett (1996), Soreng et al. (2003), Barkworth

(2007), Barkworth et al. (2008) and Romaschenko et al. (2008, 2010).

Molecular methods

Total genomic DNA was extracted from herbarium and silica dried leaf material using a column-based genomic extraction kit according to the instructions of the manufacturer (Macherey and Nagel, Düren, Germany). Polymerase chain reaction (PCR) was performed using standard protocols with annealing temperatures varying between 50 and 55°C for the different primer combinations. Primers used for nr ITS1–5.8S gene–ITS2 were ITS-A, -B, -C and -D (Blattner 1999). Primers used for the 3' part of the chloroplast *matK* gene with following intron and 3'*trnK* exon (named 3'*trnK* region in the following) were PO-*matK*1300F and *psbA*-R (Döring et al. 2007; Döring 2009; Schneider et al. 2009). Sequencing reactions were performed with the PCR primers and the ET-Terminator sequencing premix (GE Healthcare, Little Chalfont, UK) in accordance with the manufacturer's instructions. Reactions were analyzed on a MegaBace 1000 sequencer (GE Healthcare). Chromatograms of forward and reverse reactions were hand-edited, and final alignments were made by eye in Sequencher 4.6 (Genecodes Corp., Ann Arbor, MI, USA). All DNA sequences were deposited in EMBL with accession nos. FN434473–FN434608, HE586634–HE586637 for ITS and FN434204–FN434355 for cp sequences. Alignments of both regions were unambiguous except for two regions with simple sequence repeats in ITS. Inclusion or exclusion made no difference, and they were included. Potentially informative indels were also from these simple sequence repeats and were not additionally coded for analysis. A nexus file with all data is available from K.B.v.H. upon request.

Phylogenetic analysis

Both data sets (ITS, 3'*trnK* region) were analyzed separately using PAUP* 4.0b10 (Swofford 2002) under the maximum parsimony criterion. Standard parameters used were: Multrees, 100 random taxon additions, maxtrees = 20,000, and TBR. Branch support was evaluated with 200 bootstrap replicates, the closest taxon addition option and maxtrees = 300. Tree length and rescaled consistency indices (RC) were taken directly from PAUP. The resulting trees of both data sets were partly incongruent, but nevertheless we combined both data sets and performed two further analyses with PAUP parameters as above. The first analysis comprised all taxa, and in the second analysis we excluded all taxa that were incongruent between the foregoing individual analyses. Incongruence was defined by a >50% bootstrap support (BS) threshold of contradicting branches, or it was based on differing major clade membership of cp and ITS DNA sequences.

Table 1 List of taxa studied

Taxon	Collector and collection no. (or date), [herbarium acronym]	Origin or reference	ITS	Cp
<i>Achnatherum</i> P. Beauv.				
<i>A. brandisii</i> (Mez) Z.L. Wu	Anders 5279 [KAS]	Afghanistan	FN434513	FN434247
<i>A. calamagrostis</i> P. Beauv.	Hagen G112 [HAL]	Halle BG; seeds from Oxford BG	FN434520	FN434255
<i>A. caragana</i> (Trin. & Rupr.) Nevski 1	(1963) [TK]	Kazakhstan	FN434479	FN434210
<i>A. caragana</i> 2	Freitag 1629 [KAS]	Afghanistan	FN434527	FN434262
<i>A. chingii</i> (Hitc.) Keng	Miehe 9220 11 [Miehe]	China	FN434473	FN434204
<i>A. confusum</i> (Litv.) Tzvelev	Hilbig (27.07.1986) [HAL]	Mongolia	FN434534	FN434269
<i>A. duthiei</i> (Hook. f.) P.C. Kuo & S.L. Lu	Miehe 05 049 20 [Miehe]	China	FN434474	FN434205
<i>A. inebrians</i> (Hance) Keng 1	Mirkin (17.06.1972) [HAL]	Mongolia	FN434476	FN434207
<i>A. inebrians</i> 2	Hensen 430 [HAL]	China	FN434475	FN434206
<i>A. Jacquemontii</i> (Jaub. & Spach) P.C. Kuo & S.L. Lu	Freitag 1756 [KAS]	Afghanistan	FN434551	FN434289
<i>A. occidentale</i> subsp. <i>californicum</i> (Merr. & Burt Davy) Barkworth	Hagen G285 [HAL]	Halle BG; seeds from Bydgoszcz BG	FN434521	FN434256
<i>A. pekinense</i> (Hance) Ohwi 1	Freitag (14.08.1976) [KAS]	Kassel BG; seeds from Wladiwostok	FN434541	FN434278
<i>A. pekinense</i> 2	Hagen G229a [HAL]	Halle BG; seeds from Copenhagen BG	FN434542	FN434277
<i>A. pelliottii</i> (Dangu) M. Röser & H.R. Hamasha 1	Hilbig (24.06.1979) [HAL]	Mongolia	FN434502	FN434234
<i>A. pelliottii</i> 2	Hensen 540 [HAL]	Tibet	FN434503	FN434235
<i>A. pelliottii</i> 3	Miehe 96-021-02 [HAL]	Mongolia	FN434504	FN434236
<i>A. sibiricum</i> (L.) Keng ex Tzvelev 1	Hilbig (06.07.1985) [HAL]	Mongolia	FN434596	FN434338
<i>A. sibiricum</i> 2	Ebel & Reichel (22.10.1964) [HAL]	Halle BG; seeds from W Himalaya	FN434595	FN434339
<i>A. splendens</i> (Trin.) Nevski 1	Heklau R507 [HAL]	Mongolia	FN434477	FN434208
<i>A. splendens</i> 2	Hensen (10.07.2004) [HAL]	Tibet	FN434478	FN434209
<i>Aristella</i> Bertol.				
<i>A. bromoides</i> (L.) Bertol. 1	Hamasha (01.04.2006) [HAL]	Jordan	FN434517	FN434250
<i>A. bromoides</i> 2	Freitag 13500 [KAS]	Azerbaijan	FN434515	FN434251
<i>A. bromoides</i> 3	Meusel (29.04.1979) [HAL]	Greece	FN434516	FN434252
<i>A. bromoides</i> 4	Hilbig (13.06.1970) [HAL]	Bulgaria	FN434506	FN434240
<i>A. keniensis</i> (Pilg.) M. Röser & H.R. Hamasha 1	Wesche 734 [HAL]	Kenya	FN434555	FN434293
<i>A. keniensis</i> 2	Boulos (31.01.1978) [KAS]	Kenya	FN434538	FN434274
<i>Austrostipa</i> S.W.L. Jacobs & J. Everett				
<i>A. drummondii</i> (Steud.) S.W.L. Jacobs & J. Everett	Provided by S.W.L. Jacobs and M.E. Barkworth		S.W.L. Jacobs, unpubl.	
<i>A. elegantissima</i> (Labill.) S.W.L. Jacobs & J. Everett	Hagen G256 [HAL]	Halle BG; seeds from Liberec BG	FN434540	FN434276
<i>A. scabra</i> (Lindl.) S.W.L. Jacobs & J. Everett	Röser 10869 [HAL]	Australia	FN434594	FN434337
<i>A. setacea</i> (R. Br.) S.W.L. Jacobs & J. Everett	Provided by S.W.L. Jacobs and M. Barkworth		S.W.L. Jacobs, unpubl.	
<i>A. velutina</i> (Vickery, S.W.L. Jacobs & J. Everett) S.W.L. Jacobs & J. Everett	Provided by S.W.L. Jacobs and M.E. Barkworth		SW.L. Jacobs, unpubl.	

