

Multivariate morphometric analysis of the *Stipa turkestanica* group (Poaceae: *Stipa* sect. *Stipa*)

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Abstract Based on numerical analyses of macromorphological characters (cluster analysis, principal coordinate analysis and principal component analysis), scanning electron microscopy observation of lemma and lamina micromorphology, as well as field observations, five taxa belonging to the *Stipa turkestanica* group have been recognized in the mountain area of Central Asia. They are *S. turkestanica* subsp. *turkestanica*, *S. turkestanica* subsp. *trichoides*, *S. macroglossa* subsp. *macroglossa*, *S. macroglossa* subsp. *kazachstanica* and *S. kirghisorum*. As a result of this study, we propose one new combination, *S. macroglossa* var. *pubescens*, and designate lectotypes for *S. turkestanica* subsp. *trichoides* and *S. macroglossa* var. *pubescens*, and an epitype for *S. kirghisorum*. Illustrations of micromorphological structures of the lemma, patterns of leaf hairiness and an identification key are provided. A taxonomic synopsis including information on nomenclatural types, synonyms, descriptions of the

taxa, and, as supplementary information, a list of the specimens examined is also presented.

Keywords Distribution · Identification key · Micromorphology · Middle Asia · Nomenclature · Numerical analysis · Stipeae · Typification

Introduction

The mountains of Central Asia have been recognized as being among the world's top 34 biodiversity hotspots (Mittermeier et al. 2005). There are more than 8000 vascular plant species but, despite this, it contains several regions that are still significantly underexplored (Kamelin 2002). Central Asia is also characterized by a high diversity of taxa from the genus *Stipa* L. Of the 150 species of feather grasses, ca. 70 species occur in Central Asia (Roshvitz 1934; Pazij 1968; Bor 1970; Tzvelev 1976, 2012; Freitag 1985; Kotukhov 2002; Nobis 2010, 2013, 2014) and more than half of them are generally accepted as endemic or subendemic species either to particular mountain ranges or to that region (Tzvelev 1976; Nobis 2011a, b, 2012, 2013; Nobis et al. 2013). Feather grasses of Central Asia are classified into several sections containing critical groups of closely related and similar taxa. In this study, we examined the *Stipa turkestanica* group of *Stipa* sect. *Stipa*. The group includes seven taxa: *Stipa turkestanica* Hack., *S. kirghisorum* P.A.Smirn., *S. macroglossa* P.A.Smirn., *S. trichoides* P.A.Smirn., *S. ikonnikovii* Tzvelev, *S. kazachstanica* Kotukhov and *S. nikitinae* Tzvelev, which occur throughout Central Asia and in surrounding areas but are particularly abundant in the Altai, Tian-Shan, Kopet Dag, Pamir, Alai, Hindu Kush and Kunlun mountain ranges. The main, striking characters of this group are:

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glabrous (smooth or scabrous) column (lower part of awn), more or less scabrous leaves of the vegetative shoots and a relatively short antherium, less than 17 mm long, without a ring of hairs at the apex. Because of morphological similarity, some of taxa from the *S. turkestanica* group were treated at different taxonomic levels or merged with other species (Table 1).

Due to the high phenotypic plasticity observed within the *Stipa turkestanica* group, narrow species concept or taxonomic splitting (e.g., Kotukhov 2002; Tzvelev 2012) may cause many difficulties in determination of species. On the other hand, too broad species concept can also create problems in understanding patterns of diversity (Freitag 1985; Gonzalo et al. 2013). Thus, well-documented delimitation of individual taxa supported by specific combination of morphological traits, habitats requirements and distribution range is highly necessary. Additionally, clarification of the boundaries between particular species of the examined group is of crucial significance in terms of correct identification and delimitation of the taxa arisen through hybridisation, such as *S. × alaiica* Pazij, *S. × manrakica* Kotukhov, *S. okmiri* Dengub. or *S. × talassica* Pazij, for which they are one of the parental species (Nobis 2013).

