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A Numerical Taxonomic Investigation of *Stipa* Sect. *Smirnovia* and *S. Sect. Subsmirnovia* (Poaceae)

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Abstract—Multivariate and univariate analyses were used to investigate the morphological variation among the species of *Stipa* sections *Smirnovia* and *Subsmirnovia*. The MODECLUS procedure using Gower's similarity coefficient and UPGMA were used to discover how the selected specimens segregated. Subsequently different analyses were applied to qualitative and quantitative characters to determine which were the most discriminating and to determine group placement for each specimen. This study recognizes 18 taxa for section *Smirnovia*, whereas section *Subsmirnovia* comprises only one species, *S. gaubae*, which is clearly distinguished by its 3-styled ovary and its long basal leaf ligule. Both qualitative and quantitative characters are necessary for species delimitation. The present work has corroborated previously used diagnostic characters, such as: lemma and awn length, lemma indumentum, awn shape, column indumentum, seta/column length ratio, callus indumentum and shape, presence of coronula, basal leaf ligule cilia, and the number of styles. Likewise, some characters not previously studied in detail, were significant in species delimitation such as the presence of falcate trichomes on the callus of *S. caucasica* subsp. *drobovii* and the subdorsal and lateral rows of fused trichomes in *S. klemenzi*. Finally, a key to species in subsections *Smirnovia* and *Subsmirnovia* is provided.

Keywords—Asia, grass, MODECLUS, multivariate, phenetics, Stipeae.

Stipa L. is classified within the recently expanded tribe Stipeae that comprises between 400 and 600 species and 21 genera (Barkworth et al. 2008; Romaschenko et al. 2007, 2010; Cialdella et al. 2010). *Stipa* is the largest genus with about 300–400 species distributed throughout the temperate and subtropical regions of both hemispheres (Bor 1968; Tzvelev 1976; Cope 1982; Clayton and Renvoise 1986; Moraldo 1986; Freitag 1985; Watson and Dallwitz 1992). Current taxonomies recognize a narrow concept of *Stipa* with several segregate genera: *Hesperostipa* (Elias) Barkworth, *Austrostipa* S. W. L. Jacobs & J. Everett, *Celtica* F. M. Vázquez & Barkworth, *Amelichloa* Arriaga & Barkworth, and *Pappostipa* (Speg.) Romasch., P. M. Peterson & Soreng. As a consequence, *Stipa* s. s. has been reduced to ca. 140 species and is now limited to Asia, Europe, and North Africa (Romaschenko et al. 2007; Barkworth et al. 2008).

Spikelets in *Stipa* are 1-flowered, and the antherium disarticulates above the glumes leaving a sharp-pointed callus attached at its base. The lemma is often long and narrow, terete, indurate, and strongly convolute, terminating in a prominent awn. The callus, lemma, and the palea considered together is called the antherium. The awn is unigeniculate or bigeniculate and usually twisted below the first bend. The portion below the bend is referred to as the column and above the bend is referred to as the seta.

Stipa includes some of the most taxonomically difficult species in Poaceae. They exhibit plasticity in morphological characters thus making taxonomic assessments difficult. The lack of stable morphological structures and the difficulty in establishing clear morphological boundaries between taxa, has resulted in the creation of a high number of taxa at the specific and infraspecific ranks (Roshevitz 1916, 1924, 1932, 1934; Martinovský 1980; Kotukhov 1987, 1989, 1991, 1994). These problems were previously pointed out by Tzvelev (1974, 1976), Scholz (1985), Freitag (1985), and Strid (1991).

The infrageneric classification of *Stipa* traditionally has been based on awn features. Dumortier (1824) was the first author who provided an infrageneric classification. Two Sections were recognized: *Eriostipa* Dumort. (= Sect. *Stipa*), that included species with pubescent or plumose awns, and

Leiostipa Dumort., including those species with scabrous or glabrous awns. The first taxon with unigeniculate and plumose seta was *Stipa caucasica* Schmalh. which was described in 1896. Subsequently, Roshevitz (1932) proposed dividing *Stipa* into seven series, mostly based on awn features. Thus, eight species with unigeniculate awns and plumose seta were included in Ser. *Brevigeniculatae* Roshev. Roshevitz (1932), however, included in this series only those species with columns 1/10–1/8 the length of the seta and excluded *S. caucasica* because its column was 1/4–1/2 the length of the seta. More recently, Tzvelev (1974) considered *S. caucasica* the type species of a newly described Section *Smirnovia*, which included all the species with unigeniculate awns and plumose seta. The most relevant characters besides awn length were the intravaginal branching, acuminate or long acuminate glumes, coriaceous lemmas, terete or laterally compressed lemmas with overlapping margins, acute calluses, and ovaries with two styles. Section *Smirnovia* comprises 18 taxa that are endemic to Asia and the Caucasus with the highest diversity in central Asia with seven endemic species.

Parolly and Scholz (2004) described *S. cacuminis* H. Scholz & Parolly from Turkey as a species transitional between Sections *Barbatae* A. Junge and *Smirnovia*, (and relatively close to *S. hohenackeriana* Trin. & Rupr.) because of its combination of characters: the absence of coronula, an indistinctly unigeniculate awn, and plumose seta with trichomes ca. five mm long. But in our view, those characters bring it closer to *S. turkestanica* Hack. in Sect. *Stipa*, where it is frequent to find specimens whose awns are indistinctly bent in the lower portion. Therefore, *S. cacuminis* is not considered a member of Sect. *Smirnovia* and is therefore excluded from this study.

Additionally, *S. gaubae* Bor, endemic to Azerbaijan and North Iran, was included in the multivariate analysis and is the only species of Sect. *Subsmirnovia* Tzvelev (1976). It can be distinguished from Sect. *Smirnovia* by the presence of three styles and longer ligules (Tzvelev 1993). The similar awn structure and affinity with species of Sect. *Smirnovia*, made it necessary to include *S. gaubae* in the morphometric analyses.

Several species of Sections *Smirnovia* and *Subsmirnovia* have been included in floras or regional studies, but a

comprehensive taxonomic treatment does not exist. The present study aims to use morphometric and numerical taxonomic analyses to identify which characters (new and previously used) are the most consistent in distinguishing the different taxa. This paper is a preliminary step towards establishing a comprehensive taxonomic treatment of both Sections.

MATERIALS AND METHODS

Plant Material—This study is based on the examination of 852 specimens from 25 different herbaria: B, BM, BR, C, COI, E, FI, G, GH, H, JE, K, L, LD, LE, M, MEL, NY, PR, S, U, UPS, W, WAG, and WU. Unfortunately, many specimens were immature, incomplete, or fragmented and thus could not be included in this study. From the material studied, 265 specimens were selected and measured in an attempt to best cover the range of morphological variation in characters across the taxa. Each specimen measured was considered an operational taxonomic unit (OTU).

Specimens were initially identified and assigned to 20 taxa of Sect. *Smirnovia* and one taxon of Sect. *Subsmirnovia* as recognized in the most recent taxonomic treatments (Tzvelev 1976, 2000; Freitag 1985; Wu and Phillips 2006). *Stipa okmirii* Dengub., *S. talassica* Pazij, and *S. kopetdaghensis* Czopanov, are known only from the type locality and were excluded from the multivariate analyses. In total, 18 taxa were included in the multivariate analyses, 17 taxa from Sect. *Smirnovia* and *S. gaubae* from Sect. *Subsmirnovia* (Table 1).

Morphological Data and Analyses—The spikelet measurements were taken from the second most apical node from the longest branch of the panicle. Species of the two sections studied have cleistogamous spikelets, consequently the sizes of the structures that are enclosed by the floret were determined by the size of the lemma, having a limited value for species delimitation. Therefore, only qualitative characters of the palea, lodicules, and anthers were considered. All measurements were performed using a Mitutoyo CD-15CD digital caliper (see Fig. 1 for some floral structure measurements).

Initially, 68 quantitative and qualitative characters were recorded but because of missing data, many were excluded thus reducing the number to 47 (Appendix 1). Of these, 23 were quantitative, three were derived ratios, one discrete, and 20 qualitative (binary). Different subsets of these 47 characters were used depending upon the type of analysis and group being considered.

For each quantitative character, exploratory analyses were performed, including descriptive statistics and normality tests, such as the Kolmogorov-Smirnov and Skewness (Pimentel et al. 2007) using the STATISTICA package. To represent the variability of each character within species, box plots containing medians and percentiles were prepared for the most relevant characters (Figs. 2–9). Additionally, the univariate contingency tables were constructed and the Lambda coefficient was estimated to evaluate the predictive value of the qualitative characters analyzed (Legendre and Legendre 1998; Saint-Laurent et al. 2000; Pimentel et al. 2007).

To assess overall morphological variation, Gower's similarity was calculated for the combined and qualitative data using the program MVSP Version 3.13q for Windows (Kovach Computing Services, Anglesey, U. K.). All similarity matrices were converted to a distance matrix by subtracting the coefficients from one (Saint-Laurent et al. 2000). This coefficient allows the use of quantitative, discrete, and qualitative data. The resulting distance matrix was subjected to two types of clustering methods to group the OTUs. For the first method, the distance matrix was subjected to a non-parametric cluster analysis by the procedure MODECLUS (SAS. 9.2, SAS Institute Inc. 1997). This procedure has an advantage over most clustering methods in that no assumption of variable distribution is required, plus the resulting clusters are not biased toward having the same shape, variance, or dispersion (Saint-Laurent et al. 2000). The number of clusters in which the OTUs are segregated is specified by the user as a smoothing parameter called "K" which has a range of 2–80 (Baum and Bailey 1991). K specifies the number of neighbors to use for the Kth nearest neighbor density estimation and clustering. When the number of modal clusters stabilizes over a range of K, this suggests the number of clusters in the data (Baum and Bailey 1991). Although this method is not widespread in plant taxonomic analyses, it has been used successfully in other studies (Baum and Bailey 1991; Saint-Laurent et al. 2000; Binns et al. 2002). The MODECLUS procedure is explained further in Saint-Laurent et al. 2000. For the second method, a hierarchical UPGMA cluster analysis was used (Sneath and Sokal 1973). To assess the goodness of fit of the dendrogram, the cophenetic value matrix was compared with the dissimilarity matrix by Mantel's correlation coefficient (Pimentel et al. 2007). The analysis was performed using the program NTSYS pc version 1.

The validity of the number of clusters and their dispersions was assessed by canonical discriminant analysis (CDA). Likewise, CDA was performed for each cluster to see the variation among its included taxa, and to ascertain the distinctiveness of related taxa. Non-quantitative characters were deleted (despite their value for identification) because the CDA method relies on the assumption that characters are quantitative (Binns et al. 2002). Subsequently, a cross validation discriminant analysis (DA) was carried out on the same dataset and for each of the clusters of the MODECLUS 5-cluster solution. For cross validation, 25% of the specimens were randomly excluded from the dataset and the discriminant functions were calculated for the remaining specimens. This method requires a priori assignment of OTUs to groups and allows one to determine whether the recognized groups are statistically definable entities or if there is too much variation within groups to allow classification (Sneath and Sokal 1973). Finally, for those clusters with only two taxa, a *t* test was performed to determine the importance of each quantitative character in differentiating taxa.

RESULTS

The number of clusters suggested by the MODECLUS procedure stabilized at two clusters for K = 44–49, three cluster for K = 26–27 and again at K = 31–43, four clusters for K =

TABLE 1. Cluster size for each K value of the areas of stability evaluated in the present study. Species identified in each cluster using the most recent floras.

| Taxa | 3-cluster | N° Specimens | 5-cluster | N° Specimens | 13-cluster | N° Specimens |
|--|-----------|--------------|-----------|--------------|------------|--------------|
| <i>Stipa aktauensis</i> | 1 | 82 | 1 | 82 | 1 | 16 |
| <i>Stipa longiplumosa</i> | — | — | — | — | 2 | 12 |
| <i>Stipa tianschanica</i> subsp. <i>tianschanica</i> | — | — | — | — | 3 | 16 |
| <i>Stipa tianschanica</i> subsp. <i>gobica</i> | — | — | — | — | 4 | 23 |
| <i>Stipa klemenzi</i> | — | — | — | — | 5 | 16 |
| <i>Stipa lingua</i> subsp. <i>lingua</i> | 2 | 62 | 2 | 62 | 6 | 31 |
| <i>Stipa lingua</i> subsp. <i>magnifica</i> | — | — | — | — | — | — |
| <i>Stipa lingua</i> subsp. <i>lipskyi</i> | — | — | — | — | 7 | 13 |
| <i>Stipa karataviensis</i> | — | — | — | — | 8 | 18 |
| <i>Stipa caucasica</i> subsp. <i>caucasica</i> | 3 | 118 | 3 | 69 | 9 | 29 |
| <i>Stipa caucasica</i> subsp. <i>glareosa</i> | — | — | — | — | 10 | 19 |
| <i>Stipa caucasica</i> subsp. <i>desertorum</i> | — | — | — | — | — | — |
| <i>Stipa caucasica</i> subsp. <i>drobovii</i> | — | — | — | — | 11 | 21 |
| <i>Stipa caucasica</i> subsp. <i>iskanderkulica</i> | — | — | — | — | — | — |
| <i>Stipa mongolorum</i> | — | — | 4 | 23 | 12 | 23 |
| <i>Stipa gaubae</i> | — | — | — | — | — | — |
| <i>Stipa alaica</i> | — | — | 5 | 26 | 13 | 26 |
| <i>Stipa gegarkunii</i> | — | — | — | — | — | — |