Table 1 continued

Taxon	Collector and collection no. (or date), [herbarium acronym]	Origin or reference	ITS	Cp
<i>Celtica</i> F.M. Vázquez & Barkworth				
<i>C. gigantea</i> (Link) F.M. Vázquez & Barkworth	Röser 9476 [HAL]	Portugal	FN434544	FN434281
<i>Jarava</i> Ruiz & Pav.				
<i>J. ichu</i> Ruiz & Pav.	Hensen (01.01.2007) [HAL]	Bolivia	FN434550	FN434288
<i>J. neaei</i> (Nees ex Steud.) Peñail.	Hagen G152 [HAL]	Halle BG; seeds from Leipzig BG	FN434566	FN434306
<i>Macrochloa</i> Kunth				
<i>M. tenacissima</i> (L.) Kunth	Eckerlein (28.06.1964) [HAL]	Algeria		FN434345
<i>Nassella</i> (Trin.) E. Desv.				
<i>N. formicarum</i> (Delile) Barkworth	Hagen G138 [HAL]	Halle BG; seeds from Nantes BG	FN434543	FN434279
<i>N. hyalina</i> (Nees) Barkworth	Hagen G270a [HAL]	Halle BG; seeds from Copenhagen BG	FN434549	FN434287
<i>N. lepida</i> (Hitcch.) Barkworth	Rose (May 1936) [HAL]	USA		FN434300
<i>N. poeppigiana</i> (Trin. & Rupr.) Barkworth	Hagen G282 [HAL]	Halle BG; seeds from F. Wollborn	FN434577	FN434319
<i>N. trichotoma</i> (Nees) Hack. ex Arechav.	Provided by S.W.L. Jacobs and M.E. Barkworth		S.W:L Jacobs, unpubl.	
<i>N. viridula</i> (Trin.) Barkworth	Ebel & Reichel (24.04.1965) [HAL]	Halle BG	FN434608	FN434355
<i>Oloptum</i> M. Röser & H.R. Hamasha				
<i>O. miliaceum</i> (L.) M. Röser & H.R. Hamasha		Schneider et al. (2009)	FM179427	AM234597
<i>Orthoraphium</i> Nees				
<i>O. roylei</i> Nees	Miehe 14901 [KAS]	Nepal	FN434590	FN434333
<i>Pappostipa</i> (Speg.) Romasch., P.M. Peterson & Soreng				
<i>P. humilis</i> (Cav.) Romasch.	Hagen G237a [HAL]	Halle BG; seeds from F. Wollborn	FN434548	FN434286
<i>Piptatherum</i> P. Beauv.				
<i>P. aequiglume</i> Munro ex Duthie	Freitag 5949 [KAS]	Afghanistan	FN434482	FN434213
<i>P. angustifolium</i> Munro ex Aitch.	Freitag 5792 [KAS]	Afghanistan	FN434483	FN434214
<i>P. baluchistanicum</i> Freitag	Freitag 3431 [KAS]	Afghanistan	FN434484	FN434215
<i>P. barbellatum</i> Mez 1	Freitag 6369 [KAS]	Afghanistan	FN434485	FN434216
<i>P. barbellatum</i> 2	Anders (25.06.1970) [KAS]	Afghanistan		FN434217
<i>P. coeruleascens</i> P. Beauv.	Holtz et al. (13.05.1978) [KAS]	Turkey	FN434486	FN434218
<i>P. flaccidum</i> Freitag	Anders 4584 [KAS]	Afghanistan	FN434487	FN434219
<i>P. gracile</i> Mez	Freitag (25.07.1989) [KAS]	Pakistan	FN434488	FN434220
<i>P. hilariae</i> Pazij	Anders 5310 [KAS]	Afghanistan	FN434489	FN434221
<i>P. holciforme</i> Roem. & Schult.	Baierle et al. 82/1531 [KAS]	Saudi Arabia	FN434490	FN434222
<i>P. laterale</i> (Regel) Roshev.	Freitag 1431 [KAS]	Afghanistan	FN434491	FN434223
<i>P. munroi</i> Mez 1	Hensen (06.08.2004) [HAL]	Tibet	FN434480	FN434211
<i>P. munroi</i> 2	Freitag 2853 [KAS]	Afghanistan	FN434492	FN434224
<i>P. pamiralaicum</i> (Grigorj.) Roshev.	Freitag 3545 [KAS]	Afghanistan	FN434493	
<i>P. platyanthum</i> Nevski	Anders 4431 [KAS]	Afghanistan	FN434494	FN434225
<i>P. purpurascens</i> (Hack. ex Paulsen) Roshev.	Anders 8035 [KAS]	Afghanistan	FN434495	FN434226
<i>P. rechingeri</i> (Bor) Freitag	Freitag 1533 [KAS]	Afghanistan	FN434496	FN434227
<i>P. tibeticum</i> Roshev.	Hensen (09.08.2004) [HAL]	Tibet	FN434481	FN434212

Table 1 continued

Taxon	Collector and collection no. (or date), [herbarium acronym]	Origin or reference	ITS	Cp
<i>P. vicarium</i> (Grigorj.) Roshev.	Freitag 2812 [KAS]	Afghanistan	FN434497	FN434228
<i>Piptochaetium</i> J. Presl				
<i>P. avenaceum</i> (L.) Parodi	Moore (May 1955) [HAL]	USA	FN434507	FN434241
<i>Ptilagrostis</i> Griseb.				
<i>P. concinna</i> (Hook.) Roshev.	Miehe 8455 [Miehe]	China	FN434533	FN434268
<i>P. dichotoma</i> Keng ex Tzvelev 1	Miehe 05 041 47 [Miehe]	Tibet	FN434498	FN434229
<i>P. dichotoma</i> 2	Hensen (06.08.2004) [HAL]	Tibet	FN434499	FN434230
<i>P. mongholica</i> (Turcz. ex Trin.) Griseb. 1	Miehe 00 228 37 [Miehe]	Bhutan	FN434501	FN434231
<i>P. mongholica</i> 2	Hilbig (20.08.1981) [HAL]	Mongolia	FN434500	FN434232
<i>P. mongholica</i> 3	Hilbig (1972) [TK]	Mongolia		FN434233
<i>Stipa</i> L.				
<i>S. anomala</i> P.A. Smirn.	Hagen G261a [HAL]	Halle BG; seeds from Kiev BG	FN434505	FN434238
<i>S. arabica</i> Trin. & Rupr.	Hamasha (01.04.2006) [HAL]	Jordan		FN434239
<i>S. baicalensis</i> Roshev.	Hilbig (03.08.1981) [HAL]	Mongolia	FN434508	FN434242
<i>S. basi-plumosa</i> Munro ex Hook. f.	Hensen (29.07.2004) [HAL]	Tibet	FN434510	FN434244
<i>S. bhutanica</i> Noltie	Miehe 00 347 03 [Miehe]	Bhutan	FN434511	FN434245
<i>S. borysthencia</i> Klovov ex Prokudin	Hagen N113 [HAL]	Halle BG; seeds from Olomouc BG	FN434512	FN434246
<i>S. breviflora</i> Griseb.	Miehe 96-088-02 [Miehe]	Mongolia	FN434514	FN434248
<i>S. brevifolia</i> Phil.	(1932) [TK]	Kyrgyzstan		FN434249
<i>S. bungeana</i> Trin. ex Bunge 1	Hagen G269a [HAL]	Halle BG; seeds from Beijing BG	FN434518	FN434253
<i>S. bungeana</i> 2	Hensen (29.07.2004) [HAL]	Tibet	FN434519	FN434254
<i>S. capillacea</i> Keng	Hensen (15.07.2004) [HAL]	Tibet	FN434523	FN434258
<i>S. capillata</i> L. 1	Röser 6152 [HAL]	Italy	FN434525	FN434260
<i>S. capillata</i> 2	Schlegel (25.07.1972) [HAL]	Germany	FN434526	FN434261
<i>S. caucasica</i> Schmalh.	(1932) [TK]	Kazachstan	FN434529	FN434264
<i>S. caucasica</i> subsp. <i>desertorum</i> (Roshev.) Tzvelev	(1932) [TK]	Kyrgyzstan	FN434530	FN434265
<i>S. caucasica</i> subsp. <i>glareosa</i> (P.A. Smirn.) Tzvelev 1	Miehe 96 151 05 [HAL]	Mongolia	FN434531	FN434266
<i>S. caucasica</i> subsp. <i>glareosa</i> 2	Hilbig (24.07.1974) [HAL]	Mongolia	FN434532	FN434267
<i>S. cretacea</i> P.A. Smirn.	Wolodina (05.06.1974) [KAS]	Russia	FN434535	FN434270
<i>S. dasyphylla</i> Czern. ex Trautv. 1	Rauschert (18.05.1965) [HAL]	Hungary	HE586634	
<i>S. dasyphylla</i> 2	Rauschert (10.06.1978) [HAL]	Germany	HE586637	FN434271
<i>S. decipiens</i> P.A. Smirn.	(1972) [TK]	Mongolia	FN434536	FN434272
<i>S. densiflora</i> Hughes	(19279) [TK]	Russia	FN434537	FN434273
<i>S. ehrenbergiana</i> Trin. & Rupr.	(28.05.1950) [KAS]	Armenia	FN434539	FN434275
<i>S. eriocalis</i> Borbás		Schneider et al. (2009)	FM179438	AM234577
<i>S. gaubae</i> Bor	Takhtajan et al. (01.06.1990) [KAS]	Azerbaijan		FN434280
<i>S. gobica</i> Roshev.	Miehe 96-003-07 [Miehe]	Mongolia		FN434282
<i>S. grandis</i> P.A. Smirn.	Hilbig (03.02.1976) [HAL]	Mongolia	FN434545	FN434283
<i>S. himalaica</i> Roshev.	Freitag 2863 [KAS]	Afghanistan	FN434546	FN434284
<i>S. holosericea</i> Trin.	Holz et al. 730 [KAS]	Turkey	FN434547	FN434285
<i>S. joannis</i> Celak. 1	Hilbig (05.07.1988) [HAL]	Russia	FN434552	FN434290
<i>S. joannis</i> 2	Schaberg (06.07.1973) [HAL]	Germany	FN434553	FN434291