Despite the uniformity of the epidermal characters, micromorphological traits such as presence and shape of long cells, silica bodies, cork cells, hooks, prickles and hairs on lemmas and/or laminas display specific patterns within *Stipa* and have proved to be taxonomically useful (e.g., Barkworth and Everett 1987; Romaschenko et al. 2012; Nobis 2013, 2014; Nobis et al. 2014b, 2015). However, up to now within the *S. turkestanica* group, patterns of the lemma micromorphology are known only for *S. turkestanica* s. lato (Nobis and Nobis 2013; Nobis et al. 2015). Thus, we endeavored to test the micromorphological patterns of the lamina and lemma micromorphology to identify characters which would provide additional support for the taxonomical findings.

The aims of this paper were: (a) to clarify patterns of macromorphological and micromorphological variations within the *Stipa turkestanica* group; (b) to disclose the level of morphological differentiation for recognized taxa; (c) to indicate the most informative characters for identification of the taxa; (d) to provide a key, descriptions and notes on ecology and distribution of all members of the studied group.

Materials and methods

Plant material

This study is based on plant material deposited in the herbaria of FRU, GAT, GOET, KFTA, KHOR, KRA,

Table 1 Taxonomic treatment of the *Stipa turkestanica* group

Taxon	References	S. kirghisorum	S. kirghisorum	S. kirghisorum	S. pennata subsp. kirghisorum	Kotukhov (2002)	Gonzalo et al. (2013)
<i>Stipa kirghisorum</i>	S. kirghisorum	S. kirghisorum	S. kirghisorum	S. pennata subsp. kirghisorum	S. kirghisorum	S. kirghisorum	S. kirghisorum
<i>Stipa macroglossa</i> subsp. <i>macroglossa</i>	S. macroglossa	S. macroglossa	S. macroglossa	—	S. macroglossa	S. macroglossa	S. turkestanica subsp. <i>macroglossa</i>
<i>Stipa macroglossa</i> subsp. <i>kazachstanica</i>	—	—	—	—	S. kazachstanica	S. kazachstanica	S. turkestanica subsp. <i>turkestanica</i>
<i>Stipa turkestanica</i> subsp. <i>turkestanica</i>	S. turkestanica	S. turkestanica	S. turkestanica subsp. <i>turkestanica</i>	S. turkestanica	—	—	S. turkestanica subsp. <i>turkestanica</i>
<i>Stipa turkestanica</i> subsp. <i>trichoides</i>	S. trichoides	S. trichoides	S. turkestanica subsp. <i>trichoides</i>	S. turkestanica	—	—	S. turkestanica subsp. <i>trichoides</i>
<i>Stipa nikitinae</i>	—	—	S. nikitinae	S. pennata subsp. kirghisorum	—	—	S. kirghisorum
<i>Stipa ikonnikovii</i>	—	—	S. ikonnikovii	—	—	—	S. kirghisorum

KRAM, LE, LECB, M, MSB, MW, PR, PRC, TAD, TASH, TK, W, WA, WU. In total, over 500 sheets were revised. A list of selected specimens examined is provided in the Online Resource 1. Morphological characters of vegetative and reproductive structures were examined in all specimens of the group.

Characters scored for morphometric analyses

The numerical analyses are based on 108 specimens of *Stipa turkestanica* subsp. *turkestanica*, 90 of *S. turkestanica* subsp. *trichoides*, 121 of *S. macroglossa* subsp. *macroglossa*, 6 of *S. macroglossa* subsp. *macroglossa* var. *pubescens*; 44 of *S. macroglossa* subsp. *kazachstanica*, 123 of *S. kirghisorum*, 5 of *S. ikonnikovii*, and 2 of *Stipa nikitinae*. Measurements were conducted on each well-developed specimen, using digital calipers or a ruler. A total of 26 most informative quantitative and qualitative morphological characters were chosen for analysis (see

Table 2). Measured morphological characters of the anthercium and the awn are illustrated in Fig. 1.