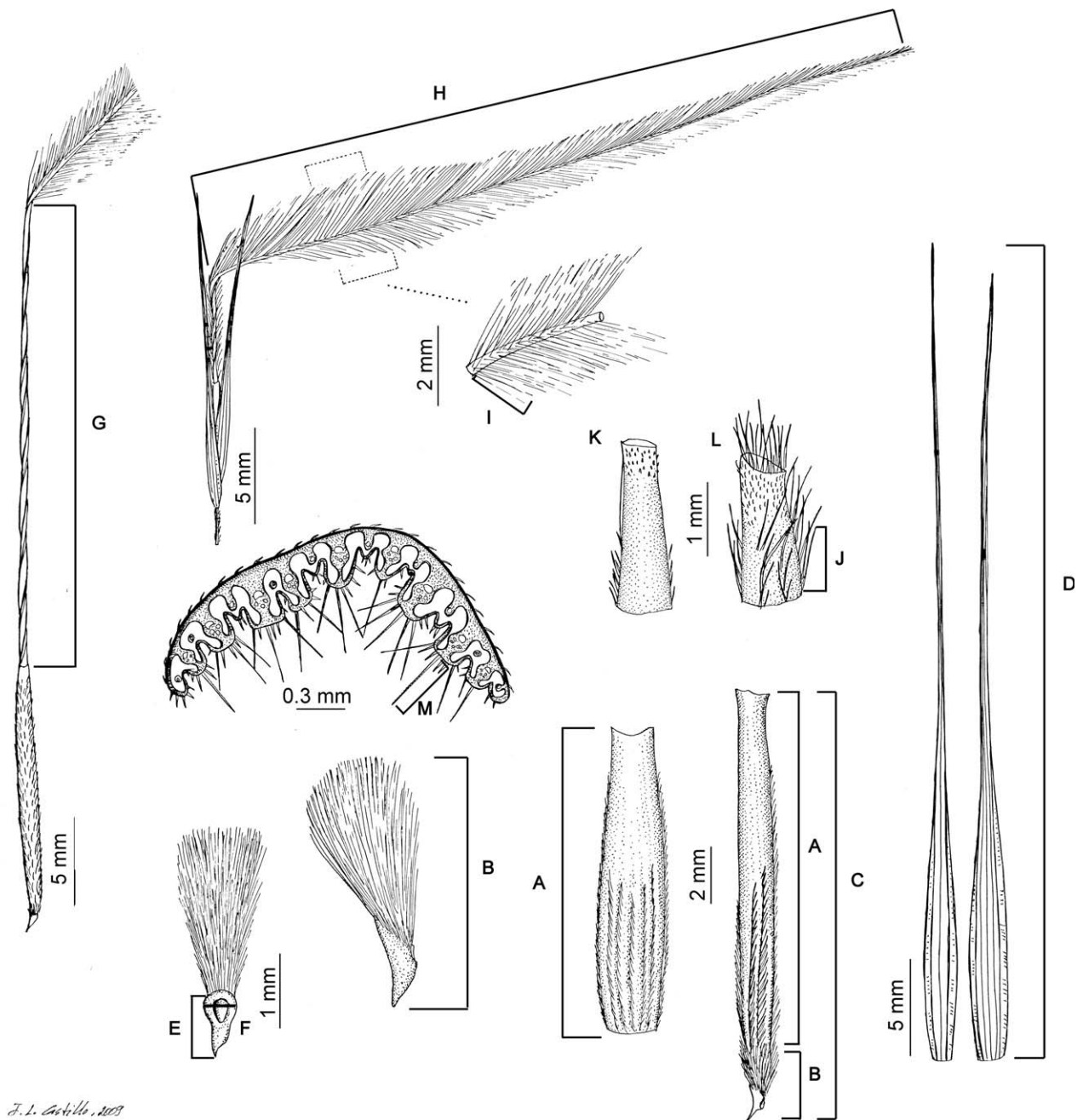


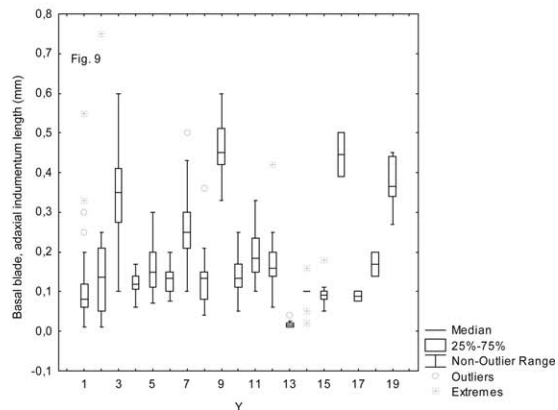
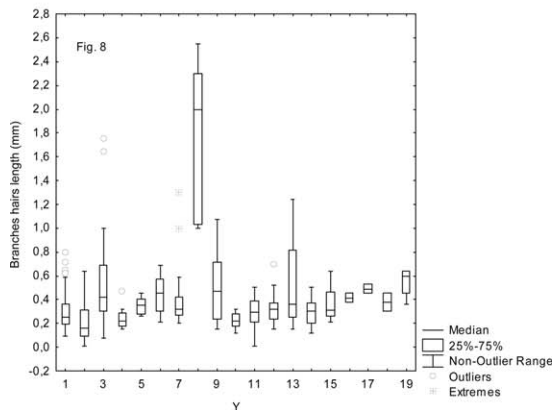
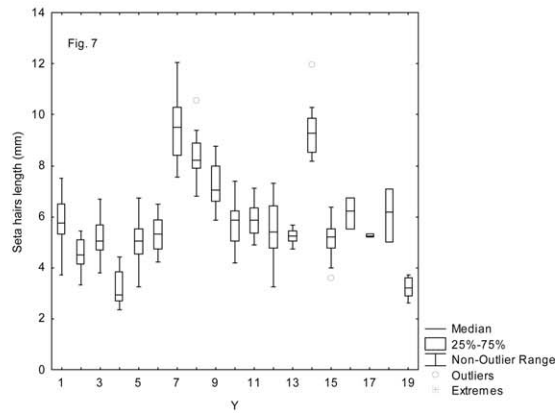
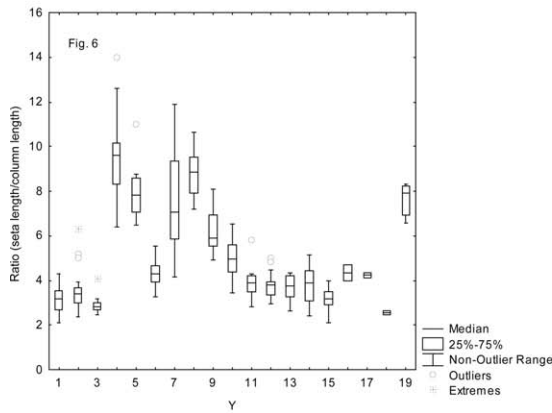
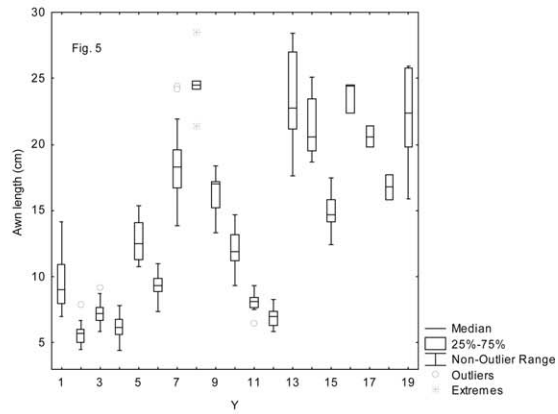
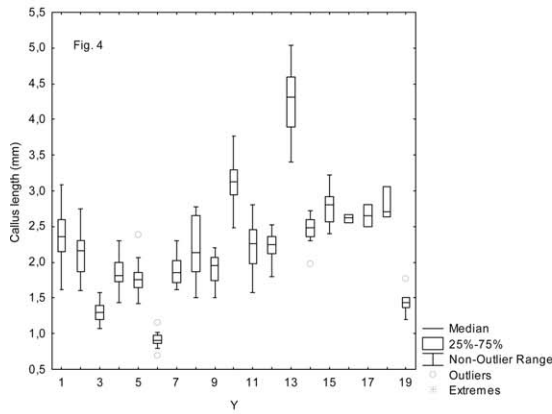
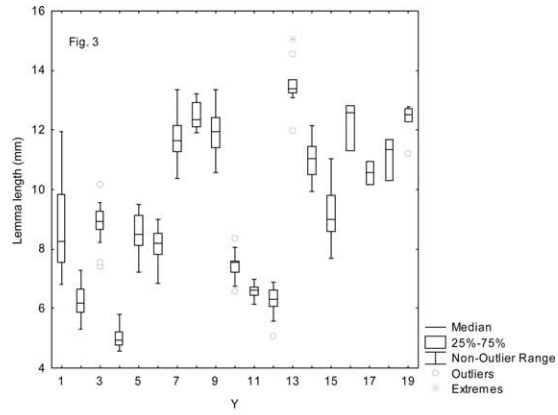
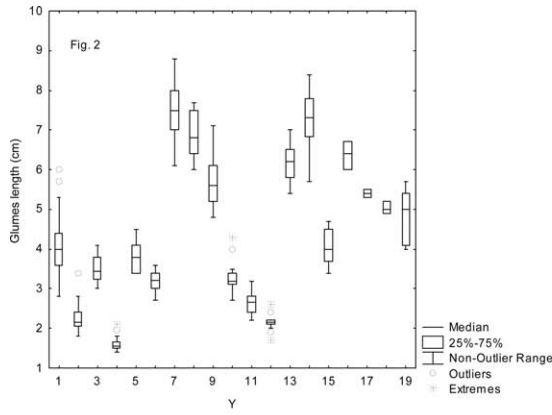
FIG. 1. The characters measured in *Stipa*. A. Lemma length. B. Callus length. C. Anthecium length. D. Glume length. E. Callus peripheral ring length. F. Callus peripheral ring width. G. Column length. H. Seta length. I. Trichome length of the seta. J. Trichome length of the lemma. K. Lemma apex glabrous. L. Coronula of lemma apex. M. Trichome length from the adaxial surface of basal leaves.

24–25, five clusters for $K = 21$ –23 and thirteen clusters for $K = 11$ –12 (Fig. 10). Despite the variability in cluster number resulting from different K values, the whole dataset was split in similar ways (Table 1). The 2-cluster ($K = 44$ –49) and 4-cluster ($K = 24$ –25) solutions were rejected because the number of specimens assigned to each cluster varied at the different K values.

The 3-cluster solution for $K = 26$ –27 and $K = 31$ –43, placed the same number of specimens into the same clusters (82, 62, and 118, respectively), and also the same specimens were found in each cluster (Table 1). The 5-cluster solution for $K = 21$ –23 was also identical, each of them suggesting 82, 62, 69, 23, and 26 specimens for each cluster and with the same specimens. Likewise, the correspondence in the assignment

to clusters between solutions with different numbers of clusters was compared, and it appears that two clusters of the 5-cluster solution are composed of the same specimens as from the two clusters resulting from the 3-cluster solution (the clusters with 62 and 82 specimens). The remaining specimens are gathered in one cluster in the 3-cluster solution, while in the 5-cluster solution they were segregated in three clusters (Table 1). In this case, the 5-cluster solution was retained because the number of clusters suggested was quite similar to the UPGMA dendrogram (Fig. 11) and gave more information of the species relationships.

The 13-cluster solution at $K = 11$ –12 was identical in size and the specimens were the same in each cluster for both K



FIGS. 2-9. Box plots of a selections of studied variables: 1. *S. caucasica* subsp. *caucasica*; 2. *S. caucasica* subsp. *glareosa*; 3. *S. caucasica* subsp. *drobovii*; 4. *S. mongolorum*; 5. *S. aktauensis*; 6. *S. karataviensis*; 7. *S. lingua*; 8. *S. magnifica*; 9. *S. lipskyi*; 10. *S. tianschanica* subsp. *tianschanica*; 11. *S. tianschanica* subsp. *gobica*; 12. *S. segarkunii*; 13. *S. longiplumosa*; 14. *S. klemenzii*; 15. *S. alaiica*; 16. *S. okmirii*; 17. *S. gaubae*; 18. *S. talassica*; 19. *S. kopetdaghensis*.

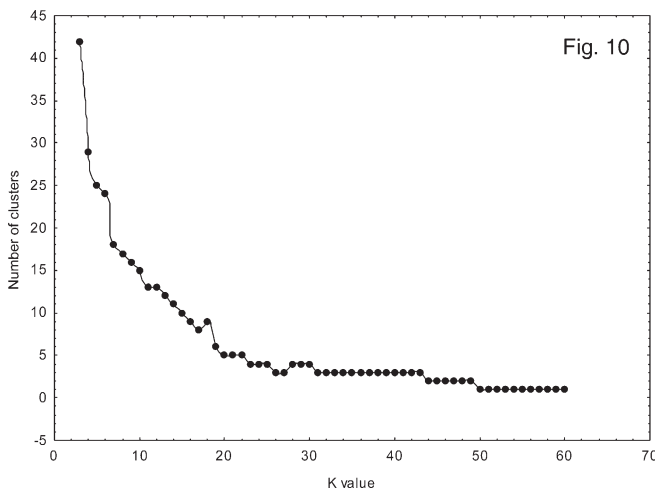


FIG. 10. Plot of the number of clusters into which the specimens of *Stipa* were placed according to the MODECLUS procedure for K values from 2–60.

values. Although the number of clusters was higher than in the 5-cluster solution, two of the clusters in this solution were composed of the same specimens as in the 5-cluster solution (the clusters with 23 and 26 specimens, respectively). The remaining clusters of the 5-cluster solution were segregated in 11 clusters in the 13-cluster solution (Table 1).

The UPGMA dendrogram constructed from the Gower's similarity matrix showed four clearly separated groups (Fig. 11). Group I was the largest and could be subdivided into three subgroups: A. composed of the widespread *S. caucasica* and *S. aktauensis* Roshev., B. composed of *S. klemenzi* Roshev., *S. tianschanica* Roshev., and *S. longiplumosa* Roshev., and C. composed of *S. gegarkunii* P. A. Smirn. and *S. alaica* Pazij. Group II contained specimens of the *S. lingua* A. Junge complex and *S. karataviensis* Roshev., which were also clearly segregated into two different clusters.

Finally groups III and IV were well differentiated, each comprising one taxon, *S. gaubae* and *S. mongolorum* Tzvelev, respectively. The Mantel cophenetic correlation obtained was high ($r = 0.84$), indicating a good fit between values from the cluster analysis and those of the dissimilarity matrix. The clusters were similar to those found using the MODECLUS procedure, with the exception of *S. aktauensis*, which appeared in the same group as *S. caucasica*, not with *S. tianschanica*, *S. klemenzi*, and *S. longiplumosa*.

The lambda values associated with each of the qualitative values (Table 2) indicated that several characters influenced both species delimitation and OTU grouping. The highest values corresponded to the presence of a coronula (COR), scar shape (SCAR), the presence of a foot-like expanded callus (CALLFLE, especially important for the delimitation of group II), a glabrous or pubescent column (COLIND, useful for the delimitation of subgroup A and B), and a falcate (SETFA) or straight (SETS) awn. For UPGMA, glabrous apex (GLAPM) was also important, whereas for the MODECLUS procedure, a scabrous (ABINDSC) or glabrous (ABINDG) abaxial basal leaf blade surface was important.

The CDA 1 of the 5-cluster solution showed that only clusters 4, 5 and more weakly cluster 2 were successfully differentiated, while the other clusters showed high overlap. The first three canonical axis explained 56%, 22% and 16% of the variance, respectively. The most important characters for axis

1 were PERL/PERW and seta trichome length, both responsible for the segregation of cluster 2, which marginally overlapped with cluster 3. SET/COL was the most important character of axis 2 and was responsible of the segregation of cluster 4 (Fig. 12). The plot of axis 2 against axis 3 (Fig. 13) segregated cluster 5. In this case the callus length, awn length, column trichome length, and ligule length (LL and LUL) were the most relevant characters (Table 3).

CDA 2 of the 13-cluster solution, as well as CDA 1 (above), did not provide justification for the clusters segregated by the MODECLUS procedure. The first three axes explained 37%, 25% and 14% of the variance, respectively. In a plot of axis 1 against axis 2, only cluster 6 and 12 were clearly segregated. The characters that contributed more to this separation were glume length and column trichome length for axis 1, responsible for the differentiation of cluster 6, whereas column trichome length and seta trichome length were the most relevant characters for axis 2 and responsible for the segregation of cluster 12 (Fig. 14). A plot of axis 2 against axis 3 (Fig. 15) segregated cluster 8. In this case, glume length, callus length, awn diameter, and seta trichome length were the most relevant characters (Table 3).