Table 1 continued

Taxon	Collector and collection no. (or date), [herbarium acronym]	Origin or reference	ITS	Cp
<i>S. juncea</i> L.	Izco (14.05.1967) [HAL]	Spain	FN434554	FN434292
<i>S. koelzii</i> R.R. Stewart	Miehe 12126 [KAS]	Nepal	FN434556	FN434294
<i>S. krylovii</i> Roshev. 1	(1932) [TK]	Russia		FN434297
<i>S. krylovii</i> 2	Hagen N109 [HAL]	Halle BG; seeds from Jakutsk BG	FN434558	FN434295
<i>S. lagascae</i> Roem. & Schult. 1	Hamasha (01.04.2006) [HAL]	Jordan	FN434559	FN434298
<i>S. lagascae</i> 2	Meusel (11.08.1981) [HAL]	Morocco	FN434560	FN434299
<i>S. lessingiana</i> Trin. & Rupr. 1	Hagen G151a [HAL]	Halle BG; seeds from Göttingen BG	FN434561	FN434301
<i>S. lessingiana</i> 2	Meusel (13.08.1978) [HAL]	Turkey	FN434562	FN434302
<i>S. lingua</i> Junge	Freitag 6588 [KAS]	Afghanistan	FN434563	FN434303
<i>S. margelanica</i> P.A. Smirn.	Freitag 6518 [KAS]	Afghanistan	FN434564	FN434304
<i>S. milleri</i> Noltie	Miehe 00 211 12 [Miehe]	Bhutan	FN434565	FN434305
<i>S. offneri</i> Breistr. 1	Hagen N108 [HAL]	Halle BG; seeds from Paris Nat. Hist. Museum	FN434568	FN434308
<i>S. offneri</i> 2	Röser 4174 [HAL]	Spain	FN434569	FN434309
<i>S. orientalis</i> Trin. ex Ledeb.	Miehe 6374 [KAS]	Pakistan	FN434570	FN434310
<i>S. penicillata</i> Hand.-Mazz.	Miehe 98 30201a [Miehe]	China	FN434574	FN434314
<i>S. pennata</i> L. subsp. <i>kirghisorum</i> (P.A. Smirn.) Freitag	Miehe 6698 [Miehe]	Pakistan	FN434575	FN434315
<i>S. pennata</i> subsp. <i>pulcherrima</i> (K. Koch) Á. Löve & D. Löve	Jäger (12.08.1977) [HAL]	Russia		FN434316
<i>S. pennata</i> subsp. <i>zalesskii</i> (Wilensky) Freitag 1	Hagen G265 [HAL]	Halle BG; seeds from Kiev BG	FN434576	FN434317
<i>S. pennata</i> L. subsp. <i>zalesskii</i> 2	Werner (19.06.1974) [HAL]	Russia		FN434318
<i>S. poetica</i> Klovov	Hagen G263 [HAL]	Halle BG; seeds from Kiev BG	FN434578	FN434320
<i>S. pontica</i> P.A. Smirn.	Hagen G168 [HAL]	Halle BG; seeds from Leipzig BG	FN434579	FN434321
<i>S. purpurea</i> Griseb. 1	Miehe 6221 [KAS]	Karakorum	FN434582	FN434324
<i>S. purpurea</i> 2	Hensen (06.08.2004) [HAL]	Tibet		FN434325
<i>S. regaliana</i> Hack. 1	Hensen (09.07.2004) [HAL]	Tibet	FN434584	FN434326
<i>S. regaliana</i> 2	Dickorée 8925 [KAS]	Tibet	FN434583	FN434327
<i>S. richterana</i> Kar. & Kir.	Feldkamp 7323 [KAS]	Afghanistan	FN434586	FN434329
<i>S. roborowskyi</i> Roshev.	Miehe 05 104 04 [Miehe]	Tibet	FN434587	FN434330
<i>S. rohmooiana</i> Noltie	Miehe 93 256 39 [Miehe]	Tibet	FN434589	FN434332
<i>S. rubens</i> Smirnnow	Rauschert (21.05.1965) [HAL]	Czech Republic	FN434591	FN434334
<i>S. sareptana</i> A.K. Becker 1	Hilbig (23.07.1979) [HAL]	Mongolia	FN434592	FN434335
<i>S. sareptana</i> 2	Roshevitz (1926) [HAL]	Kazachstan	FN434593	FN434336
<i>S. stenophylla</i> Czern. ex Trautv.	Hilbig (13.06.1978) [HAL]	Germany		FN434343
<i>S. subsessiliflora</i> Roshev.	Miehe 6201 [KAS]	Pakistan	FN434600	FN434344
<i>S. thessala</i> Hausskn.	Hagemann 1099 [KAS]	Greece	FN434601	FN434346
<i>S. tianschanica</i> Roshev. 1	Wuendisch 952 [Miehe]	China	FN434602	FN434347
<i>S. tianschanica</i> 2	Miehe 04 159 15 [Miehe]	Tibet	FN434603	FN434348
<i>S. tirsa</i> Steven	Hagen N14 [HAL]	Halle BG; seeds from Göttingen BG	FN434605	FN434350
<i>S. trichoides</i> P.A. Smirn.	(1936) [TK]	Kyrgyzstan		FN434351
<i>S. turkestanica</i> Hack. 1	Hagen G211 [HAL]	Halle BG; seeds from Leipzig BG	HE586635	FN434352