Multivariate morphometric analyses

Each specimen was treated as an Operational Taxonomic Unit (OTU), in accordance with the methods used in numerical taxonomy (Sokal and Sneath 1963). The assumptions of normality were examined using the Lilliefors test. Those variables that did not meet the assumptions of normality were Box–Cox transformed to find the optimal normalizing transformation in each case. The Pearson correlation coefficients or non-parametric Spearman correlation coefficients were then calculated to check if any strong correlation (>0.90) exists between variables which could potentially affect the results of further multivariate analyses. If the correlation coefficients for the logically correlated pairs of variables exceeded $r=0.90$, they were excluded from the multivariate analyses.

Table 2 A list of morphological characters used in the analyses

Abbreviation	Character
Quantitative characters	
AC	Width of the awn column (mm)
AL	Length of the anthercium (mm)
AwnL	Length of the awn (mm)
Call	Length of the callus (mm)
CvH	Length of hairs on the ventral part of the callus (mm)
CdH	Length of hairs on the dorsal part of the callus (mm)
Col ₁ L	Length of the lower segment of column (mm)
CRL	Length of the peripheral ring of the callus base (mm)
CRW	Width of the peripheral ring of the callus base (mm)
DDL	Distance from the end of dorsal line of hairs to the top of anthercium (mm)
DVL	Distance from the end of ventral line of hairs to the top of anthercium (mm)
LG	Length of the lower glume (mm)
LHB	Length of hairs on the adaxial surface of blades of vegetative shoots (mm)
LHD	Length of hairs in the dorsal line on the lemma (mm)
LHV	Length of hairs in the ventral line on the lemma (mm)
LigC	Length of ligules of the middle cauline leaves (mm)
LigV	Length of ligules at the vegetative shoots (mm)
SHL	Length of hairs on seta (mm)
SL	Length of seta (mm)
SL/CL	Ratio length of seta to the length of column (Col ₁ L + Col ₂ L)
UG	Length of the upper glume (mm)
WVS	Width of blades of vegetative shoots (mm)
Qualitative characters	
CC	Color of column (1—green; 2—light-red; 3—red-purple)
ColS	Scabrousness of column (1—smooth; 2—slightly scabrous; 3—strongly scabrous)
HVS	Character of abaxial surface of leaves of the vegetative shoots (1—slightly scabrous; 2—scabrous; 3—hairy scabrous; 4—pubescent)
HCL	Character of cauline leaf sheaths (1—slightly scabrous; 2—scabrous to hairy scabrous; 3—pubescent)

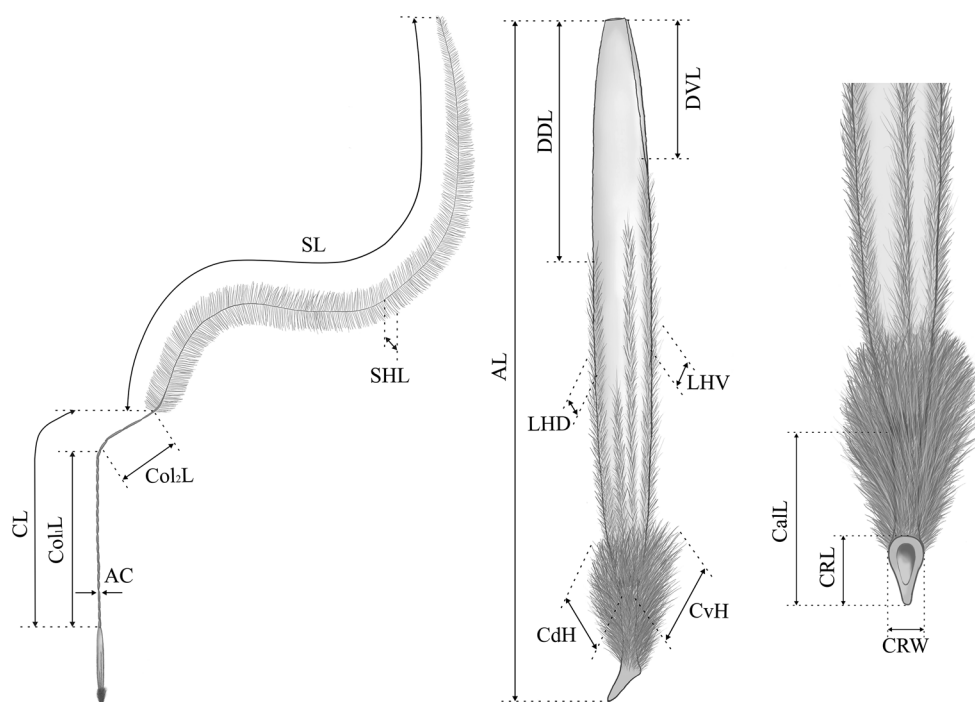


Fig. 1 Measured morphological characters of the antherium and the awn. For character abbreviations see Table 2