New analyses (CDA, DA, and *t* test) were performed for each of the clusters from the 5-cluster solution. This was done to ascertain the distinctiveness of the species associated with each cluster.

Regarding the MODECLUS procedure, cluster 1 contained *S. longiplumosa*, *S. aktauensis*, *S. klemenzi*, and *S. tianschanica* (Table 1). The 13-cluster solution separated each of the species, as well as the two subspecies, of *S. tianschanica*, *gobica* (Roshev.) D. F. Cui and *tianschanica*, (with the exception of two specimens of subsp. *tianschanica* that segregated with subsp. *gobica* and vice versa). CDA 3 was performed for cluster 1, excluding *S. longiplumosa* and *S. aktauensis* because they are obviously distinct from the remainder of the species in the cluster (Figs. 11, 14, 15). This was done to ascertain the distinctiveness of the three remaining taxa. However, CDA 3 only provided justification for *S. klemenzi* with the first axis explaining 95% and the second 5% of the variation. In the plot of axis 1 against axis 2 (Fig. 16), there was a marginal overlap between subsp. *tianschanica* and subsp. *gobica*, while *S. klemenzi* was clearly segregated. The characters that most contributed were lengths of the callus, lemma, glume, and awn (Table 4). Using discriminate analysis, all the specimens of *S. klemenzi* were well classified (as in the MODECLUS procedure), while two specimens of subsp. *tianschanica* and two of subsp. *gobica* were misclassified as the other subspecies.

Cluster 2 was identified as *S. karataviensis* and the *S. lingua* complex (*S. lingua* subsp. *lingua*, *S. lingua* subsp. *lipskyi* (Roshev.) R. Gonzalo and *S. lingua* subsp. *magnifica* (A. Junge) R. Gonzalo). The most important characters used for this differentiation were: lemma length, awn length, column ornamentation, basal blades adaxial surface trichome or papillae length, callus ornamentation, and the swollen upper leaf sheath.

The CDA 4 was performed for the four latter species recognized by Tzvelev (2000) and Pazij (1968) using additional morphological characters (Table 4). The first two axis explained 81% and 16% of the variation, respectively. Only *S. karataviensis* and *Stipa lingua* subsp. *lipskyi* were well segregated by CDA 4, whereas the CDA was not able to explain the difference between subsp. *magnifica* and subsp. *lingua*. The plot of axis 1 against axis 2 (Fig. 17) shows a clear differentiation for

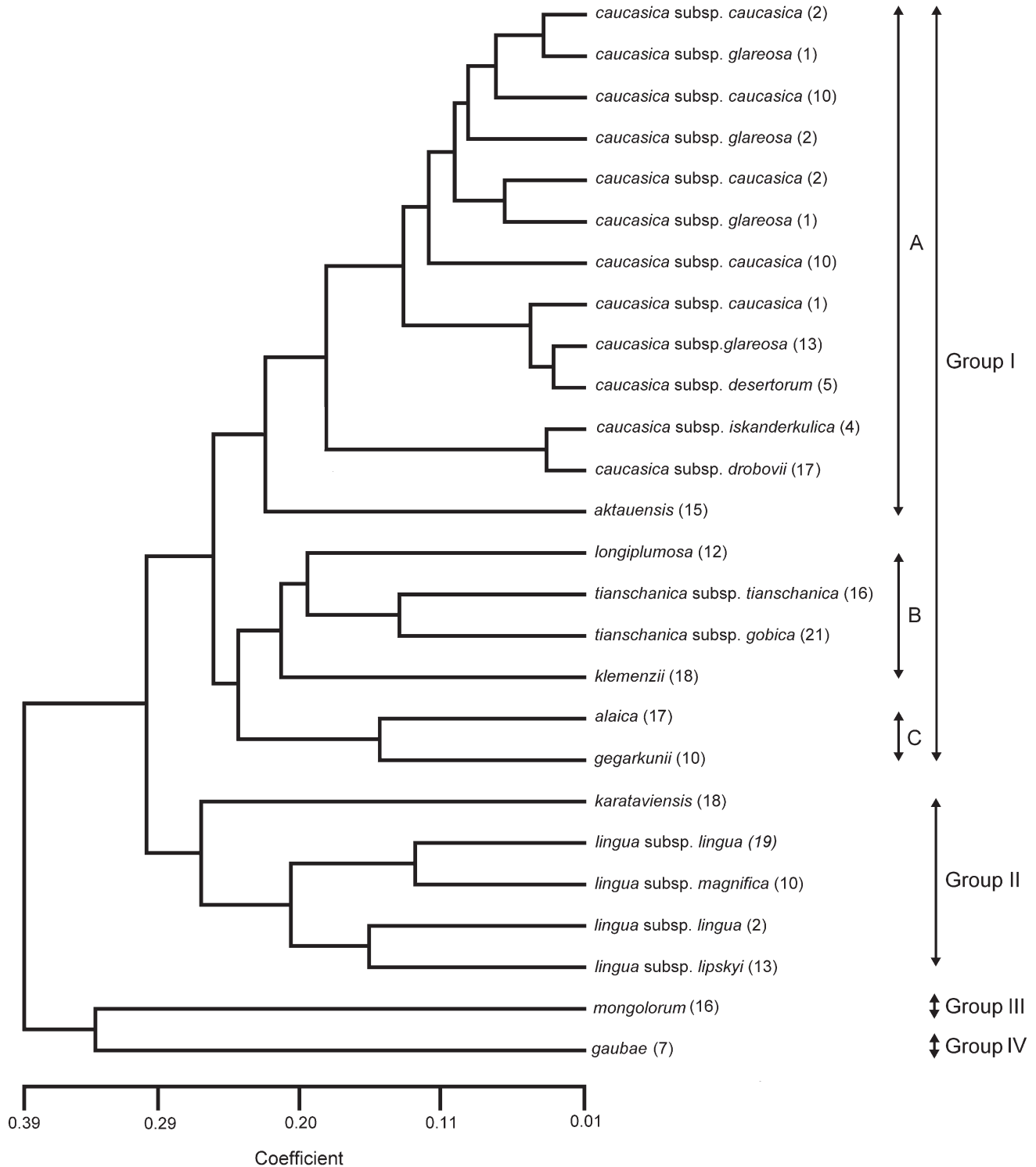


FIG. 11. UPGMA dendrogram of 262 specimens using a dissimilarity matrix calculated from 45 characters (1-Gower's coefficient of similarity). The number of specimens is given between parentheses.

S. karataviensis and for *S. lingua* subsp. *lipskyi*. Axis 1 was responsible for the differentiation of *S. karataviensis*, with glume length, lemma length, callus length, coronula length, awn length, awn diameter, and seta length contributing most to this separation. Axis 2 was responsible for the differentiation of *S. lingua* subsp. *lipskyi*, with adaxial indumenta length

as the most important character (Table 4). In the DA, 90% of the specimens were well identified. All the specimens of *S. karataviensis* and *S. lingua* subsp. *lipskyi* were well identified, whereas *S. lingua* subsp. *lingua* had two specimens misidentified as *S. lingua* subsp. *magnifica* and *S. lingua* subsp. *magnifica* had four misidentified as *S. lingua* subsp.

TABLE 2. Lambda values for the qualitative characters studied. For 5-cluster solution and UPGMA see Table 1 and Fig. 11, respectively, and for character codes see Appendix 1. Characters in bold show the highest values obtained for the lambda coefficient.

| Characters | Species | 5-cluster | UPGMA | Characters | Species | 5-cluster | UPGMA |
|------------|--------------|--------------|--------------|------------|--------------|--------------|--------------|
| BRDISP | 0.126 | 0.128 | 0.164 | COLIND | 0.411 | 0.419 | 0.595 |
| COR | 0.382 | 0.313 | 0.461 | SETS | 0.374 | 0.470 | 0.360 |
| SCAT | 0.216 | 0.225 | 0.258 | SETFA | 0.356 | 0.418 | 0.304 |
| GLAPM | 0.248 | 0.183 | 0.355 | SETFL | 0.081 | 0.053 | 0.053 |
| LEMAP | 0.185 | 0.013 | 0.075 | ADIND | 0.251 | 0.119 | 0.099 |
| PALIN | 0.168 | 0.091 | 0.095 | ABINDG | 0.303 | 0.336 | 0.219 |
| LIGSH | 0.057 | 0.037 | 0.075 | ABINDSC | 0.301 | 0.340 | 0.236 |
| CALI | 0.187 | 0.213 | 0.167 | ABINDDP | 0.017 | 0.027 | 0.010 |
| LSDF | 0.141 | 0.020 | 0.091 | NSTY | 0.057 | 0.037 | 0.075 |
| SCAR | 0.320 | 0.413 | 0.419 | CALLFLE | 0.278 | 0.512 | 0.440 |

lingua. A t test was performed for *S. lingua* subsp. *magnifica* and *S. lingua* subsp. *lingua* (Table 5). The characters that contributed significantly ($p < 0.01$) were: lengths of awns, lemmas, seta, glumes, adaxial trichomes, and three new characters, lengths of coronula trichomes, panicle branch cilia, and ligule cilia. *Stipa lingua* subsp. *lingua* and subsp. *magnifica* were identified with all those characters. A new DA was performed for the four taxa in which 100% of the specimens were well identified. Likewise, removing the length of the adaxial indumenta from the analysis, *S. lingua* subsp. *lipskyi* is placed close to *S. lingua* subsp. *lingua* (data not shown), with 3 specimens misidentified as *S. lingua* subsp. *lingua*.

Cluster 3 was identified as the *S. caucasica* complex. Five subspecies were recognized (*caucasica*, *glareosa* (P. A. Smirn.) Tzvelev, *iskanderkulica* Tzvelev, *desertorum* (Roshev.) Tzvelev and *drobovii* Tzvelev) based on characters such as awn length, lemma length, basal leaf abaxial ornamentation, and basal leaf adaxial trichome length. In the DA performed for the five subspecies, only 79% of the specimens were correctly identified. However, in the 13-cluster solution, *S. caucasica* complex was segregated in three clusters identified as the following subspecies: *caucasica* (cluster 9), *glareosa* plus *desertorum* (cluster 10), and *drobovii* plus *iskanderkulica* (cluster 11). A t test

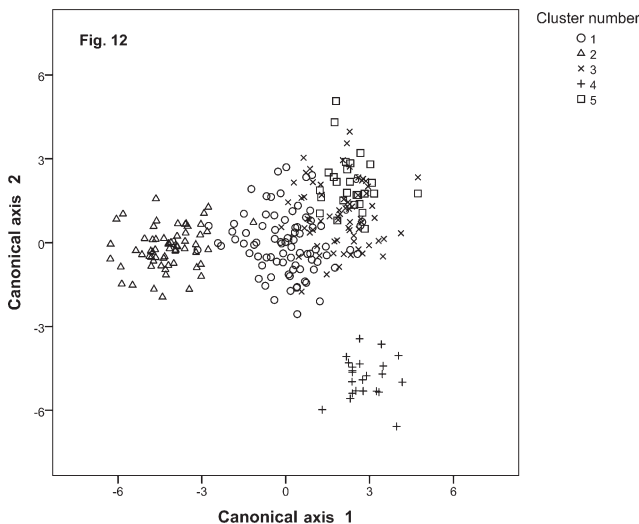


FIG. 12. CDA 1. Canonical discriminant plot of the 262 OTUs, for the 5-cluster solution from the MODECLUS procedure. The numbers correspond to each cluster, assigned to each OTU by MODECLUS as in Table 1.

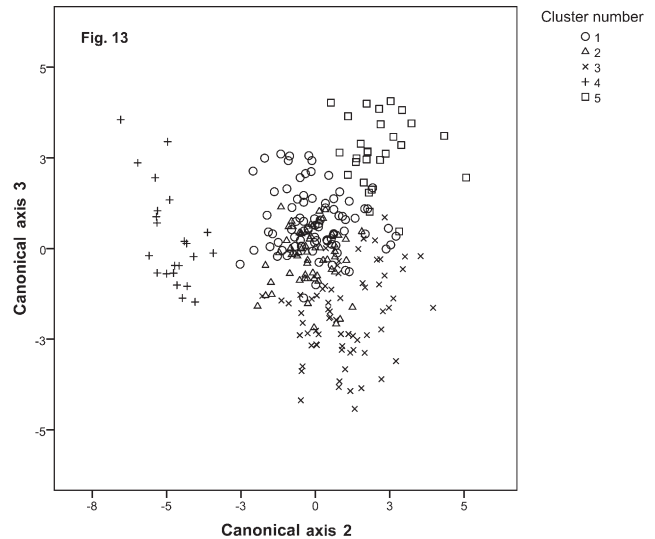


FIG. 13. CDA 1. Canonical discriminant plot of the 262 OTUs, for the 5-cluster solution from the MODECLUS procedure. The numbers correspond to each cluster, assigned to each OTU by MODECLUS as in Table 1.

was performed for subsp. *glareosa* plus *desertorum* and for subsp. *drobovii* plus *iskanderkulica* (Table 5), with no differences found within each pair of subspecies. As a result, we recognize three subspecies: subsp. *caucasica* (cluster 9), subsp. *glareosa* (cluster 10), and subsp. *drobovii* (cluster 11). These three subspecies were well segregated using canonical discriminant analysis (CDA 5), with the first and the second axis explaining 72% and 28% of the variance, respectively. The plot of axis 1 against axis 2 (Fig. 18) showed a high degree of separation between the three subspecies. The characters that contributed most to this differentiation were lemma trichome length and two new characters, callus length, and CDH/CVH for axis 1, responsible for the separation of subsp. *drobovii*, and glume length, lemma length and diameter, and awn length and diameter (Table 4) for axis 2, responsible for the differentiation of subsp. *caucasica* and *glareosa*. Another

TABLE 3. Standardized coefficient obtained in the CDA for the 5- and 3-cluster solution of the MODECLUS procedure. Bold values show the highest standardized coefficient of the three first canonical axes.