Table 1 continued

Taxon	Collector and collection no. (or date), [herbarium acronym]	Origin or reference	ITS	Cp
<i>S. turkestanica</i> 2	Freitag 1008 [KAS]	Afghanistan	FN434606	FN434353
<i>S. turkestanica</i> 3	Hagen G213 [HAL]	Halle BG	HE586636	
<i>S. ucrainica</i> Steud.	Hagen G251 [HAL]	Halle BG	FN434607	FN434354
<i>Stipella</i> (Tzvelev) M. Röser & H.R. Hamasha				
<i>S. capensis</i> (Thunb.) M. Röser & H.R. Hamasha	Hamasha (01.04.2006) [HAL]	Jordan	FN434522	FN434257
<i>S. capensis</i> 2		Schneider et al. (2009)	FM179437	AM234576
<i>S. capensis</i> 3	Meusel (06.05.1955) [HAL]	Morocco	FN434585	FN434328
<i>S. nitens</i> (Bor) M. Röser & H.R. Hamasha	Meusel (13.12.1961) [HAL]	Morocco	FN434567	FN434307
<i>S. parviflora</i> (Desf.) M. Röser & H.R. Hamasha	Hamasha (01.04.2006) [HAL]	Jordan	FN434571	FN434311
<i>S. parviflora</i> 2	Röser No.4138 [HAL]	Spain	FN434572	FN434312
<i>S. staintonii</i> (Bor) M. Röser & H.R. Hamasha	Miehe 01 122 04 [Miehe]	Nepal	FN434598	FN434341
<i>S. tigrensis</i> (Chiov.) M. Röser & H.R. Hamasha	Müller-Hohenstein (29.03.1983) [KAS]	Yemen	FN434604	FN434349
Outgroup				
<i>Ampelodesmos mauritanicus</i> (Poir.) T. Durand & Schinz		Schneider et al. (2009)	AF019799	AM234569
<i>Anisopogon avenaceus</i> R. Br.		Schneider et al. (2009)	FM179386	AM234575
<i>Avena macrostachya</i> Coss. & Durieu		Schneider et al. (2009)	FM179443	FM253118
<i>Brachyelytrum erectum</i> (Schreb.) P. Beauv.		Schneider et al. (2009)	AF019794	AM234584
<i>Brachypodium distachyon</i> (L.) P. Beauv.		Schneider et al. (2009)	AF303399	AM234568
<i>Bromus erectus</i> Huds.		Schneider et al. (2009)	FM179394	AM234570
<i>Brylkinia caudata</i> F. Schmidt		Schneider et al. (2009)	FM179442	FM253121
<i>Danthoniastrum compactum</i> (Boiss. & Heldr.) Holub		Schneider et al. (2009)	FM179398	AM234544
<i>Diarrhena americana</i> P. Beauv.		Schneider et al. (2009)	FM179400	FM253123
<i>Duthiea brachypodium</i> (P. Candargy) Keng & Keng f.		Schneider et al. (2009)	FM179402	AM234547
<i>Echinopogon</i> sp.		Schneider et al. (2009)	FM179403	AM234609
<i>Glyceria nemoralis</i> (Uechtr.) Uechtr. & Körn.		Schneider et al. (2009)	FM179405	AM234578
<i>Littledalea tibetica</i> Hemsl.		Schneider et al. (2009)	FM179416	AM234572
<i>Lygeum spartum</i> L.		Schneider et al. (2009)	FM179417	AM234579
<i>Melica picta</i> K. Koch		Schneider et al. (2009)	FM179418	AM234580
<i>Nardus stricta</i> L.		Schneider et al. (2009)	FM179420	AM234573
<i>Phaenosperma globosa</i> Benth.		Schneider et al. (2009)	FM179423	AM234574
<i>Schizachne purpurascens</i> Swallen		Schneider et al. (2009)	FM179432	FM253126
<i>Sinochasea trigyna</i> Keng		Schneider et al. (2009)	FM179436	AM234548

Taxon, collector and standard herbarium code or reference, geographical origin and EMBL/GenBank sequence entries

BG Botanical Garden, [Miehe] private collection of G. and S. Miehe, Geographical Institute, University of Marburg

To obtain phylogenetic relationships and branch support with a different methodology, we used a Bayesian approach. MrModeltest 2.3 (Nylander 2004) was used to determine the model that best fit the cp and nr DNA data. The hierarchical likelihood ratio tests (hLRTs) selected

HKY + I + G as the best fit model for the cp DNA data, whereas the Akaike information content criteria (AIC) selected model GTR + I + G. For the nr ITS data, hLRTs and AIC correspondingly selected GTR + I + G as the best fit model. The results of these tests were used as priors

for Bayesian inference using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Separate analyses of the cp DNA data sets under the models HKY + I + G and GTR + I + G yielded congruent tree topologies with only slightly different posterior probabilities for some nodes as shown in Figs. S1 and S2 of the electronic supplementary material (differences <0.07). In the analyses of the combined cp and nr DNA data the priors thus were set according to GTR + I + G as a single model. In all analyses (cp, ITS and combined data), four Markov chains were run simultaneously for 3–5 million generations, and these were sampled every 1,000 generations. After the chains had reached stationarity as judged from plots of likelihood and from split variances, data from the first 10–25% of generations were discarded as “burn-in.” A 50% majority-rule consensus tree was constructed, and posterior probabilities (P) of nodes were calculated from the remaining sample.

The complete trees and results of the Bayesian analyses are contained in Figs. S1–S4 of the electronic supplementary material. Detailed maximum parsimony strict consensus trees with tree statistics (cp, ITS and combined data) are shown in Figs. S5–S7.

Results

The cp 3'trnK region alignment was 870 base pairs long. The length of the >20,000 most parsimonious trees was 503 steps, and the RC was 0.608. A simplified strict consensus tree with BS and Bayesian values on major branches is shown in Fig. 1a. The complete trees are available in the electronic supplementary material (Figs. S1, S2 and S5). The nr ITS alignment was 663 base pairs long. The length of the >20,000 most parsimonious trees was 1,365 steps, and the RC was 0.326. A simplified overview of the strict consensus tree with BS and Bayesian values is shown in Fig. 1b. The entire trees are Figs. 3 and 6 in the electronic supplementary material. Taxa with incongruent position between the cp and the nr ITS analyses (definition of incongruence in “Materials and methods”) are indicated in Fig. 1a, b. The combined analysis with all taxa included was less resolved than the separate analyses, and most branches were comparably weakly supported (not shown). A combined analysis with incongruent taxa excluded, however, was better resolved than the separate analyses, and also branch support was distinctly higher. The strict