Cluster analysis was performed on all the OTUs using all 26 characters, to obtain information about general relationships and similarities between them. The similarity between two OTUs was calculated on the basis of Gower's general similarity coefficient. The dendrogram was prepared using UPGMA method.

A principal coordinate analysis (PCoA) was performed on the basis of all quantitative and qualitative characters. The goal of PCoA was positioning of objects (individuals) in a space of reduced dimensionality while preserving their distance relationships.

Subsequently, a principal component analysis (PCA) was conducted on all quantitative characters, on the basis of the correlation matrix (Sokal and Sneath 1963). The specimens were grouped with no a priori assumptions. Each specimen was then marked with the symbol on the scatter plot corresponding to a particular taxon. The analysis enabled the determination of reduced set of variables (features), which were most strongly correlated with the principal components. Factors with eigenvalues >1 were chosen according to the Kaiser criterion (Kaiser 1960). The characters which had the highest factor loadings on first three principal components ($r > 0.60$) were selected.

Next, descriptive statistics of characters for previously recognized groups were calculated. To reveal significant differences between means of particular characters across all examined groups (after using Levene's test to assess the equality of variances), one-way analysis of variance

(ANOVA) followed by Tukey's HSD test for unequal sample frequencies was calculated.

Data analyses and statistical calculations were performed using Statistica software version 9.1 (Statsoft Inc. 2011), XLSTAT version 2013.1.02 and MVSP 3.1 (Kovach 1999).

Scanning electron microscopy (SEM) observation

Using scanning electron microscopy (SEM) observation, pattern of the lemma micromorphology and hairiness of vegetative leaves (adaxial surface of blades) were studied in all of the examined taxa of the group. We analyzed 28 samples of 7 species. A list of voucher specimens used in the study is given in Table 3. For SEM observation, samples were coated with gold using a JFC-1100E Ion sputter manufactured by JEOL. Micromorphological structures of lemmas and laminas were observed and photographs taken by means of the scanning electron microscope Hitachi S-4700, at various magnifications. Lemmas (removed from mature spikelets in the middle part of the panicle) were studied from the base to the distal portions. Qualitative and quantitative characters were studied for the abaxial lemma surface: length of long cells, shape of silica bodies, presence and shape of hooks and prickles, length and distribution of macrohairs. The terminology used was adopted from Thomasson (1978, 1981), Ellis (1979), Snow (1996) and Nobis (2013, 2014). The patterns of hairiness of leaves (adaxial surface of blades)

Table 3 Specimens used in the micromorphological examination of lemmas and leaves