| Characters | MODECLUS 5-cluster solution | | | MODECLUS 13-cluster solution | | |
|------------|-----------------------------|--------------|---------------|------------------------------|---------------|--------------|
| | Axis 1 | Axis 2 | Axis 3 | Axis 1 | Axis 2 | Axis 3 |
| GLL | 0.210 | 0.193 | -0.130 | 0.316 | 0.197 | 0.387 |
| LEML | 0.172 | 0.199 | -0.130 | 0.226 | 0.121 | 0.261 |
| LEMD | 0.119 | 0.248 | -0.104 | 0.165 | 0.139 | 0.275 |
| CORL | 0.065 | 0.073 | 0.247 | 0.294 | -0.194 | 0.175 |
| CAL | -0.152 | 0.251 | -0.396 | -0.227 | 0.041 | 0.494 |
| PERL/PERW | 0.541 | -0.132 | 0.040 | 0.293 | 0.250 | -0.228 |
| AWN | 0.186 | 0.085 | -0.413 | 0.195 | 0.177 | 0.249 |
| AWND | 0.083 | 0.295 | -0.082 | 0.135 | 0.138 | 0.540 |
| SETH | 0.319 | 0.287 | 0.019 | 0.222 | 0.307 | 0.320 |
| SET | 0.124 | 0.015 | 0.007 | 0.107 | 0.011 | 0.018 |
| COLH | -0.021 | -0.145 | 0.375 | 0.336 | -0.451 | 0.006 |
| SET/COL | -0.241 | 0.564 | 0.227 | -0.155 | 0.078 | 0.298 |
| LEMH | 0.281 | 0.282 | 0.134 | 0.291 | 0.220 | -0.051 |
| PANCIL | 0.138 | 0.099 | 0.139 | 0.125 | 0.132 | 0.067 |
| BASD | 0.132 | 0.044 | -0.049 | 0.136 | 0.032 | 0.076 |
| ADIL | 0.091 | -0.093 | 0.231 | 0.077 | -0.052 | 0.012 |
| LL | -0.177 | -0.182 | -0.392 | -0.184 | -0.070 | -0.042 |
| LCILL | 0.177 | 0.127 | 0.158 | 0.058 | 0.081 | -0.007 |
| LUL | -0.145 | -0.142 | -0.301 | -0.083 | -0.046 | -0.025 |

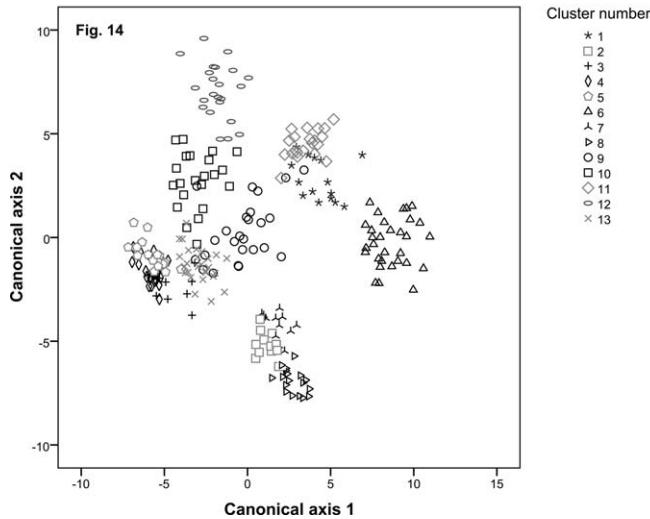


FIG. 14. CDA 2. Canonical discriminant plot of the 262 OTUs, for the 13-cluster solution from the MODECLUS procedure. The numbers correspond to each cluster, assigned to each OTU by MODECLUS as in Table 1.

DA was performed with these three subspecies, where only 8% of the specimens were wrongly identified, two specimens of subsp. *glareosa* as subsp. *caucasica* and vice versa.

Finally, the last clusters (4 and 5) of the 5-cluster solution included the same specimens as the 13-cluster solution (12 and 13), with 23 and 26 specimens, respectively (Table 1). Specimens of cluster 4 were identified as *S. gaubae* and *S. mongolorum*, while specimens of cluster 5 were identified as *S. gegarkunii* and *S. alaica*. Only two species were involved for each cluster, and a *t* test was performed to test which characters might be used to separate both taxa with the highest probability. For cluster 4 (*S. gaubae* and *S. mongolorum*), besides the difference in the number of styles, all the quantitative characters excluding lemma trichome length, seta trichome length, and CDH/CVH contributed to their differentiation (Table 5). Within cluster 5 (*S. gegarkunii* and *S. alaica*), besides the different shape of the seta, both species were dif-

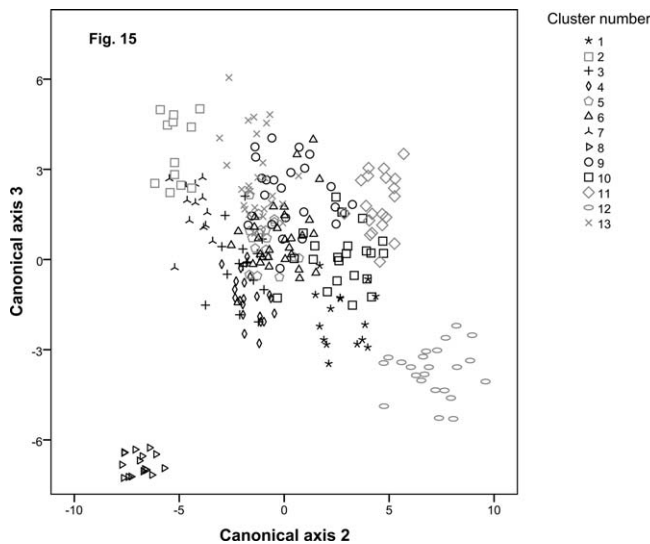


FIG. 15. CDA 2. Canonical discriminant plot of the 262 OTUs, for the 13-cluster solution from the MODECLUS procedure. The numbers correspond to each cluster, assigned to each OTU by MODECLUS as in Table 1.

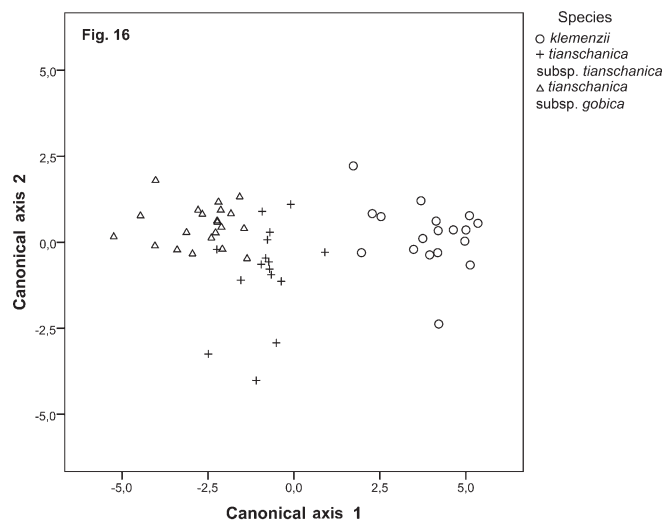


FIG. 16. CDA 3. Canonical discriminant plot for *S. tianschanica* subsp. *tianschanica* and subsp. *gobica* and *S. klemenzii*.

ferent in all the quantitative characters except the lengths of the lemma trichomes, seta trichomes, seta, the uppermost leaf ligule, CDH/CVH, and PERL/PERW (Table 5).

DISCUSSION

The MODECLUS procedure yielded 3-, 5- and 13-cluster solutions, which were not justified with the canonical discriminant analysis (CDA 1 and 2). This was mainly because CDA utilizes only quantitative data, thus the important qualitative data that are useful in identification were not employed. However, the MODECLUS procedure and UPGMA analysis yielded similar results, with the exception of the placement of *S. aktauensis*. This difference is mainly due to the importance that each analysis gives to the qualitative data (Table 6). *Stipa aktauensis* and *S. caucasica* are morphologically

TABLE 4. Standardized coefficient obtained in the CDA, from the clusters 1, 2, and 3 of the 5-cluster solution. Bold values show the highest standardized coefficient of the two first canonical axes.

| Characters | CDA 3 (Fig. 16) | | CDA 4 (Fig. 17) | | CDA 5 (Fig. 18) | |
|------------|-----------------|---------------|-----------------|---------------|-----------------|--------------|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| GLL | 0.432 | 0.406 | 0.530 | 0.134 | 0.258 | 0.653 |
| LEML | 0.362 | 0.052 | 0.473 | 0.021 | 0.359 | 0.431 |
| LEMD | 0.070 | 0.029 | 0.135 | 0.037 | 0.112 | 0.309 |
| CORL | — | — | 0.302 | 0.174 | 0.202 | -0.147 |
| CAL | 0.363 | -0.419 | 0.411 | -0.058 | -0.457 | 0.409 |
| CDH/CVH | 0.123 | 0.186 | — | — | 0.416 | -0.193 |
| PERL/PERW | -0.021 | 0.080 | -0.078 | 0.151 | 0.039 | 0.147 |
| AWN | 0.624 | 0.166 | 0.382 | 0.130 | 0.100 | 0.567 |
| AWND | 0.215 | -0.018 | 0.400 | -0.248 | 0.044 | 0.371 |
| SETH | 0.028 | 0.231 | 0.276 | 0.130 | 0.052 | 0.301 |
| SET | -0.110 | -0.041 | 0.362 | 0.125 | 0.147 | 0.004 |
| COLH | — | — | — | — | 0.278 | -0.298 |
| SET/COL | -0.216 | 0.122 | -0.190 | -0.061 | 0.103 | 0.079 |
| LEMH | -0.230 | 0.250 | -0.148 | 0.088 | 0.430 | 0.220 |
| PANCIL | 0.074 | 0.187 | 0.058 | 0.136 | 0.090 | 0.057 |
| BASD | -0.058 | 0.042 | -0.121 | 0.100 | 0.144 | 0.268 |
| ADIL | -0.064 | 0.225 | -0.135 | -0.587 | 0.172 | -0.168 |
| LL | 0.065 | 0.173 | -0.036 | -0.019 | 0.012 | 0.025 |
| LCILL | -0.052 | 0.280 | -0.041 | 0.179 | -0.096 | 0.018 |
| LUL | 0.040 | -0.269 | -0.039 | 0.010 | 0.042 | 0.035 |

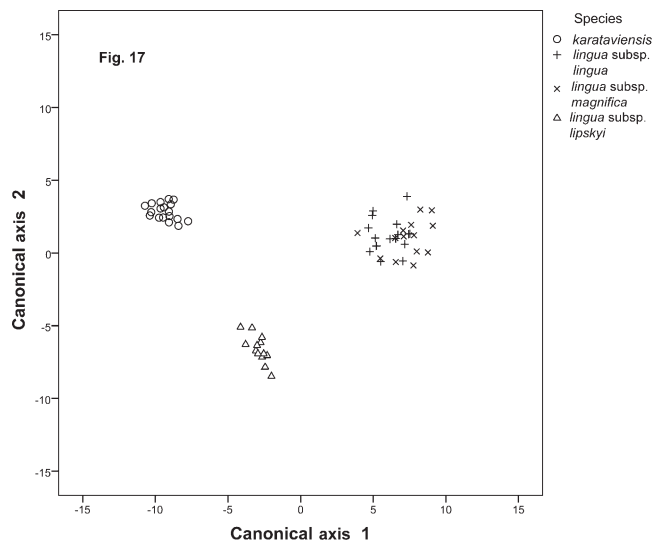


FIG. 17. CDA 4. Canonical discriminant plot for *S. lingua*, *S. lipskyi*, *S. magnifica*, and *S. karataviensis*.

similar, and they are usually placed together in the keys to species of *Stipa* (Pazij 1968; Tzvelev 1976). Spikelets of both species are similar in size, and both have a coronula and a pubescent column. For this reason both species are clustered on the UPGMA dendrogram (Fig. 11). Awn shape easily separates both species, which is falcate in *S. caucasica* and straight in *S. aktauensis*. The awn shape is also responsible for the segregation of *S. aktauensis* in cluster 1 of the 5-cluster solution (Table 1). Moreover, *S. aktauensis* has an awn slightly longer than *S. caucasica* and the column is 1/7–1/10 the length of the awn, whereas in *S. caucasica* the column is 1/2–1/4 the length of the awn (Figs. 5, 6).

Stipa longiplumosa shares with the other species of cluster 1 the straight awn and the scabrous basal leaf, but it can be easily distinguished by its larger spikelets (Figs. 2–5, 14, 15).

TABLE 5. Result of the Student's *t* test for pair of taxa of the 13-cluster solution, level of significance 0.01; ns not significant.

| Characters | <i>S. lingua</i> subsp. <i>lingua</i> and <i>S. lingua</i> subsp. <i>magnifica</i> | <i>S. caucasica</i> subsp. <i>glareosa</i> and <i>S. caucasica</i> subsp. <i>desertorum</i> | <i>S. caucasica</i> subsp. <i>drobovii</i> and <i>S. caucasica</i> subsp. <i>iskanderkulica</i> | <i>S. gaubae</i> and <i>S. mongolorum</i> | <i>S. gegarkunii</i> and <i>S. alaiica</i> |
|------------|---|--|--|---|--|
| | <i>p</i> value | <i>p</i> value | <i>p</i> value | <i>p</i> value | <i>p</i> value |
| GLL | > 0.01 | ns | ns | > 0.01 | > 0.01 |
| LEML | > 0.01 | ns | ns | > 0.01 | > 0.01 |
| LEMD | 0.070 | ns | ns | > 0.01 | > 0.01 |
| CORL | > 0.01 | ns | ns | — | — |
| CAL | 0.017 | ns | ns | > 0.01 | > 0.01 |
| CDH/CVH | — | ns | ns | 0.480 | 0.260 |
| PERL/PERW | 0.628 | ns | ns | 0.015 | 0.300 |
| AWN | > 0.01 | ns | ns | > 0.01 | > 0.01 |
| AWND | 0.225 | ns | ns | > 0.01 | > 0.01 |
| SETH | 0.025 | ns | ns | 0.600 | 0.840 |
| SET | > 0.01 | ns | ns | > 0.01 | > 0.01 |
| COLH | — | ns | ns | — | — |
| SET/COL | 0.06 | ns | ns | 0.020 | 0.060 |
| LEMH | 0.013 | ns | ns | 0.440 | 0.080 |
| PANCIL | > 0.01 | ns | ns | — | — |
| BASD | 0.048 | ns | ns | > 0.01 | > 0.01 |
| ADIL | > 0.01 | ns | ns | > 0.01 | > 0.01 |
| LL | 0.500 | ns | ns | > 0.01 | > 0.01 |
| LCILL | > 0.01 | ns | ns | > 0.01 | > 0.01 |
| LUL | 0.450 | ns | ns | > 0.01 | > 0.01 |

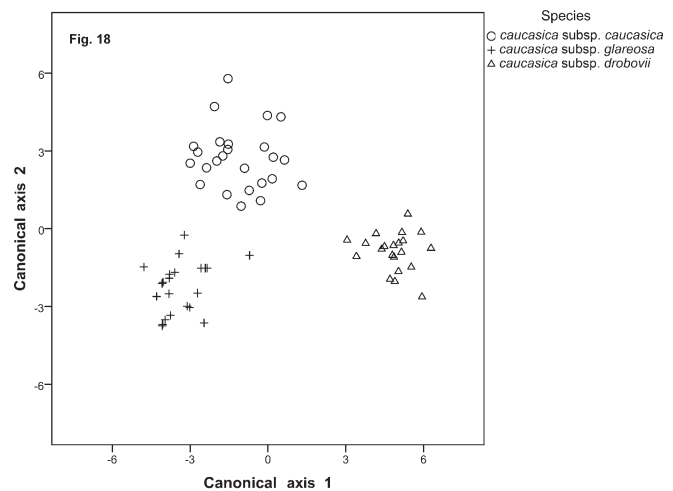


FIG. 18. CDA 5. Canonical discriminant analysis for the three subspecies of *S. caucasica*.