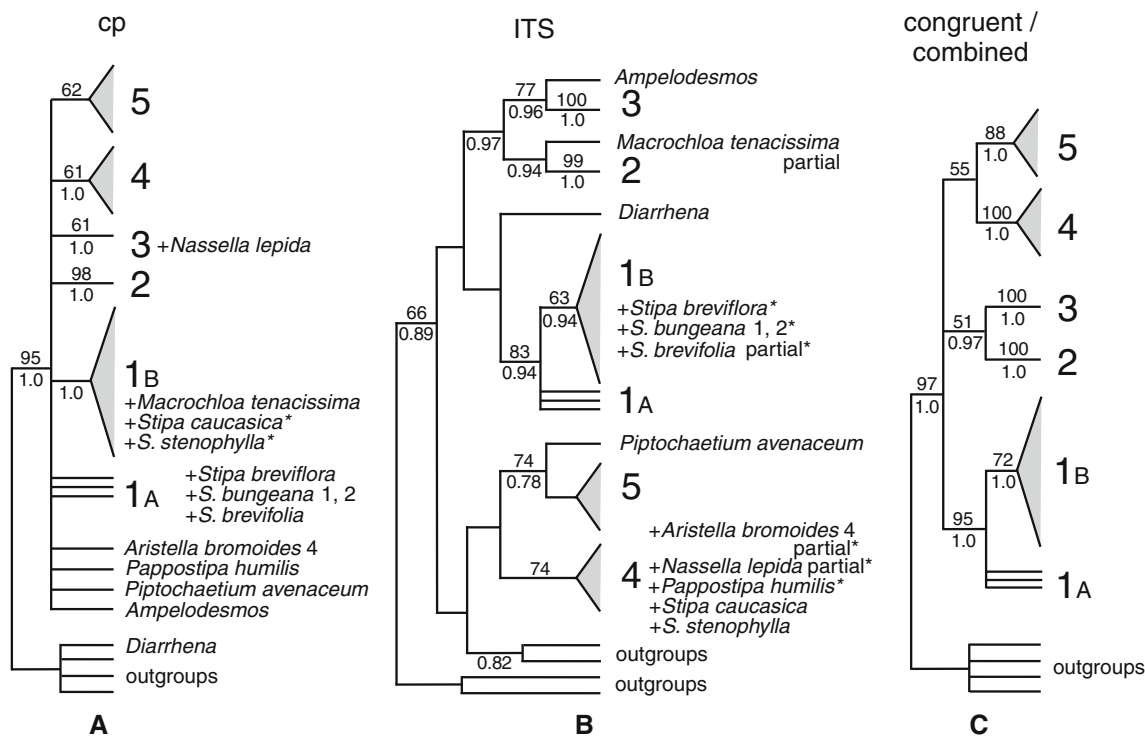


Fig. 1 Overview of phylogenetic trees derived from maximum parsimony analyses of the different data sets. **a** Generalized strict consensus tree based on cp data. **b** Generalized strict consensus tree based on nuclear ITS data. **c** Generalized strict consensus tree based on combined data. Definition of groups 1–5 as in Fig. 2. Bootstrap support >50% for major groups is given above, Bayesian support of $P > 0.50$ below branches. Parsimony and Bayesian analyses were nearly congruent for all three data sets (but see text for minor

exceptions). Taxa regarded as incongruent between cp and nuclear trees are named in **a** and **b**, and were not included in the data set used for **c**. The probable correct phylogenetic position of some of these taxa is denoted by an asterisk, and for four of them only partial ITS sequences could be obtained. The complete strict consensus trees used for **a–c** are shown in the electronic supplementary material Figs. S5–S7, the full Bayesian trees in Figs. S1–S4

consensus tree of the >20,000 trees (1,965 steps, RC = 0.358) with branch support values on major branches is shown as a simplified overview in Fig. 1c. This tree is shown completely in Fig. S7 of the electronic supplementary material, and the Bayesian 50% majority rule tree is illustrated in Fig. S4.

Parsimony and the Bayesian approach yielded very similar relationships (Figs. 1, S1–S7). The few exceptions must be regarded as minor or very minor only, e.g., in the combined analysis several *Achnatherum* lineages and *Aristella* were in one clade in the Bayesian tree ($P = 0.97$; Fig. S4), but these were unresolved with parsimony (Fig. S7). This difference is indicated by a dashed line in the bootstrap 50% majority-rule consensus tree of Fig. 2b. Several subclades in major group 1B received some bootstrap support in the combined analysis, whereas Bayesian support was low or absent ($P < 0.94$; Figs. 2a, S4). With cp data *Aristella bromoides* 4 was in an unresolved position in the parsimony tree (Figs. 1a, S5) and at the very base of group 4 (below *Celtica*) in the Bayesian analysis ($P = 1.0$; Figs. S1, S2). Both positions are hard to explain when compared with the three other conspecific accessions (*A. bromoides* 1–3), which were nested in group 4. Therefore, there is no need to discuss the parsimony and Bayesian results separately.

Several major groups were consistently found in the separate nr and cp analysis (Fig. 1a, b; termed clades 1–5). They also appeared in the combined analysis of both data sets with improved branch support after removal of the incongruent taxa (Figs. 1c, 2, S4, S7). The monophyly of Stipeae was well supported with the combined data set, but branching order among the five major clades was essentially unresolved (e.g., BS < 60%). The large majority of species were kept by most authors under *Stipa* even in a very narrow circumscription grouped in the Eurasian to Mediterranean clade 1. Clade 2 was the major *Piptatherum* clade and encompassed all of its Eurasian members including Asian species sometimes treated before under *Oryzopsis* Michx., with the exception of *Oloptum miliaceum* (formerly *Piptatherum miliaceum*), which was nested in clade 4. Clade 3 included the two accessions of the Asian *Achnatherum splendens*. Clade 4, also named “Transcontinental Stipeae Clade” in the remainder of this article, encompassed the type species of *Achnatherum*, *A. calamagrostis* and several other species of this genus including *Achnatherum pelliottii*, a species that has previously been included in *Ptilagrostis*. Parts of this clade were the mainly South American *Nassella* and *Jarava*, including *J. ichu*, type species of *Jarava* and Australian *Austrostipa*. In addition, it further included the Eurasian to African *Oloptum miliaceum*, and the species treated here under the genera *Stipella* and *Aristella*. *Celtica gigantea* was sister to the remainder of clade 4 (Figs. 2, S4, S7). Clade 5

encompassed mainly Himalayan, Mongolian, Siberian and Chinese species included by previous authors under *Achnatherum*, *Orthoraphium*, *Ptilagrostis* and *Stipa*.

Discussion

Congruence and incongruence between data sets

The major phylogenetic lineages retrieved from both partial molecular data sets were largely identical (Figs. 1a, b, S1–S3, S5, S6). A minor difference was that the ITS tree was better structured for the deeper nodes, but this did receive less than 50% bootstrap and $P < 0.5$ Bayesian support. A major difference was that the positions of the genera *Ampelodesmos* and *Diarrhena*, and a part of the outgroup taxa were not consistent. The monotypic genus *Ampelodesmos* was affiliated with clade 3 (77% BS, $P = 0.96$) in the ITS trees (Figs. 1b, S3, S6), but stood in the large polytomy of clades 1–5 in the cp DNA data (Figs. 1a, S1, S2, S5). This is a similar result to those obtained in previous studies, the exact position being dependent on the sampling of Stipeae taxa (e.g., Döring et al. 2007; Jacobs et al. 2007; Barkworth et al. 2008; Bouchenak-Khelladi et al. 2008; Döring 2009; Schneider et al. 2009). Origin of *Ampelodesmos* within the tribe Stipeae rather than outside of it (i.e., a separate Ampelodesmeae Tutin) seems increasingly likely, especially in view of our extensive outgroup sampling (cf. Davis and Soreng 2007; Schneider et al. 2009; Romaschenko et al. 2010). *Ampelodesmos* was recently suggested to be a separate subtribe, *Ampelodesminae* Conert, within the Stipeae (Schneider et al. 2009).

In the ITS trees *Diarrhena americana* was unsupported as sister to Stipeae clades 1A and B in parsimony analysis (Figs. 1b, S6), whereas in Bayesian inference it was unsupported as sister to an unsupported assemblage of clades 1A and B and 4 (Fig. S3). *Diarrhena* grouped with the outgroup taxa in the cp DNA tree (Figs. 1a, S1, S2). Placement of *Diarrhena* within Stipeae or even Meliceae, though consistently without strong support, was also found in previous ITS analyses (e.g., Grass Phylogeny Working Group 2001; Jacobs et al. 2007; Schneider et al. 2009), whereas all cp DNA data, including the present study, provide strong support for its exclusion from the Stipeae (Fig. 1a; cf. Catalán et al. 1997; Grass Phylogeny Working Group 2001; Döring et al. 2007; Davis and Soreng 2007; Schneider et al. 2009). We believe that the relatively high degree of homoplasy of the ITS data is the main cause for the different placements of *Ampelodesmos* and *Diarrhena* in the trees.

There are ten other taxa with clearly incongruent positions between the cp and ITS trees (listed in Fig. 1a, b).