However, *S. longiplumosa* is most similar to *S. lingua* subsp. *lipskyi*, mostly because of overall similarity of their spikelets (Fig. 14, 15). This resemblance has frequently led to their misidentification in areas where the two species coexist. Roshevitz (1932) emphasized the longer column of *S. longiplumosa*, 1/3–1/5 the length of the seta, whereas in *S. lingua* subsp. *lipskyi* the column is 1/6–1/9 the length of the seta (Fig. 6). Additionally, several qualitative characters (Table 6) traditionally used for the identification of *S. longiplumosa*, such as the absence of a coronula and scabrous basal leaf blades (Ovczinnikov 1957; Pazij 1968; Tzvelev 1976), were responsible for its segregation from the *S. lingua* complex in the MODECLUS procedure and with UPGMA (Fig. 11).

Regarding cluster 1, the three remaining taxa (*S. klemenzii*, *S. tianschanica* subsp. *tianschanica* and subsp. *gobica*), have been considered closely related and occur together in West Mongolia. *Stipa klemenzii* traditionally has been considered related to *S. tianschanica*, the two differing in their spikelet sizes (Roshevitz 1924; Tzvelev 2000). Several taxonomists have not considered this variation sufficient to recognize two species, and therefore reduced *S. klemenzii* to a variety of either *S. gobica* or *S. tianschanica* (Wu and Phillips 2006; Norlindh 1947). Tzvelev (1976) kept the specific status intact, although he left open the possibility of considering it a subspecies of *S. tianschanica*. Our results suggest a clear differentiation between both taxa, supporting the maintenance of *S. klemenzii* as a different species. Besides the different spikelet structure sizes (Figs. 2–5, 16), there are solid diagnostic qualitative characters that have not been used in the keys of *Stipa* that provide useful information for species identification (Table 6). One of these is awn shape, e.g. falcate in *S. klemenzii*, straight in *S. tianschanica*, that has been reported in the description of the species (Tzvelev 2000; Wu and Phillips 2006), but has not been used in the keys. In addition, we have noticed that in *S. klemenzii* the subdorsal and lateral rows of the lemma are fused, whereas they are distinct in *S. tianschanica*.

Multivariate analysis showed that *S. tianschanica* subsp. *gobica* and subsp. *tianschanica* are morphologically similar, overlapping in most of the characters studied (Fig. 16). Subspecies *gobica* is almost confined to Mongolia and subsp.

TABLE 6. Main qualitative and discrete characters in *Stipa* sect. *Smirnovia* and *Subsmirnovia*.

| Accepted taxa | Branch | Lemma apex | Lemma surface | Scar shape | Callus surface | Column surface | Seta shape | Basal abaxial surface | Basal adaxial surface | N° Styles |
|---|-----------------|------------------------------|-------------------------------|----------------------|------------------|-------------------------|------------------|-------------------------------|--------------------------------------|-----------|
| Sect. <i>Smirnovia</i> | | | | | | | | | | |
| <i>S. caucasica</i> | Erect-spreading | Coronula | 7 rows of trichomes | Circular to elliptic | Villous | Pilose | Falcate | Glabrous, rarely scabrous | Minutely pubescent, rarely pubescent | 2 |
| subsp. <i>caucasica</i> | Erect-spreading | Coronula | 7 rows of trichomes | Elliptic | Villous | Pilose | Falcate | Scabrous, rarely glabrous | Minutely pubescent, rarely pubescent | 2 |
| <i>S. caucasica</i> subsp. <i>glareosa</i> | Erect-spreading | Coronula | 7 rows of trichomes | Elliptic | Villous | Pilose | Falcate | Glabrous, rarely scabrous | Pubescent | 2 |
| <i>S. caucasica</i> subsp. <i>drobovii</i> | Erect | Scattered pilose | Pubescent | Elliptic | Villous | Pilose | Straight | Glabrous | Pubescent or minutely pubescent | 2 |
| <i>S. mongolorum</i> | Erect-spreading | Coronula | 7 rows of trichomes | Circular to elliptic | Villous | Pilose | Straight | Glabrous or scabrous | Pubescent or minutely pubescent | 2 |
| <i>S. karataviensis</i> | Erect-spreading | Glabrous or scattered pilose | 3 rows of trichomes, rarely 5 | Circular | Glabrous | Glabrous | Straight | Glabrous | Pubescent | 2 |
| <i>S. lingua</i> subsp. <i>lingua</i> | Erect-spreading | Coronula | 7 rows of trichomes | Circular | Usually glabrous | Pilose | Straight | Glabrous | Pubescent | 2 |
| <i>S. lingua</i> subsp. <i>magnifica</i> | Erect-spreading | Coronula | 7 rows of trichomes | Circular | Villous | Pilose | Straight | Glabrous | Minutely pubescent, rarely pubescent | 2 |
| <i>S. lingua</i> subsp. <i>lipskyi</i> | Erect-spreading | Coronula | 7 rows of trichomes | Circular | Villous | Tuberculate | Straight | Glabrous | Pubescent | 2 |
| <i>S. longiplumosa</i> | Erect-spreading | Usually glabrous | 7 rows of trichomes | Circular | Villous | Glabrous | Straight | Scabrous | Scabrous | 2 |
| <i>S. tianschanica</i> subsp. <i>tianschanica</i> | Erect-spreading | Coronula | 7 rows of trichomes | Elliptic | Villous | Tuberculate or glabrous | Straight | Scabrous, rarely glabrous | Pubescent | 2 |
| <i>S. tianschanica</i> subsp. <i>gobica</i> | Erect-spreading | Usually glabrous | 7 rows of trichomes | Elliptic | Villous | Tuberculate or glabrous | Usually straight | Scabrous or glabrous | Pubescent | 2 |
| <i>S. gogarkunii</i> | Erect-spreading | Scattered pilose | 7 rows of trichomes | Elliptic | Villous | Scabrous | Flexuous | Glabrous | Papillae | 2 |
| <i>S. klemenzi</i> | Erect-spreading | Glabrous | 7 rows of trichomes | Elliptic | Villous | Glabrous | Falcate | Glabrous or sparsely prickly | Pubescent | 2 |
| <i>S. altaica</i> | Erect-spreading | Scattered pilose | 7 rows of trichomes | Circular to elliptic | Villous | Scabrous | Falcate | Glabrous | Pubescent | 2 |
| <i>S. okmirii</i> | Erect-spreading | Coronula | 7 rows of trichomes | Elliptic | Villous | Scabrous | Flexuous | Scabrous | Pubescent | 2 |
| <i>S. talassica</i> | Erect-spreading | Scattered pilose | 7 rows of trichomes | Elliptic | Villous | Scabrous | Straight | Scabrous | Minutely pubescent | 2 |
| <i>S. kopetdaghensis</i> | Erect-spreading | or glabrous scattered pilose | 7 rows of trichomes | Elliptic | Villous | Scabrous | Falcate | Scabrous | Minutely pubescent | 2 |
| Sect. <i>Subsmirnovia</i> | | | | | | | | | | |
| <i>S. gaulbae</i> | Erect-spreading | Glabrous | Pubescent | Elliptic | Villous | Glabrous | Straight | Pubescent or sparsely prickly | Pubescent | 3 |

tianschanica is a more western taxon, mostly confined to the Tian Shan range. Nevertheless, both taxa are found in east Mongolia, where the differences between them become blurred. Most of the taxonomic revisions (Roshevitz 1924; Norlindh 1947; Wu and Phillips 2006) revealed little differentiation between the taxa, differences consisting of the smaller size of the glumes, lemma and awn in subsp. *gobica* (Figs. 2, 3, 5). Maybe the clearest difference between these taxa is the lemma apex, which is glabrous in subsp. *gobica* and with a coronula in subsp. *tianschanica*. The overall similarity in their floral and vegetative structures could justify a subspecies treatment.

The *Stipa lingua* complex is one of the most widespread groups of sect. *Smirnovia*, plus it shows great morphological variation. Besides the straight and long awn, the most characteristic feature is its foot-like expanded callus that is shared with *S. karataviensis*; it is likely this character that causes both species to be placed together in the 5-cluster solution, as well as in the UPGMA dendrogram (Fig. 11). In addition to spikelet size differences (Fig. 14, 15), the presence of three instead of seven rows of trichomes is noteworthy and is extensively used in regional floras to differentiate *S. karataviensis* from other species (Roshevitz 1932; Tzvelev 1976).

The three taxa of the *S. lingua* complex have been traditionally treated as different species (Pazij 1968; Tzvelev 1976), but our results indicate that the morphological differences are not clear. *Stipa lingua* subsp. *lipskyi* can be distinguished from *S. lingua* subsp. *lingua* and *S. lingua* subsp. *magnifica* by its glabrous column (Fig. 11, 12). Additionally, it usually has longer trichomes on the adaxial surface of the basal leaves (Fig. 9, 17). No other distinctive qualitative characters are evident and resemblances in size and shape of the spikelets of *S. lingua* subsp. *lingua* and *S. lingua* subsp. *lipskyi* was noticed before by Tzvelev (1976) and Gonzalo et al. (2011), both of whom suggested the subspecies rank for *S. lipskyi*.

Considering our results, the morphological differentiation between *S. lingua* subsp. *lingua* and *S. lingua* subsp. *magnifica* is difficult based on traditionally used characters (Junge 1910; Pazij 1968; Tzvelev 1976). However, our analyses yielded small differences in the awn and lemma lengths, and added three new diagnostic characters (coronula trichome length, panicle branch cilia length, and ligule cilia length). Furthermore, *S. lingua* subsp. *magnifica* is separated geographically from the other subspecies, being endemic to the Alai range of Kirghizstan where no specimens of *S. lingua* subsp. *lingua* have been collected. Our DA, conducted with specimens identified according to the new characters, allowed the differentiation of both taxa. Nevertheless, the slight morphological differentiation observed and the overall resemblance of their spikelets and panicles indicates that a subspecific rank could be suitable for *S. magnifica* (Gonzalo et al. 2011).

Stipa caucasica is the most widespread species of sect. *Smirnovia*, distinguished from the other species of the section by having a falcate and completely pubescent awn. Throughout its geographical range it is morphologically variable and numerous specific and infraspecific names have been applied to plants of this species. Tzvelev (1974, 1976) recognized five subspecies based on the size of the lemma and the awn, with special attention to the surface of the basal leaves. A broader concept was adopted by Freitag (1985), who reduced the number to two subspecies (subsp. *caucasica* and *glareosa*) based on differences in spikelet structure and size, culm size, and surface of the abaxial face of the basal leaves. Our study

supports the recognition of three taxa that we recognize here as subspecies.

Stipa caucasica subsp. *glareosa* has been separated from subsp. *caucasica* basically by its shorter awn and lemma (Fig. 18) and the ornamentation of the abaxial surface of the basal leaves (Smirnow 1929; Tzvelev 1976). However, Freitag (1985) noticed that the differences between these two subspecies are not always obvious. Specimens of *S. caucasica* subsp. *caucasica* growing at higher altitudes or under harsher environmental conditions are shorter with smaller spikelets, thus resulting in overlap in quantitative characters with the alpine subsp. *glareosa*. Special emphasis has been given to the indumentum of the basal leaves, but as with other widespread taxa of *Stipa* (i.e. *S. capensis* Thunb., *S. capillata* L., *S. lagascae* Roem. & Schult., *S. pennata* L.), this feature is variable. The scabrous abaxial surface of the basal leaf blades has been traditionally considered characteristic of subsp. *glareosa* (Smirnow 1929), with subsp. *caucasica* being glabrous. However, populations of subsp. *caucasica* can have scabrous leaves whereas subsp. *glareosa* (= subsp. *desertorum*) may have glabrous or smooth leaves across its distributional area. Even though subsp. *glareosa* is a more delicate plant with smaller spikelets (Fig. 18), it has been misclassified with small specimens of subsp. *caucasica*. Therefore, and in agreement with recent floras (Tzvelev 1976; Freitag 1985; Wu and Phillips 2006), we consider *S. glareosa* as a subspecies of *S. caucasica*.

The third subspecies, *drobovii*, was first described by Drobow (1925) as *Stipa bella* Drobow. This taxon is characterized by having the rows of trichomes reach the lemma apex, and the trichomes of the lemma and the column are longer than in *S. caucasica*. Tzvelev (1974) reduced it to subspecies rank as *S. caucasica* subsp. *drobovii*, and specifically emphasized the dense and short pubescence (0.2–0.3 mm long) on the adaxial side of the basal leaves. Freitag (1985) considered the variation in these characters to reside within that of the type subspecies, thus he did not recognize it as a different taxon. Our result supports its differentiation, mostly based in its short callus, its longer lemma trichomes, and its dorsal trichomes which are longer than its ventral ones. This latter feature is reported here for the first time, and has not been documented in any other species of the genus.

Stipa caucasica subsp. *iskanderkulica* has been described from Gissar-Darvaz, characterized by having the abaxial surface of the basal leaves pubescent, becoming glabrous towards the apex. However, this pubescence pattern is also found in other species of the genus (i.e. *S. iberica* Martinovský, *S. pulcherrima* K. Koch, and *S. lagascae*). Likewise, populations with pubescent blades are also found in Iran. Populations with pubescent leaves share the same distinctive features as subsp. *drobovii* and both taxa represent the same subspecies (Table 5).

Stipa mongolorum and *S. gaubae* are segregated together in the MODECLUS procedure, but both taxa are different in most of the quantitative characters and grow in different areas. *Stipa mongolorum* apparently resembles *S. caucasica* subsp. *glareosa* and both are similar ecologically and biogeographically (Tzvelev 2000). Likewise, they are morphometrically similar and frequently found on the same herbarium sheet, thus leading to misidentifications. *Stipa gaubae* morphologically resembles *S. lingua*, sharing a long and straight awn with the column 1/7–1/10 the seta length (Fig. 6). However, *S. mongolorum* and *S. gaubae* share a completely pubescent

lemma, seta with trichomes shorter than 4 mm, and an awn with the column 1/10 of the seta (Figs. 6, 7), thus explaining their clustering in MODECLUS. Besides, these two species have unique features not shared with the other taxa of the section that are responsible for their clear segregation on the UPGMA dendrogram (Fig. 11). *Stipa mongolorum* is characterized by its somewhat loose panicle with erect branches, whereas the other taxa have contracted panicles with spreading or erect-spreading branches (Tzvelev 2000). *Stipa gaubae* is characterized by its long ligules and its 3-styled ovary (Freitag 1985), whereas the remaining taxa have short ligules and a 2-styled ovary. The affinity of both species are obscure, displaying unique features that suggest hybrid origins. For *S. mongolorum*, possible parentals are *S. glareosa* × *S. pelliottii* (Danguy) Grubov or *S. glareosa* × *S. breviflora* Griseb. (Tzvelev 2000), whereas *S. gaubae* has been segregated in the section *Subsmirnovia* (Tzvelev 1974).

Finally, the MODECLUS procedure and the UPGMA analysis grouped *S. alaica* and *S. gegarkunii* together. Both taxa share several qualitative characters (Table 6), but the

most interesting is the presence of a unigeniculate or subbigeniculate awn. Despite the subbigeniculate awn, both species are distinguished by the obviously longer lemma of *S. gegarkunii* (Table 5), and by the awn shape, which is flexuous in *S. gegarkunii* and falcate in *S. alaica*. In addition, both taxa have different distributions: *S. gegarkunii* is endemic of Armenia, while *S. alaica* is distributed in Pamir and more recently has been found in East Kazakhstan.

The present work has highlighted some new quantitative and qualitative characters that, together with others already used, are useful in identifying the studied taxa. Referring to both qualitative and quantitative characters, it was possible to adequately distinguish morphologically 18 taxa in section *Smirnovia* and one taxon for section *Subsmirnovia* (Table 6). Based upon the characters examined in this study, a new key to taxa is presented, modified from that in Tzvelev (1976, 2000) and Wu and Phillips (2006). Finally, this study highlights the need for future explorations, especially in those species excluded from the multivariate analyses, to improve the species descriptions and delimitations.

KEY TO TAXA

1. Column pubescent all over its length 2
2. Column/seta ratio = (2.1–)2.8–3.5(–6.3); seta falcate 3
3. Callus (1.07)1.2–1.34(1.57) mm long, dorsal trichomes falcate and longer than ventral ones *S. caucasica* subsp. *drobovii*
3. Callus (1.62–)1.95–2.47(–2.82) mm long, dorsal trichomes straight and shorter than ventral ones 4
4. Abaxial surface of basal leaves usually scabrous; glumes (1.8–)2.1–2.4(–2.8) cm long; anthercium (7.4–)7.8–8.9(–9.5) mm long; awn (4.5–)5.1–5.8(–8) cm long *S. caucasica* subsp. *glareosa*
4. Abaxial surface of basal leaves usually glabrous; glumes (3.1–)4.2–3.6(–6) cm long; anthercium (9.6–)10–12.4(–13.1) mm long; awn (7–)7.9–10.7(–13.4) cm long *S. caucasica* subsp. *caucasica*
2. Column/seta ratio = (4.2–)7.6–9.8(–14); seta straight 5
5. Anthercium (3.7–)6.3–7.2(–8) mm long; lemma pubescent throughout; awn (4.4–)5.7–6.8(–7.7) cm long; seta with trichomes (2.3–)2.6–3.9(–4.3) mm long *S. mongolorum*
5. Anthercium (9.9–)11.5–14.1(–16) mm long; lemma with seven distinct rows of trichomes; awn (10.8–)14.2–22.1(–28.1) cm long; seta with trichomes (3.9–)6.2–9.4(–12) mm long 6
6. Glumes (3.4–)3.6–4.3(–4.7) cm long; anthercium (9.9–)10–11.2(–11.5) mm long; awn (10.8–)11.7–14.5(–15.4) mm long; seta with trichomes (3.2–)4.5–5.5(–6.3) mm long *S. aktauensis*
6. Glumes (6–)6.8–8(–9.1) cm long, anthercium (12.1–)13.3–14.5(–16) mm long; awn (13.9–)16.9–24.4(–28.5) mm long; seta with trichomes (6.8–)8–10.4(–12) mm long 7
7. Panicle branches with trichomes (0.2–)0.3–0.4(–1.3) mm long; culms below the nodes pilose; dorsal side of the callus usually glabrous; seta (13.9–)16.7–19.7(–24.4) cm long *S. lingua* subsp. *lingua*
7. Panicle branches with trichomes 1–2.2(–2.5) mm long; culms below the nodes glabrous; dorsal side of the callus villous; seta (19–)21–22(26–) cm long *S. lingua* subsp. *magnifica*
1. Column glabrous, tuberculate or scabrous, rarely with a few trichomes near the bend 8
8. Lemma pubescent throughout or up to $\frac{3}{4}$ the length of the lemma; styles 3 *S. gaubae*
8. Lemma with 3–7 distinct rows of trichomes; styles 2 9
9. Lemma with 3 distinct rows, more rarely with 5 rows of trichomes; callus glabrous *S. karataviensis*
9. Lemma with 7 distinct rows of trichomes; callus villous 10
10. Awn straight; callus with foot like expansion or not 11
11. Glumes (2.2–)2.7–2.9(–3.2) cm long; anthercium (7.2–)8.2–8.9(–9.4) mm long; awn (6–)6.3–8.1(–9.3) mm long 12
12. Glumes (2.2–)2.7–2.9(–3.2) cm long; awn (6.5–)7.8–8.3(–9.3) cm long; anthercium with coronula *S. tianschanica* subsp. *tianschanica*
12. Glumes (1.9–)2.15–2.4(–2.7) cm long; awn (6–)6.3–7.3(–8) cm long; anthercium apex glabrous, rarely with scattered trichomes *S. tianschanica* subsp. *gobica*
11. Glumes (4.8–)5.6–7.5(–9) cm long; anthercium (12.3–)13–13.9(–14.7) mm long; awn (13.3–)17–22(–25) cm long 13
13. Awn (13.3–)15.9–17.3(–18.4) cm long; callus (1.5–)1.7–2.1(–2.2) mm long; blades abaxial surface glabrous, adaxial surface pilose *S. lingua* subsp. *lipskyi*
13. Awn (19–)19.8–23.6(–25.1) cm long; callus (2.3–)2.4–2.7(–2.8) mm long; blades abaxial surface scabrous, adaxial surface scabrous or papillose (rarely minutely pubescent) 14
14. Ligule replaced by a line of trichomes or shortly truncate, up to 0.15 mm long; column glabrous; seta with trichomes (8.2–)8.7–10(–12) mm long *S. longiplumosa*
14. Ligule 0.89–1.7 mm long, rounded; column somewhat scabrous, seta with trichomes 5.2–5.31 mm long *S. talassica*
10. Awn flexuous or falcate; callus base not expanded 15
15. Glumes (1.9–)2.15–2.4(–2.7) cm long; anthercium (7.2–)8.1–8.8(–9.3) mm long; awn (6–)6.3–7.3(–8) cm long *S. tianschanica* subsp. *gobica*
15. Glumes (3.1–)4.6.2(–9) cm long; anthercium (9.6–)11–15.2(–19.8) mm long; awn (9.8–)13.3–19.9(–28.4) cm long 16
16. Seta falcate 17
17. Lemma apex glabrous, peripheral ring (0.35–)0.45–0.58(–0.63) mm long; awn (9.9–)11.3–13.2(–14) cm long; lemma subdorsal and lateral rows of trichomes fused $\frac{3}{4}$ their length *S. klemenzi*

17. Lemma apex with scattered trichomes or with coronula, peripheral ring (0.7–)0.76–0.86(–0.93) mm long; awn (12.4–)14.2–16.5(–17.7) cm long; lemma with distinct rows of trichomes 18
18. Blades abaxial surface glabrous; anthecium (10.1–)11.3–12.5(–12.6) mm long, with erect-spreading trichomes; column (2.3–)3.2–3.6(–4) cm long *S. alaiica*
18. Blades abaxial surface distinctly scabrous; anthecium 13–14.4 mm long, with erect trichomes; column 4.3–4.7 cm long *S. kopetdaghensis*
16. *Seta flexuosa* 19
19. Anthecium (16.1–)17.1–18.1(–19.8) mm long, the ventral row reaching the top or ending not less than 0.33 mm below the top; blades abaxial surface glabrous and adaxial surface papillose *S. gegarkunii*
19. Anthecium (12.7–)13.8–15.2(–15.5) mm long, the ventral row ending 2–2.5 below the top; blades abaxial surface distinctly scabrous and adaxial surface pilose or minutely pubescent 20
20. Lemma with coronula; blades adaxial surface pilose, with trichomes ca. 0.5 mm; glumes (6–)6.1–6.7(–6.8) cm long; awn 22.4–24.5 cm long *S. okmirii*
20. Lemma apex glabrous or with scattered trichomes; blades adaxial surface minutely pubescent with trichomes up to 0.1 mm long; glumes 5.3–5.6 cm long; awn 19.8–21.3 cm long *S. talassica*

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APPENDIX 1. Variables studied in this paper.

Quantitative characters: GLL: Glumes length (cm); LEML: Lemma length (mm); LEMD: Lemma width (mm); LCIL: Ligule's cilia length (mm); CORL: Lemma apex trichome length (mm); CAL: Callus length (mm); CDH: Callus dorsal trichome length (mm); CVH: Callus ventral trichome length (mm); CDH/CVH: Ratio of callus dorsal trichome length and callus ventral trichome length; PERL: Peripheral ring length (mm); PERW: peripheral ring width (mm); PERL/PERW: Ratio of peripheral ring length and peripheral ring width; AWN: Awn length (cm); AWND: Awn diameter (mm); COL: Column length (cm); SET: Seta length (cm); SETH: Seta trichome length (mm); COLH: Column trichome length (mm); SET/COL: Ratio seta length and column length; LEMH: Lemma trichome length (mm); ADIL: Length of the adaxial trichomes of the basal leaf blade (mm); PANCIL: Panicle branches cilia length (mm); BASD: Basal blade leaf diameter (mm); LL: Ligule length (mm); LUL: Ligule uppermost leaf length (mm); LCILL: Ligule cilia length (mm).

Discrete character: ROH: Number of lemma rows.

Qualitative characters: BRDISP: Branch disposition respect the panicle: Spreading or erect-spreading (0); Erect (1). COR: Coronula: absent (0); present (1). SCAT: Lemma apex with scattered trichomes: absent (0); present (1). GLAPM: Lemma apex glabrous: no (0); yes (1). LEMAP: Lemma trichomes: appressed to erect-spreading (0); spreading (1). LSDF: Laterally and subdorsal lines of the lemma fused: absent (0); present (1). CALLFE: Callus shape: Callus not foot-like expanded (0); callus foot-like expanded (1). SCAR: Scar shape: elliptic or slightly elliptic (0); circular (1). CALI: Callus surface: glabrous (0); villous (1); COLIND: Column surface: glabrous, tuberculate or scabrous (0); pubescent (1). SETS: Seta straight: absent (0); present (1). SETFA: Seta falcate: absent (0); present (1). SETFL: Seta flexuous: absent (0); present (1). NSTY: Number of styles: 2 styles (0); 3 styles (1). PALIN: Palea surface: glabrous (0); with a central row of trichomes (1). ADIND: Adaxial surface of basal leaf: not pubescent (0); pubescent (1). ABINDG: Abaxial surface of basal blade leaf glabrous: no (0); yes (1). ABINDSC: Abaxial surface of basal blade leaf scabrous: no (0); yes (1). ABINDP: Abaxial surface of basal blade leaf pubescent: no (0); yes (1). LIGSH: Ligule absent or not lanceolate (0); ligule lanceolate (1).

APPENDIX 2: List of specimens measured and used for the morphological and numerical studies.

Stipa aktauensis Roshev. UZBEKISTAN. Sands of SW Kyzyl-Kum. Bukan-tau, Araslai forest zone, 42° 36' N 63° 28' E, 8 Jun 1932, Nikitin and Michailova s. n. (LE); Kyzyl-Kum desert, Aktau mountains, 40° 15' N 66° 10' E, 3 Jun 1932, Muralvoljansky 82 (H, FI, JE, LE, W); SE Kyzyl-Kum desert. Between Jdangueldi spring and Taidaras, Kul'dzhuktau mountain, 40° 45' N 63° 50' E, 21 May 1937, Bochantsev 536 (LE); SE Kyzyl-Kum desert. Surroundings Aiak-Kudjumda mountain, 38° 28' N 65° 14' E, 12 May 1937, Bochantsev 351 (LE); Buchara province, Singrun tau mountain, 40° 45' N 63° 50' E, 11 Jun 1948, Negaeva s. n. (LE); Syr Darya province, Aktau inter opp. Turkestan et Petro-Aleksandrowsk, 40° 15' N 66° 10' E, 6 May 1916, Filatov 219 (LE); Central Kyzyl-Kum, Attau Tamdinskiy, 42° 00' N 65° 00' E, 24 Apr 1972, Kamelin et al. 472 (LE); Between Kayak-Ati and Adam-Kirulgan, 1873, Korolkovym and Krauze s. n. (LE); Samarkand, Sangrun-Tau, 41° 15' N 65° 10' E, 10 Jun 1948, Nekaeva 385 (LE).

Stipa alaica Pazij. KAZAKHSTAN. Jugi Manrak pars centralis, locus Sagyndyk Majo, 47° 25' N 84° 20' E, 27 Jun 1986, Kotukhov s. n. (LE); Saur-Tarbagatai, NO Saykan, 46° 25' N 80° 38' E, 16 Jul 1993, Kotukhov s. n. (LE); Saur-Tarbagatai. NW Saur range, Kensay forest, 42° 53' N 70° 08' E, 14 Jul 1992, Kotukhov s. n. (LE); Saur-Tarbagatai. NW Saur range, forest of Kiziltas, 47° 5' N 85° 30' E, 17 Jul 1993, Kotukhov s. n. (LE); Saur-Tarbagatai, brachia australi-occidentalia jugi Saur, in viciniis hibernaculi Kesek, 47° 05' N 85° 30' E, 14 Jul 1992, Kotukhov s. n. (LE). KYRGYZSTAN. East of Sarik-Mogola, 39° 55' N 72° 47' E, 17 Apr 1961, Ikonnikov 12746 (LE); Semirechenskaya province, Przhevals district, Toguz-Torau forest, close to Kargalyk-Pereval pass, 41° 17' N 74° 10' E, 9 Jun 1913, Saposhnikov s. n. (LE). TAJIKISTAN. West Pamir, Vakhani-Ishkashimskii district, eastern hillsides to Abkharv river between Shenade and Dibane, 36° 49' N 71° 34' E, 30 Jun 1935, Ovczinnikov and Afanasiev 832 (LE); Vakhani-Ishkashimskii district, at western slope of Katta-Khorob, Ishkashish, 36° 50' N 71° 45' E, 9 Jul 1935, Ovczinnikov and Afanasiev 1024 (2 LE); West Pamir, Vakhani-Ishkashimskii district, eastern hillsides to Abkharv River between Shenade and Dibane, 30 Jun 1935, Ovczinnikov and Afanasiev 832 (LE).