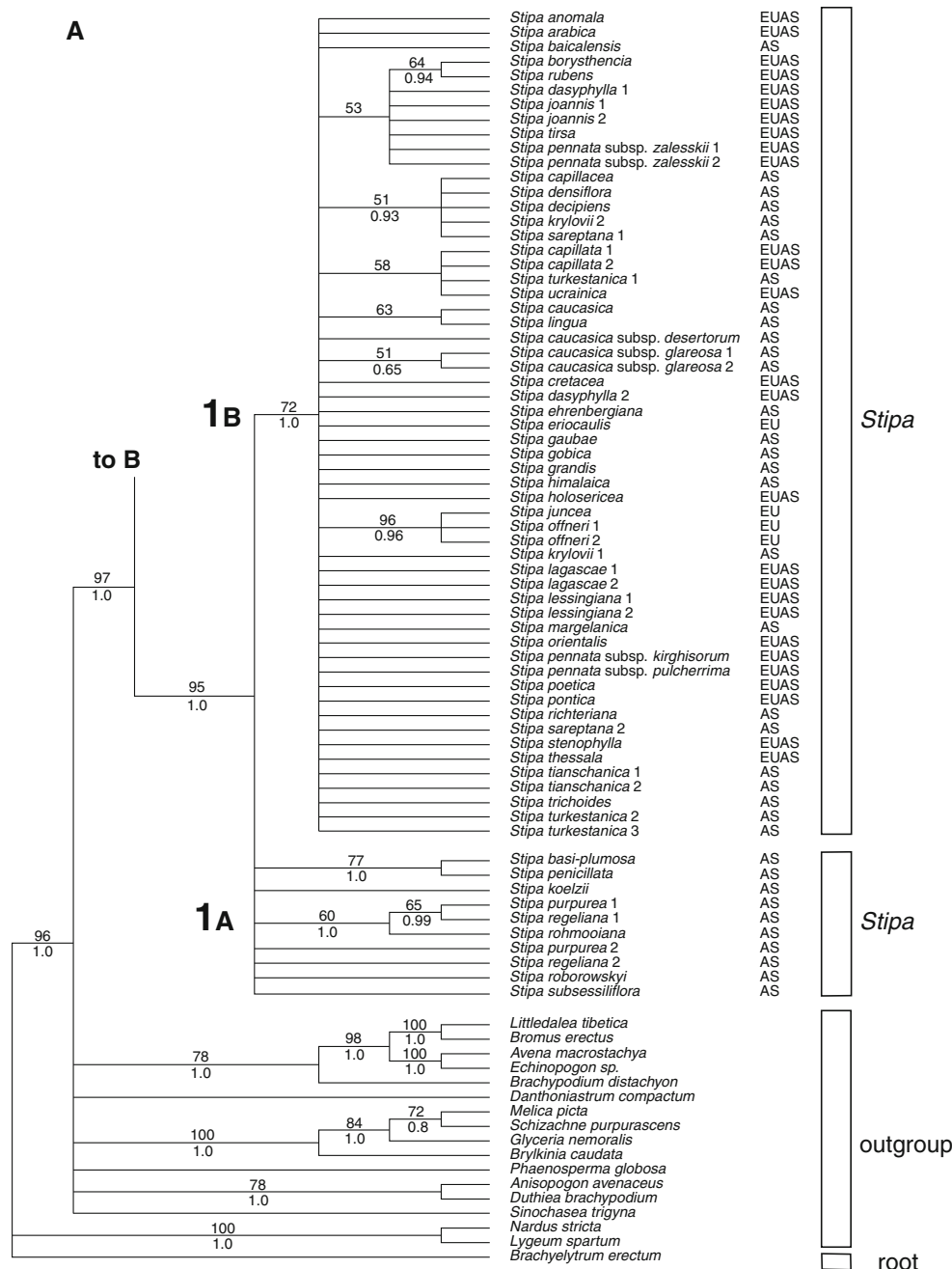


Fig. 2 Lower (a) and upper (b) half of the 50% majority-rule bootstrap tree from maximum parsimony analyses of the combined data set with incongruent taxa excluded. Bootstrap values >50% above, Bayesian support of $P > 0.95$ below branches. The dashed line indicates the single branch with reasonable support from Bayesian inference that was not found in the parsimony analyses. The general geographical distribution of species is given behind

species names (AS Asia, EUAS Eurasia, AF Africa, NA North America, SA South America, AUS Australia). When available, names of existing segregate genera were used. *Oloptum* and *Stipella* are new genus names. The two *Stipa* species in clade 5 are not known very well and probably will have to be renamed. The type of *Achnatherum*, *A. calamagrostis*, is contained in group 4, and some other *Achnatherum* lineages probably will have to be renamed in the future

These taxa are firmly nested within Stipeae, and judging from morphology and geography, it seems that one of the DNA regions analyzed yields a very reasonable phylogenetic position while the other does not (indicated by an asterisk in Fig. 1). Our difficulties in obtaining complete

ITS data (indicated by the suffix “partial” in Fig. 1b) even after multiple amplifications point to the presence of slightly different copies in *Nassella lepida*, *Pappostipa humilis*, *Macrochloa tenacissima* and *Aristella bromoides* 4 (Figs. 1a, b, S3, S6). The consistency of the pattern for

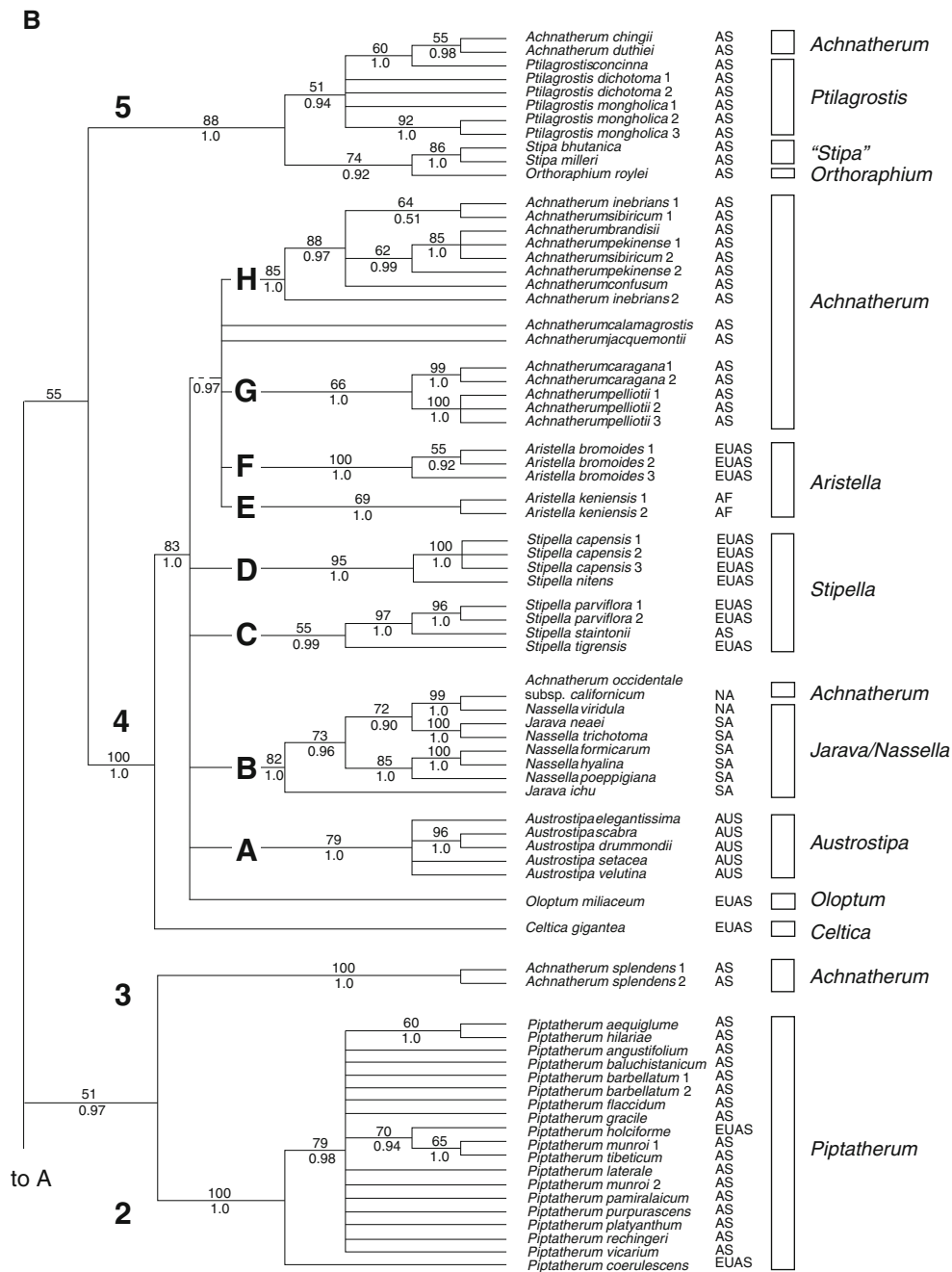


Fig. 2 continued

Stipa breviflora, *S. brevifolia*, and *S. bungeana* 1 and 2 suggests that the problem in these taxa is the result of lineage sorting or introgression (Figs. 1a, b, S3, S6). The latter may also account also for the position of *S. stenophylla* and one of the *S. glareosa* accessions along with clade 4 in the ITS data (Figs. 1b, S3, S6). This position is supported by parsimony analysis (BS = 74) but not by Bayesian inference ($P < 0.5$). We have no explanation for the placement of *Piptochaetium avenaceum*; however, very

few of putatively related American taxa have been sampled in this study. We believe that it is important to explicitly include these problematic accessions in our results even if at present we cannot draw any conclusions from them.

Major lineages of *Stipa* and Stipeae

A hierarchical branching order of the major lineages could not be identified with reasonable support. Branching order

was also unresolved by previous treatments based predominantly on morphology and an intuitive order of character evolution in the Stipeae (e.g., Tzvelev 1977; Freitag 1985; Barkworth and Everett 1987). Nevertheless, our results give new insights into what the “core” genus *Stipa* actually encompasses and which lineages of Old World Stipeae are the closest relatives of the typical American and Australian lineages, among them *Nassella*, *Jarava* or *Austrostipa*.

Stipa = clade 1 (Old World)

Clade 1B in Fig. 2 includes among others most sampled species of *Stipa* section *Stipa* and all of *Stipa* section *Barbatae* Junge emend. Freitag in the circumscription of Freitag (1985). These species belong to sections *Stipa*, *Leiostipa* Dumort. and *Smirnovia* Tzvelev in the circumscription of Tzvelev (1976). The sampled species from section *Pseudoptilagrostis* Tzvelev as treated by Freitag (1985) are represented only in clade 1A. The distribution of these two “core” *Stipa* clades is strictly Eurasian to Mediterranean, with a clear centre of diversity in the Asian mountain and steppe regions. This finding supports the exclusion of the species of clades 2–5 from *Stipa* (Fig. 2), as has already been recommended for most taxa already by various previous treatments, though generally different generic delineations were employed. An alternative would be to reinstate an extremely broad genus *Stipa* with an elaborate system of subgenera or sections comparable to that of Freitag (1985), which in principle could give the same information. On the basis of the clear-cut molecular phylogenetic data for clade 1, we argue for narrow genera in Stipeae (cf. below), admitting that their morphological differences alone would not justify acceptance of some of the segregate genera as emphasized, for example, by Freitag (1985) and Clayton and Renvoize (1986).

Clade 1 in Fig. 1 showed an interesting internal structure, because the early diverging species (group 1A) were almost always from the Himalayas, while the species from the larger group 1B were from other sections and only very rarely from this region. We were astonished that sequence divergence in clade 1B is close to zero in the cp data and very low in the ITS data, although the group contains several dozen species. This seems to be the main cause for the low phylogenetic resolution found and not incongruence between genes (e.g., due to lineage sorting) within clade 1B in Fig. 2 (but see Fig. 1 for possible lineage sorting in incongruent taxa between clades 1A and B).

Piptatherum (clade 2)

Monophyly and thus maintenance of genus *Piptatherum* were corroborated in this study, which included the large

majority of its Old World species (Fig. 2b), some of which had been transferred in previous treatments to *Oryzopsis*. Based on morphological and molecular phylogenetic studies (Freitag 1975; Barkworth 1993; Romaschenko et al. 2010), the type species of *Oryzopsis*, *O. asperifolia* Michx., which was not sampled in this study, is different from *Piptatherum*, so the name *Oryzopsis* is not applicable to Old World species. Here again the low sequence divergence between most species precluded resolution of the internal phylogeny of *Piptatherum* with one exception. The Old World species *P. miliaceum* was strongly supported as a distinct clade, distantly related to the other species of *Piptatherum*. For this reason we have made it the type species of a new genus named *Oloptum*.

Clade 3

Both accessions of one further species of *Achnatherum*, *A. splendens* (= *Stipa splendens*), formed this monotypic clade. This is a widespread and moderately abundant species that grows in Central Asia and the Far East (cf. Tzvelev 1976; Freitag 1985; Wu and Phillips 2006). Its special position is somewhat surprising. Tzvelev included it in *Achnatherum* sect. *Neotrinia* Tzvelev together with, e.g., *A. caragana* and *A. inebrians*; Freitag placed both *A. splendens* and *A. caragana* in *Stipa* sect. *Lasiagrostis* (Link) Hack. together with several other species. He did not treat *A. inebrians*. *Achnatherum splendens* is a very tall species and seems to be distinguished from other species of Stipeae mainly by quantitative characters in current taxonomic keys. A notable difference to the bulk of *Achnatherum* species is that its chromosome number seems to be $2n = 42$ or 48 (Tzvelev 1976) instead of mostly 24, as in other species. In conclusion, it seems necessary to base a new genus on *A. splendens*, but the appropriate treatment of the highly polyphyletic *Achnatherum* should be clarified first.

Transcontinental Stipeae clade 4

This molecularly highly supported monophyletic clade (100% BS) is extremely heterogeneous in overall morphology and geographically very widely distributed, encompassing Eurasia, Africa, the Americas and Australia. We initially considered this apparently purely ‘molecular’ clade artificial, because the taxa assembled under it had been treated before under several genera or sections of *Stipa*. Moreover, some taxa of clade 4 have been included in *Piptatherum* and *Ptilagrostis*, genera whose Eurasian members were in clades 2 and 5, respectively.

Closer morphological and taxonomic inspection showed that clade 4 could be separated into a number of reasonable morphological and biogeographical units, most of which are confined to this clade, for example, the species sampled

of American *Nassella* and *Jarava*, Australian *Austrostipa*, the Mediterranean to Middle Eastern genera *Aristella* [= *Stipa* sect. *Aristella* (Trin.) Hack.], *Celtica*, *Stipella* [= *Stipa* sect. *Stipella* Tzvelev] and *Oloptum* [= *Piptatherum* sect. *Miliacea* Roshev. ex Freitag]. *Celtica gigantea* was supported as sister to the remainder of this clade (BS 79%), thus supporting its maintenance as a monotypic genus separate from *Stipa* or other segregate genera (cf. Vázquez and Barkworth 2004; Romaschenko et al. 2010). *Oloptum miliaceum* was part of clade 4 as an outlier relative to its former congeners (*Piptatherum*), which assembled under clade 2. This species was already recognized as special by Freitag (1975, p. 356), who made it the only species of sect. *Miliacea*, arguing that some characters in lemma and palea structure appeared “primitive” and because of the shape of the disarticulation scar of the lemma. Further evidence for this was given by Barkworth and Everett (1987). All this induced us to describe a new genus *Oloptum* (cf. below nomenclature section). The actual species content of the new genus *Oloptum*, as either monotypic or encompassing further species, is yet unclear. Preliminary analysis of an ITS 1 sequence available from EMBL suggested that *P. virescens* (Trin.) Boiss. is also part of clade 4, but no additional further sequences were available; any conclusions should await a better supported analysis.