Stipa caucasica Schmalh. subsp. *caucasica*. AFGHANISTAN. Pamir, Issiktalb, 37° 00' N 73° 19' E, 17 Aug 1975, Huss 206 (M). ARMENIA. Ad lacum Sevan prope pag. Schordsha, 40° 30' N 45° 29' E, 27 Jul 1929, Smirnow 46 (JE). CHINA. Pamir, distr. Yarkand, in Jersil valley, 38° 23' N 77° 14' E, 14 Jul 1930, Persson 107 (S); South of Taxkorgan, above Dafda, 37° 31' N 75° 27' E, 1 Aug 1991, Mieke and Mieke 5583 (GOET); South of Muji, 38° 56' N 74° 28' E, 16 Aug 1998, Wündisch 1441 (GOET). KAZAKHSTAN. Terskey Ala-tau. Gorge of Baiynkol river, at 24 km S of Tekes village, 42° 50' N 80° 16' E, 26 Jun 1950, Medvedeva et al. 133 (C, L); Semiretschensk region, Dzharkent district, pr. stat. Sary-Dzhas, 42° 54' N 79° 36' E, 27 Jun 1910, Michelson 1635 x (S); Semiretschensk region, Prjevsk district, Inilchek stream at 10 km from the glacier, 42° 03' N 79° 05' E, 1 Apr 1912, Sapojnikov and Shishkin s. n. (C); Mangischlak, 43° 30' N 52° 15' E, 2 Jun 1926, Russacoov s. n. (PR); Syr-Darya province, Aliyie-Ata district, Around Aleksandrovskaia village, 42° 56' N 75° 30' E, 16 May 1909, Minkwitz 142 (LE); Turgai province, Kyzyl-Dzhingil district, lower reaches of Sary-su River, 49° 51' N 63° 48' E, 30 May 1914, Krascheninnikov 139 (W); Lepinsk, close to Jaman-Terek stream, 45° 31' N 80° 36' E, 13 Jun 1928, Pavlov 62 (HBG); SW spur of Alatai-Djungar range, Chulak mountain, gorge of Monna-Sai river, 43° 57' N 77° 56' E, 29 May 1955, Goloskokov s. n. (GH). KYRGYZSTAN. Sufi Kurgan in Alai mountains, 40° 02' N 73° 30' E, 18 Jun 1898, Paulsen 404 (C); Issik-Kul province, Taragay, at the left of Karakoyun river, 41° 10' N 75° 44' E, 30 Aug 1964, Trulebich and Kajennikova s. n. (BR); Tian-Shan, Kirgizski khrebet, 10 km ad boreo-orientem versus ab oppido Frunze (Pishpek), in vicinitate pagi Chop-aryk, 42° 52' N 74° 36' E, 29 May 1974, Vašak s. n. (B); Fergana province, Margelan district, SW Katta-Karamuk valley river, 40° 28' N 71° 43' E, 19 Jun 1913, Desiatoff 1251 (S); Oškaya district, Altay, at 15 km south of Iski-Naijat village, 40° 16' N 72° 36' E, 9 Jun 1958, Tzvelev 39 (K); Kochkor region, 8 Km W from Tiulek village, 41° 58' N 75° 41' E, 7 Aug 1960, Kurganskaia and Udincteva s. n. (GDA). RUSSIA. Daghestan, Temir-Ch.Schura district, prope st. Atly-bujun, 42° 33' N 47° 42' E, 12 May 1901, Alexeenko s. n. (S). TURKMENISTAN. Turcomania. Aschabad province, Gaudan, 37° 39' N 58° 24' E, 29 May 1898, Litwinow 2174 (GH); Aschabad; Sulukli (Saratowka), 37° 19' N 58° 14' E, 13 Jul 1900, Hackel 882 (LD). TAJIKISTAN. Pamiriae pars borealis occidentalis, prope ostium fl. Tachta-Korum, 38° 47' N 72° 55' E, 6 Aug 1958, Tolmatceva 4759 (MA); Badakhsan, the mouth of Taxta-Korum stream. Small streams of Kak-Djar river, 28 Jul 1958, Tzvelev 860a (K).

Stipa caucasica subsp. *drobovii* Tzvelev. AZERBAIJAN. Transcaucasia, Nachrepublica prope pag Dzhulfa (Jolfa), 37° 57' N 58° 06' E, 27 May 1932, Keideman s. n. (WU). IRAN. Seman province, Touran Protected area (SE of Shahrud), E side of Kuh-e-Yazdu pass at road Ghazazan-Ahmadabad, 36° 09' N 56° 01' E, 8 May 1978, Freitag 15176 (B); South center, ca. km W of Mirza-Baylu, 37° 21' N 56° 12' E, 24 May 1995, Akhani 10928 (M); Between Mashad and Quchan, 36° 37' N 59° 07' E, 24 May 1959, Merton 3950 (K, W); N Seman, 4 km North of Bidak, along Derazi valley, 37° 18' N 55° 54' E, 18 May 1995, Akhani 10753 (B); Gorgan (Mohammed Rez Shah National Park), versus Almeh ducentum, N. Robat-e Qareh Bil, 37° 19' N 56° 26' E, 1975, Rechingen 52843 (B); NW Khorasan, W Soolgerd Guard station, 37° 27' N 56° 08' E, 27 Apr 1995, Akhani 10511 (B); Montes Elburz, summi montis Kuh Dasteh ca. 30 km a Tehran occidentem, 35° 59' N 51° 13' E, 28 Jun 1977, Rechingen 57303 (B); Gorgan, Shahpasand to Shahrud, south side of pass Gardaneh Khosh Yeilagh, 36° 16' N 51° 34' E, 22 Jun 1974, Wendelbo and Foroughi 12878 (W); 127 Km Gambadgbabons, 14 May 1966, Pabot 7813 (G); 70 km from Téhéran, close to Homand village, 35° 41' N 52° 25' E, 11 Jul 1960, Pabot 4293 (G); Region d'Aq Bolagh 90 km N de Hamadan, 1960, Pabot AB 75 (G); Mirza-Baylu plain, North of Armadlu, 37° 20' N 56° 11' E, 24 May 1995, Akhani 10894 (W); Ca. 3-4 km S Almeh, southern slopes of Chondeh-Abbas mountain, 37° 19' N 56° 8' E, 23 May 1995, Akhani 10858 (M). KAZAKHSTAN. Karatau ridges north of lake Biilikol, toward Lake Akkul, 1 Jun 1922, Drobov 285 (LE). TURKMENISTAN. Aschabad province, Transcaspia region, Kopet-Dagh mountains, 37° 57' N 58° 06' E, 16 May 1911, Michelson s. n. (WU); Central Kopet-Dag, spur of Kelyat range, 38° 33' N 57° 01' E, 21 May 1954, Medvedeva s. n. (LE) Kopet-Dag, at 16 km SW Kizil-Arvat, around Djanajir village, 38° 58' N 56° 16' E, 27 Apr 1952, Rodin et al. 3011 (LE). UZBEKISTAN. Samarkand, ad lacum Iskander-kul, 39° 04' N 68° 21' E, 21 May 1914, Dubjansky s. n. (LE); Fergana distr, Margelan, between Vuadil and Okhna village, 40° 10' N 71° 43' E, 21 May 1913, Desiatoff 610 (NY).

Stipa caucasica subsp. *glareosa* (P. A. Smirn.) Tzvelev. CHINA. Xinjiang, Pamir of China. Tashkurgan valley, W extreme of Tushkurgan mountain, 37° 46' N 75° 13' E, 13 Jun 1959, Junatov et I-Fen 603 (GH); Southern Muji valley, 38° 56' N 74° 28' E, 16 Aug 1998, Wündisch 1381 (GOET). INDIA. Salt Lake Rupshu, 32° 58' N 78° 17' E, Aug 1913, Stewart 442a (NY).

KAZAKHSTAN. Altai, Chegan-Uzuna river valley, 50° 38' N 79° 15' E, 17 Jul 1903, *Krylov s. n.* (H); Semirechenskaya province. Pishpek. North slope of Chu River, next to Ort-Tokoi village, 42° 20' E 76° 01' N, 29 May 1915, *Sovritkina 549* (C). KYRGYZSTAN. Alpes Alexandri, Turduk in valle fl. Kaschkara, 41° 45' N 72° 01' E, 7 Jun 1896, *Brotherus 148* (H); Semirechenskaya region, Przhewalskii district, in vicinny stat. Choktal (ad rip. septentr. lac. Issik-kul), 42° 35' N 76° 44' E, 28 May 1910, *Michelson 51* (H); Tian Shan, Issyk-Kul region, Issyk-Kul-See, Kara-Talaa, 42° 18' N 76° 23' E, 30 Jun 2002, *Dürbye 1684* (B); Gansu, Anxi Mazong Shan, 41° 33' N 97° 10' E, 18 Jun 1886, *Xu Lang Ren et al. s. n.* (MSB). MONGOLIA. Gobi-Altai, between Khalga and Baintukhum, 43° 45' N 103° 33' E, 9 Aug 1931, *Ikonnikov-Galitzky 3777* (NY); Tonkhil somon, west bank of lake Tonkhil-Nur, 46° 11' N 93° 54' E, 16 Jul 1947, *Junatov 2769* (LE); Ikhen-gung, close to the meteorological station, 17 Jun 1931, *Müllhlerweg 5637* (S); Shabarakh Usu, Outer Mongolia, 45° 00' N 103° 00' N, 1925, *Chaney 80* (LE, NY). RUSSIA: Baykal province, Oviurskiy region, at 17 km Ubsu-Nur lake, around Ak-Chira village, NE Amdaiguin-Joli lake, 50° 42' N 93° 18' E, 7 Aug 1973, *Timojina and Djukov 1714* (LE); Near Aya Bay, 52° 47' N 106° 36' E, Jun 1979, *Elias and Smirnov 90* (NY); Altai Oieotia, Chusk steppe, Telengt-Sartagoi, 49° 50' N 89° 0' E, 23 Jul 1937, *Kolinina s. n.* (K); Gorno-Altaiy, W Kosh Agatch, 49° 59' N 88° 40' E, 25 Aug 1978, *Elias et al. 4675* (NY). TAJIKISTAN. Pamir, Karakuli, Kara-Art valley, at 5 km from the rivers mouth, 39° 03' N 73° 35' E, 28 Aug 1962, *Ladigina and Ikonnikov 14797* (LE); East Pamir. Chechekti, 38° 20' N 74° 00' E, 6 Sep 1951, *Steshenco s. n.* (LE); Pamir, at the left of Ayujalu gorge, 38° 28' N 74° 15' E, 1 Aug 1961, *Sidorov 68* (LE); Mustagh Ata N flank, 37° 41' N 73° 45' E, 16 Sep 2002, *Dickoré 18256* (GOET).

Stipa karataviensis Roshev. KAZAKHSTAN. West Tian-Shan. Kara-Tau mountains, forest of Uzak-Uia, 47° 13' N 62° 05' E, 21 Jun 1934, *Pjataeva 336* (LE); Syr-Darya province, Perovskiy region, Balamurun forest zone close to Karatau, on the slopes close to Čili, 44° 17' N 66° 26' E, 19 May 1910, *Androsova 79* (LE); Syr-Darya province, at Karatau mountains around Ural-Tube, 43° 0' N 70° 40' E, 26 May 1963, *Goloskokov s. n.* (LE); Karatau mountains, rocky slopes on the Bukui-Tau pass, 46° 45' N 60° 45' E, 29 Jun 1931, *Pavlov 443* (LE); Tian-shan occid, Montes Karatau, 43° 50' N 69° E, 18-29 May 1930, *Lipschitz 92* (H, JE, L, S); Syr-Darya. Karatau mountains, Bala-Saukandik in Koskuli (Jamankuli) lake zone, 43° 0' N 68° 03' E, 13 May 1977, *Kamelin et al. 1394* (LE); Karatau, Syr-Darya, southern slope of Uch-Uzeni gorge, above Kogashik forest, 43° 53' N 68° 01' E, 11 May 1977, *Kamelin et al. 1255* (LE); Karatau Dschil, 1876, *Regel 493* (LE); Syr-Darya prov., Aulie-atinskii district, Gory Berk-Kara (Karatau), 42° 54' N 71° 22' E, 23 May 1909, *Minkwitz 310* (LE); Karatau of Syr-Darya, Kora-Uzen gorge at the upper reaches of Boyaldyr depp valley, 43° 33' N 68° 28' E, 9 May 1977, *Kamelin et al. 1137* (LE); Syr-Darya province, Aulie-Atinskaya, close to Golovachevki village, 42° 50' N 71° 12' E, 25 May 1917, *Dingel s. n.* (LE); Syr-Darya province, Aulie-atinskii district, Berk-Kara gorge (Karatau), 42° 54' N 71° 22' E, 23 Jun 1909, *Knorrning 283* (LE); Kora-Tau mountains. Kara-Sai tableland, 46° 00' N 64° 45' E, 12 Jun 1936, *Pjataeva s.n.* (LE). UZBEKISTAN. Naratau. Tutak-Sai, 39° 54' N 68° 07' E, 8 Jun 1951, *Neustrueva, et al. 208* (LE).

Stipa klemenzii Roshev. MONGOLIA. East Gobi, Erdeni region, Baroja-Tala forest, S Dzamin-Ude, 43° 45' N 111° 55' E, 16 Jun 1941, *Junatov s. n.* (LE); Matad region, at 20 km south of Matad, 47° 09' N 115° 32' E, 25 Jul 1956, *Dashniyam s. n.* (LE); Gobi, Artsa Bogdo range, at 3 km from the pass to Kobdo, 44° 35' N 102° 4' E, 16 Jul 1970, *Grubov, Ulziijutag and Tsereibaljid s. n.* (LE); Gobi to Juisin, 27 km E of Salt lakes by the path to Daribi, 46° 27' N 94° 7' E, 21 Jun 1971, *Grubov et al. s. n.* (LE); South Gobi, Khongor region, N Gurban-Saikhan and Dzun-Saikhan, 43° 49' N 103° 27' E, 22 Jul 1943, *Junatov s. n.* (LE); South Gobi, Jurmein region, S slope of Gurbai, 43° 49' N 103° 27' E, 19 Jul 1950, *Kalinina s. n.* (LE); Ulan-tsay region, Bailinlis mountain, 1959, *Ivanov s. n.* (LE); Central Mongolia, 15 km ad orient, Summit Wang, in Gobi, 19 Jun 1934, *Eriksson 696* (S); Selenge province, Barun-Burin region, Burgultai river valley at 3-4 km of the left side, 48° 58' N 104° 51' E, 18 Jun 1948, *Kalinina et al. s. n.* (LE); 60 km SW of Ulan Bator along the road to Ubur Hangay, 46° 36' N 107° 11' E, 18 Jul 1949, *Junatov s. n.* (LE); Ad ripam fl. Khorukha, 48° 12' N 104° 16' E, 25 Jun 1895, *Klemenz 72a* (LE); Southern Gobi, Jan-Jongor Region, at 40-45 km NWN of Dalan-Dzadagad, by the old state highway to Ulan-Bator, 43° 37' N 103° 29' E, 10 Oct 1940, *Junatov s. n.* (LE); Central Khalkha, Northwest Undzhul, 46° 47' N 105° 34' E, 27 Jun 1974, *Golubkova et al. 116* (LE). RUSSIA. Tuva Oblast, Ereinskij p-H.- okp- c. Erein. Bulun-Bazhy, 50° 16' N 95° 12' E, 22 Jul 1972, *Timojina and Mrijin 3193* (LE); Buryat province, S slope of Bartoy range, 50° 40' N 103° 23' E, 20 Jul 1972, *Petshikov s. n.* (LE); Dyresiu area, Dospedgai forest, at 6-7 km east Borgoi village, 50° 45' N 105° 50' E, 2 Aug 1936, *Petshikov s.n.* (LE).

Stipa gaubae Bor. IRAN. Kazvin. Ravandeh prope Keredj, 34° 01' N 51° 20' E, 17 Aug 1975, *Gaubae 1632* (K, W). AZERBAIJAN: Opp. Nachiczvan, Duzdag, 39° 17' N 45° 19' E, 23 Jun 1973, *Musajev and Sadychov s. n.* (LE); ARMENIA. Near Aznaberd, 39° 32' N 45° 29' E, 1 Jul 1960 *Takhtajan et al. 131078* (ERE).