The remainder of clade 4 was rather heterogeneous, but contained a selection of some partly well-defined and especially species-rich lineages, i.e., (A) that of Australian *Austrostipa* and (B) a common lineage of American *Achnatherum*, *Nassella* and *Jarava*. It might be noted here that the very large majority of species from previous molecular analyses would obviously be part of our clade 4 (Jacobs et al. 2007; Cialdella et al. 2007; Romaschenko et al. 2007, 2008, 2010; Barkworth et al. 2008). The actual phylogenetic structure seemed to be more complicated than shown here in our reduced sample, but branch support was mostly low in previous studies.

Part of clade 4 were also (C) the lineages of *Stipella parviflora*, *S. staintonii* and *S. tigrensis*, and (D) of *S. capensis* and *S. nitens*. *Stipella capensis* represents the only annual species of Stipeae in the Old World and is one of seemingly only two annual species in the entire tribe [cf. South American *Jarava annua* (Mez) Peñalillo]. It was treated by Tzvelev (1974) under a new *Stipa* section, *Stipella*, mainly because of its unusual life form. It was noted by Freitag (1985: p. 413) that *S. capensis* shared a very short palea relative to the lemma and other characters of the lemmas and lodicules with the perennials found here under the lineages (C) and (D), and he considered all of these species under an expanded section *Stipella*. Although (C) and (D) do not share explicate molecular synapomorphies, *Stipa* sect. *Stipella* is acknowledged here as a separate genus *Stipella* (cf. nomenclature section below) based

on its exceptional and seemingly synapomorphic morphological characters.

Two further elements of clade 4 (termed groups E and F in Fig. 2b) consist of Mediterranean to Middle East *Aristella bromoides* [= *Stipa bromoides* (L.) Dörfel.], and E to S African *Aristella keniensis* [= *Stipa keniensis* (Pilg.) Freitag, syn. *S. dregeana* Steud.; cf. Clayton 1970; Freitag 1989]. *Aristella bromoides* and *A. keniensis* were placed together with few Asian species under *Stipa* sect. *Aristella* (Freitag 1985, 1989), based on uncommon characters of their mature florets (awns straight and untwisted, lemmas colored brown; cf. Freitag 1985). Therefore, both species are united under the genus *Aristella* here (cf. nomenclature section below), although this has not yet been resolved with molecular data. A possible relationship of *Aristella* with parts of *Achnatherum* weakly suggested by the molecular data (dashed branch in Fig. 2b) is not backed by morphological data.

Achnatherum calamagrostis [= *Stipa calamagrostis* (L.) Wahlenb.], the type species of *Achnatherum*, and other Asian or African species ascribed to *Achnatherum* by earlier treatments are also part of clade 4. This applies to the well-supported lineage (H) of Asian *A. brandisii*, *A. confusum*, *A. pекinensis* [syn. *A. extremiorientale* (H. Hara) Keng; cf. Tzvelev 1974, 1976; Wu and Phillips 2006], *A. inebrians* and *A. sibiricum*, a lineage for which strong morphological similarities of the species were noted earlier (e.g., Tzvelev 1976, 1977; Freitag 1985; Wu and Phillips 2006). A less well-supported lineage (G) included several accessions of *A. caragana* and *A. pelliottii*, the latter also treated sometimes under *Ptilagrostis* (cf. clade 1 below). *Achnatherum pelliottii* is a lowland species of steppes and deserts of Central Asia, and disagrees in morphology and ecology from the other alpine species traditionally summarized under *Ptilagrostis* (Tzvelev 1974, 1977; Barkworth and Everett 1987; Wu and Phillips 2006; Barkworth 2007). It was considered to belong to *Achnatherum* by Barkworth and Everett (1987) because of the evenly distributed pubescence of the lemma and the types of lemma epidermal cells, but has not been formally transferred to this genus (cf. below nomenclature section). The plumose awns of *A. pelliottii*, a character also encountered in parts of core *Ptilagrostis* (Tzvelev 1976, 2001; Freitag 1985; Wu and Phillips 2006; Barkworth 2007), thus obviously reflects a common adaptation to wind dispersal, not ancestry.

Clade 5

This well-supported clade encompassed Central to East Asian species frequently included in the genera *Achnatherum* (*A. chingii*, *A. duthiei*), *Ptilagrostis* (*P. mongholica*, *P. concinna*, *P. dichotoma*) and monotypic *Orthoraphium*. The internal structure of this clade was intriguing, and few

conclusions can be drawn from it. *Orthoraphium* from the outer Himalayas is morphologically defined by a unique hair structure at the apex of the lemma. This is putatively an autapomorphic character and unsuitable to define a separate genus as argued earlier (cf. Freitag 1985: pp. 360, 403f). The two species of *Stipa* in this clade (*S. bhutanica* and *S. milleri*) were put in *S.* sect. *Lasiagrostis* because of their callus shape and are seemingly close to *Achnatherum* and *Ptilagrostis* (Noltie 1999, 2000), but to our knowledge have not yet been combined under these genera. In view of the uncertain genus delineations in this clade, no new combinations are made in this study.

Conclusions

It is worthwhile to note that most of our classificatory conclusions are not particularly new relative to previous concepts based on morphological characters, except for the firm circumscription of a narrow *Stipa* and the origin of the typical American and Australian Stipeae from the separate “Transcontinental Stipeae Clade.” An American origin of Stipeae was implied by the branching order of previous studies, but it now seems that these results were just sampling artifacts. A firm branching order within and between the five lineages identified could not be established with the molecular markers used in this study, but we consider it an interesting question for future studies.

New description and new combinations

Oloptum M. Röser & H.R. Hamasha, gen. nov.

Differt a genero *Piptathero* cicatrice disarticulationis lemmatum circulari.

Type: *Agrostis miliacea* L., Sp. Pl. 1: 61, 1753.

Oloptum miliaceum (L.) M. Röser & H.R. Hamasha, comb. nov.

Bas.: *Agrostis miliacea* L., Sp. Pl. 1: 61, 1753.

Stipella (Tzvelev) M. Röser & H.R. Hamasha, stat. et gen. nov.

Bas.: *Stipa* sect. *Stipella* Tzvelev, Novosty Sist. Vysš. Rast. 11: 15, 1974.

Stipella parviflora (Desf.) M. Röser & H.R. Hamasha, comb. nov.

Bas.: *Stipa parviflora* Desf., Fl. Atlant. 1: 98, t. 29, 1798.

Stipella staintonii (Bor) M. Röser & H.R. Hamasha, comb. nov.

Bas.: *Stipa staintonii* Bor, Bull. Bot. Surv. India 7: 133, 1965.

Stipella tigrensis (Chiov.) M. Röser & H.R. Hamasha, comb. nov.

Bas.: *Stipa tigrensis* Chiov., Ann. Bot. (Rome) 2: 336, 1905.

Stipella capensis (Thunb.) M. Röser & H.R. Hamasha, comb. nov.

Bas.: *Stipa capensis* Thunb., Prodr. Pl. Cap.: 19, 1794.

Stipella nitens (Bor) M. Röser & H.R. Hamasha, comb. nov.

Bas.: *Stipa nitens* Ball, J. Linn. Soc., Bot. 16: 712, 1878.

Achnatherum pelliottii (Dangu) M. Röser & H.R. Hamasha, comb. nov.

Bas.: *Stipa pelliottii* Dangu in Lecomte, Notul. Syst. (Paris) 2: 167, 1912.

Aristella keniensis (Pilg.) M. Röser & H.R. Hamasha, comb. nov.

Bas.: *Oryzopsis keniensis* Pilg., Notizbl. Bot. Gart. Berlin-Dahlem 9: 509, 1926.

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