Stipa gegarkunii P.A. Smirn. ARMENIA. At Sevan lake close to Schordsha village, 40° 30' N 45° 29' E, 28 Jul 1929 *Smirnov 48* (B, FI, H, JE, L, 3LE, S, W).

Stipa kopetdaghensis Czoparov. TURKMENISTAN. Montes Kopetdagh centralis, in declivitate occidentali prope apicem montis Dushak in solo argilloso, 30 Jul 1967, *Czoparov s. n.* (LE)

Stipa lingua A. Junge. AFGHANISTAN. Smangan province, 2 Km W of Kotal-e-Mirza Atbili, 36° 11' N 68° 18' E, 9 Jun 1978, *Podlech 31631* (G); Hari-rud valley, 34° 28' N 65° 03' E, *Aitchinson 1137* (G, WU); Elepasti, foothill of Band-e-Yakh, Djawzari Valley, Afghanistan, 35° 15' N 67° 30' E, 9 Jul 1976, *Rodenburg 233* (L); Parwan province, the highest part of Ghorband valley, below Shibar pass, 34° 54' N 68° 15' E, 28 Jul 1965, *Podlech 12051* (MSB); Top of Shibar pass, 34° 22' N 66° 43' E, 28 Jul 1958, *Pabot 1110* (G). TAJIKISTAN. Low part of Šachdary river, SW slope of Schugnan range, 37° 30' N 71° 35' E, 13 Jul 1964, *Grubov et al. s. n.* (LE); Schugnan. Šachdary valley. Between Drum Dar river and Čay-kilriver, 37° 13' N 72° 04' E, 26 Jun 1914, *Tuturin and Bessedin 371* (LE); West Pamir, Dasht-Baranov, close to Khorog, 37° 29' N 71° 31' E, 12 Jul 1948, *Lavrenko and Rodin 945* (LE); West Pamir, around Dasht-Baranov, close to Khorog, slope of Šachdary river gorge, 37° 29' N 71° 30' E, 11 Jul 1948, *Lavrenko and Rodin 887* (LE). TURKMENISTAN. Central Kopet-Dagh mountains, Geok-Tepinsk district, between Čuli and Časkon, 37° 58' N 58° 01' E, 29 May 1958, *Čoparov s. n.* (COI, JE); Aschabad province, Kopet-Dagh mountains, Vannovskiy, 37° 57' N 58° 06' E, 16 May 1911, *Michelson 234* (G); Transcaspia region, Kopet-Dagh mountains, 37° 50' N 58° 00' E, 17 May 1911, *Michelson 319* (M) Badkhyz, Bodkhyzskiy Zapovednik wild life reserve. Kepelya, 35° 46' N 61° 44' E, 22 Jun 1972, *Gorelova 3* (LE); Zeravshan range in the high mountains close to Kitut river mouth, 39° 15' N 69° 0' E, 7 Jun 1932, *Ovczinnikov and Slobodov s. n.* (LE); Low part of Šachdary river, the valley of Sadbargo river on the right side of Chandym affluent, 37° 13' N 72° 00' E, 1914, *Tuturin and Bessedin 379* (LE); Chashma-i-Obek, 10 km NW Obek, 34° 22' N 63° 10' E, May 1977, *Unger 117* (MSB). TURKMENISTAN. Prope Germab, 30 May 1889, *Antonov s. n.* (LE). UZBEKISTAN. Oy-Badak-Sai deep valley, S slope of Turkestan range, at 3-4 km of Kodshar village, 38° 50' N 65° 35' E, 27 Jun 1948, *Czestnaja 48* (LE).

Stipa lipskyi Roshev. UZBEKISTAN. Samarkand district, Samarkand, 39° 39' N 66° 57' E, 29 May 1897, *Lipskyi s. n.* (W); Buchara province, Nura-Tau range, S of Djizlok pass, 40° 25' N 67° 00' E, 26 May 1964, *Priajin s. n.* (LE). Samarkand district, Samarkand, 39° 39' N 66° 57' E, 27 May 1897, *Lipskyi 4530* (LE); River Siab valley, close to Samarkand, 39° 39' N 66° 58' E, 6 May 1913, *Michelson 1983* (LE). TAJIKISTAN. Koyki-Tai mountains at NW of Lyublikar village, 37° 2' N 68° 4' E, 18 May 1960, *Nepli s. n.* (LE); Koyki-Tau mountain at NW Ayvadh village, 36° 58' N 68° 01' E, 17 May 1960, *Bochantsev and Egorova 17*. (LE); Zeravshan pass, 39° 30' N 70° 30' E, 3 Jun 1932, *Ovczinnikov and Slobodov s. n.* (LE); Zeravshan pass, north slope of Gissarskiy pass, 39° 0' N 68° 30' E, 6 Jul 1948, *Kozlova 355* (LE). KAZAKHSTAN. Tian-Shan occid., Montes Karatau, 43° 05' N 70° 25' E, 23 May-8 Jun 1936, *Mikeschin 93* (G, LE, S).

Stipa longiplumosa Roshev. TAJIKISTAN. SE slope of Babatag range close to Akmecheti, 37° 34' N 74° 48' E, 5 Jun 1938, *Linchevskii 281* (LE); West slope of North Aruk-Tau, 37° 47' N 68° 32' E, 13 Jun 1959, *Chukavina 676* (LE); Jugum Babatag, fere meridiem versus ab urb Djuschambe, 38° 33' N 68° 46' E, 11 Jul 1931, *Gontscharov 94* (FI, S, W); Pamir, at the top of Babatag mountain, 38° 45' N 68° 00' E, 25 Sep 1935, *Prianishkov 126* (JE); E slope of Sarsariak range, hills below Margak, 2-3 km SW Margak village, 38° 12' N 69° 09' E, 9 Jun 1958, *Gontscharov et al. 227* (LE). KYRGYZSTAN. Oškaya province, Alai range, Clay slopes at 15 km S of Oš to Iski-Naukat, 40° 16' N 72° 36' E, 9 Jun 1958, *Tzvelev 7* (LE); Oškaya province, Altai range, at 15 km S of Oš village to Iski-Naukat village, 40° 16' N 72° 36' E, 9 Jun 1958, *Tzvelev 5* (LE).

Stipa magnifica Junge. KYRGYZSTAN. Čatkalskiy range, Bozbu-Too mountain close to Djuk-Beli pass, 41° 17' N 71° 55' E, 17 May 2005, *Lazikov s. n.* (LE); Fergana province, Sari-Kamysh-Sau gorge close to Tash-Kumyr mountain, 41° 20' N 72° 14' E, 4 May 2005, *Lazikov s. n.* (LE); Fergana province, Gulera river valley, Sufi-Kurgan, 40° 02' N 73° 30' E, 28 Jun

1901, *Alexeenko 1422* (LE); Oškaya province, Altai range at 15 km S from Ošcity to Iski-Naukat village, 40° 16' N 72° 36' E, 9 Jun 1958, *Tzvelev 7* (LE), Fergana province, Oš district, close to Gulcza, Jun 1900, *Transchel s. n.* (LE); Alai Mts, Sufi Kurgan, 18 Jun 1898, *Paulsen 407* (C).

Stipa mongolorum Tzvelev. MONGOLIA. Uburjantai, at 25 km WSW Teg mine by Bogd road, 44° 32' N 102° 20' E, 25 Jun 1972, *Banzrach, et al. s. n.* (LE); East Gobi. Ulan Baderkhu somon, west rim of Borokha-Tala region, 43° 47' N 109° 49' E, 17 Jun 1941, *Junatov 372* (LE); Tonkhil somon, west bank of lake Tonkhil-Nur, 46° 11' N 93° 54' E, 16 Jul 1947, *Junatov 2773* (LE); Left bank of Dzaijina river by Taishiri and Delger road, at 38 km of Taishiri, Tairim plain, 46° 21' N 97° 17' E, 24 Aug 1972, *Grubov et al. 1179* (LE); Shabarakh Usu, Outer Mongolia, 43° 00' N 104° 00' E, 1925, *Chaney 80* (GH, NY, W); Erdeni region, Borokha-Tala region, S of Dзамын-Ude, 44° 20' N 111° 14' E, 16 Jun 1941, *Junatov 3130* (LE); Delger Hangay somon, at 8-10 km NW extremity of Delger-Hangay mountain range, along the old road from Ulan Bator to Dalan Dzadagad, 45° 25' N 104° 83' E, 17 Jul 1943, *Junatov s. n.* (LE); Erdeni somon, Borocho-Tala region, at S of Dзамын-Ude, 10 Jun 1941, *Junatov s. n.* (LE); East Gobi, Urgen-Tsetslerlik Region, Sain-Utu baun at 40 km NW Sain-Shanda, 45° 16' N 110° 8' E, 28 Aug 1940, *Junatov s. n.* (LE).

Stipa okmirii Dengub. TAJIKISTAN. Schugnan district, close to horti Botanici Pamirensis, 14 Jun 1977, *Dengubenko 2731* (LE).

Stipa talassica Pazij. KYRGYZSTAN. Tian-Shan. Talaskii region. Talasski Alatau, Bastash river valley, 30 Jun 1927, *Sovetkina & Uspenskaya 339* (LE).

Stipa tianschanica Roshev. subsp. *tianschanica*. CHINA. Gansu province, Čianti, Altyntag mountain range 15 km south of Aksai settlement, 39° 31' N 94° 59' E, 2 Aug 1958, *Petrov s. n.* (LE); Kashgar, 58-60 km WNW of Kashgar along the road to Kensu mine and Ulugchat, 39° 48' N 74° 21' E, 17 Jun 1959, *Junatov and I-Fen 704* (LE, NY); Baikurt Settlement, 83 km NW of Kashgar by Turugart pass, 39° 59' N 75° 22' E, 19 Jun 1959, *Junatov and I-Fen 852* (GH, LE); Xinjiang province, S Tian-Shan, at 70 km NW of Kashgar, by Turugart pass, 40° 30' N 75° 57' E, 19 Jun 1959, *Junatov and I-Fen 847* (LE); Tian -Shan, upper part of Muzart river valley, 41° 15' N 83° 27' E, 8 Sep 1958, *Junatov and I-Fen 892* (K); Kashgara, Kyzylsu river between Shur-Bulak and Kshuiku, 39° 42' N 78° 39' E, 4 Jul 1929, *Popov s. n.* (LE); South Tian-Shan range, at 10-12 km N Baikurt from the road of Kashgar to Turugart, 39° 56' N 75° 32' E, 20 Jun 1959, *Junatov and I-Fen s. n.* (LE). KYRGYZSTAN. Central Tian-Shan. Sari-Dzhas at the lower part of

Kalida river mouth, 42° 12' N 79° 20' E, 1 Aug 1982, *Grubov and Popova s. n.* (LE); Kuylyu range, E of Taldy-su river valley, at 0.5 km of Saraltdaz river valley, 42° 05' N 78° 45' E, 30 Jul 1979, *Ikonnikov and Ladigina 1767* (LE). MONGOLIA. Rim of Tuilin-Tala plain Guiltar, 46° 0' N 97° 00' E, 26 Aug 1943, *Junatov s. n.* (LE). UZBEKISTAN. Tagdumbasch-Pamir, Kara-Chukur valley, pr. fl. Beik in rupibus meridionalis, 39° 26' N 65° 16' E, 18 Jul 1901, *Alexeenko 2131* (LE)

Stipa tianschanica subsp. *gobica* (Roshev.) D. F. Cui. MONGOLIA. Altai, Gobi, Ire-Togua mountain, 47° 00' N 107° 0' E, 18 Aug 1926, *Tugarikov s. n.* (LE); Eastern Gobi, Erdini region, Usun-Gulu mountain, east Erdini, 112° 0' N 44° 50' E, 14 Jun 1941, *Junatov s. n.* (LE); Southern Gobi, Jurmeni region, southern slopes of Gurban-Saykhan, 43° 49' N 103° 27' E, 19 Jul 1950, *Kalinnikov s. n.* (LE); Alasham desert, Bayan Khoto, Kamensujaitu, at 8 km SE of Bain-Ula mountain, 46° 6' N 95° 37' E, 13 Jun 1958, *Petrov s. n.* (LE); Divusumu village, 70 km S-E of Bayan Khoto, 46° 6' N 95° 37' E, 11 Jun 1958, *Petrov s. n.* (LE); Chuj-choto desert, at 10 km of the city, N Datsinshani mountain, 49° 44' N 106° 42' E, 4.VI.1958, *Petrov s. n.* (LE); Central Gobi. Region Buiantu, at 8 km N of Talan-Juduk, 107° 00' N 45° 00' E, 7 May 1941, *Tugarikov s. n.* (LE); Mongolia australis, Hutjerta-gol Camp, 49° 22' N 112° 42' E, 2 Jun 1927, *Hummel 1091* (S); idem, *Hummel 1186* (S); Eastern Gobi, at 200 km S from Sain-Shand village, northern slopes of Jutag-Ul moutain, 44° 53' N 110° 08' E, 19 Jun 1980, *Gubanov 5831* (LE); Dzum-Saychan range, by the path of Dalan-Dzadagada to Elo-Ama, 43° 34' N 104° 25' E, 21 Jul 1970, *Grubov et al. 191* (LE); Valley between Nemegetu mountains and Zomzo mountain, 43° 39' N 100° 54' E, 20 Aug 1886, *Potantin s. n.* (W); Gobi, Bani-Undur region, Juju-Us forest at 15-20 km SE of Ata-Bogdo, 43° 18' N 96° 36' E, 11 Aug 1943, *Junatov s. n.* (LE); Between Nemegetu and Zomzo Mts, 20 Aug 1886, *Potantin s. n.* (W); Mongolia interior, 7.5 km ad bor.-orient Khadain-sume, 49° 50' N 106° 35' E, 26 Jul 1936, *Eriksson 887* (S); Dzajjin, Tragan-Olom district, at 25 km W Tragan-Olom by Kobdo road, 48° 0' N 96° 0' E, 28 Aug 1944, *Junatov s. n.* (LE); 50 km along the road from In'chuan in Bayan Khoto desert, 10 Jun 1958, *Petrov s. n.* (LE); Alashan desert, Bayan-Khoto, at 80 km SE Divusumu village, Bain-Nur mountains, 43° 47' N 102° 41' E, 12 Jun 1958, *Petrov s. n.* (LE); South Gobi Jan-Bogdo district, at 1 km SE from the old station of the city, close to Glaba range, 43° 00' N 103° 00' E, 24 Sep 1940, *Junatov s. n.* (LE). CHINA. Xangai. region, Jairjan-Dulan, at 40 km SW by Bayan Khoto road, 46° 6' N 102° 50' E, 27 Jun 1941, *Tsatsekin s. n.* (LE). Kalgan, 40° 48' N 114° 50' E, 20-21 Jul, *Cowday 1519* (NY); North Shanxi province, Datun district, at 8 km W the city, 39° 42' N 112° 21' E, 21 May 1957, *Petrov s. n.* (LE).