Taxon	Locality	Voucher
<i>Stipa turkestanica</i> subsp. <i>turkestanica</i>	Tajikistan	Pamirs, 1 Jul 2009, <i>M. Nobis</i> (KRA)
		Pamirs, 2 Jul 2009, <i>M. Nobis</i> (KRA)
		Pamirs, 1 Jul 2008, <i>M. Nobis</i> (KRA)
<i>Stipa turkestanica</i> subsp. <i>trichoides</i>	Tajikistan	Zeravshan Mts, 15 Jun 2012, <i>M. Nobis</i> , <i>A. Nowak</i> (KRA)
		Zeravshan Mts, 22 Jun 2008, <i>M. Nobis</i> (KRA)
		Zeravshan Mts, 8 Jun 2011, <i>M. Nobis</i> (KRA)
<i>Stipa macroglossa</i> subsp. <i>macroglossa</i>	Tajikistan	Zeravshan Mts, 10 Jun 2011, <i>M. Nobis</i> (KRA)
		Zeravshan Mts, 4 Jun 2009, <i>M. Nobis</i> (KRA)
		Zeravshan Mts, 11 Jun 2012, <i>M. Nobis</i> , <i>A. Nowak</i> (KRA)
		Zeravshan Mts, 14 Jun 2007, <i>M. Nobis</i> (KRA)
		Kyrgyzstan
<i>Stipa macroglossa</i> subsp. <i>kazachstanica</i>	Kyrgyzstan	Kyrgyz Mts, 15 May 2011, <i>M. Nobis</i> (KRA)
	Kazakhstan	Altai Mts, 12 Jun 1992, <i>Yu. Kotukhov</i> (LE)
<i>Stipa kirghisorum</i>	Kazakhstan	Altai Mts, 4 May 1901, <i>Krylov</i> (TK)
		Altai Mts, 16 May 1914, <i>C. Kossinsky</i> (TK)
	Tajikistan	Zeravshan Mts, 17 Jun 2008, <i>M. Nobis</i> , <i>M. Kozak</i> , <i>A. Nowak</i> (KRA)
		Darvaz Mts, 6 Jul 2008, <i>M. Nobis</i> (KRA)
		Zeravshan Mts, 18 Jun 2008, <i>M. Nobis</i> , <i>M. Kozak</i> , <i>A. Nowak</i> (KRA)

from the middle part of leaves) were also studied in all of the examined taxa of the group.

Results

Numerical analysis

Cluster analysis (UPGMA) performed on the basis of all 26 quantitative and qualitative characters (Table 2), resulted in the delimitation of two main clusters (Fig. 2). The first comprises groups of OTUs belonging to *S. kirghisorum* and *S. macroglossa* and the second, OTUs of *S. turkestanica*. Within *S. macroglossa*, two subclusters are clearly distinguished: *S. macroglossa* subsp. *macroglossa* and *S. macroglossa* subsp. *kazachstanica*. A similar result was generated for the cluster of *S. turkestanica*, where *S. turkestanica* subsp. *turkestanica* and *S. turkestanica* subsp. *trichoides* are well differentiated. A comparable pattern is shown in the ordination diagrams from the PCoA, performed also on 26 quantitative and qualitative characters. The first axis clearly separated the OTUs of *S. turkestanica* subsp. *turkestanica* and *S. turkestanica* subsp. *trichoides*, which are positioned on the negative side of the axis, while all the remaining OTUs belonging to *S. kirghisorum* and *S. macroglossa* are located on the positive side. At the same time, axis 2 distinctly divides OTUs of *S. kirghisorum* from those of both subspecies of *S. macroglossa* (Fig. 3). For the purposes of comparison, we marked the OTUs of *S.*

nikitinae and *S. ikonnikovii* within *S. kirghisorum* cluster (Figs. 2, 3).

The PCA diagram, performed on 22 quantitative characters, also displays a pattern similar to that described above. The first three principal components accounted for 63.6 % of the total variance: 34.9 and 21.2 % for the first and second axis, respectively. Ten characters studied displayed highest correlations with the first axis, five with the second axis and one with the third axis (Table 4). Thirteen characters had high positive factor loadings (>0.60) on the two first axes and two had high negative factor loadings (<-0.60). A plot onto these axes (Fig. 4) revealed 3–5 neighboring or slightly overlapping groups of OTUs. The first group, located in the right upper part of the diagram, belongs to *S. kirghisorum*, which consists of three completely overlapping groups of OTUs belonging to *S. kirghisorum*, *S. ikonnikovii* (type) and *S. nikitinae* (type). The cluster in the bottom right-hand section of the diagram can be divided into two slightly overlapping subclusters. They correspond to currently recognized subspecies *S. macroglossa* subsp. *macroglossa* and *S. macroglossa* subsp. *kazachstanica*, which differ mainly in AL, CalL, DDL and LHB (Fig. 5; Table 5, Online Resource 2, 3). Apart from the indumentum of the cauline sheaths, a character not used in the analysis, the specimens of *S. macroglossa* var. *pubescens* do not differ in any other character, from those of the type variety, and consequently, they are plotted together. The two somewhat overlapping clusters in the left-hand part of the diagram correspond to

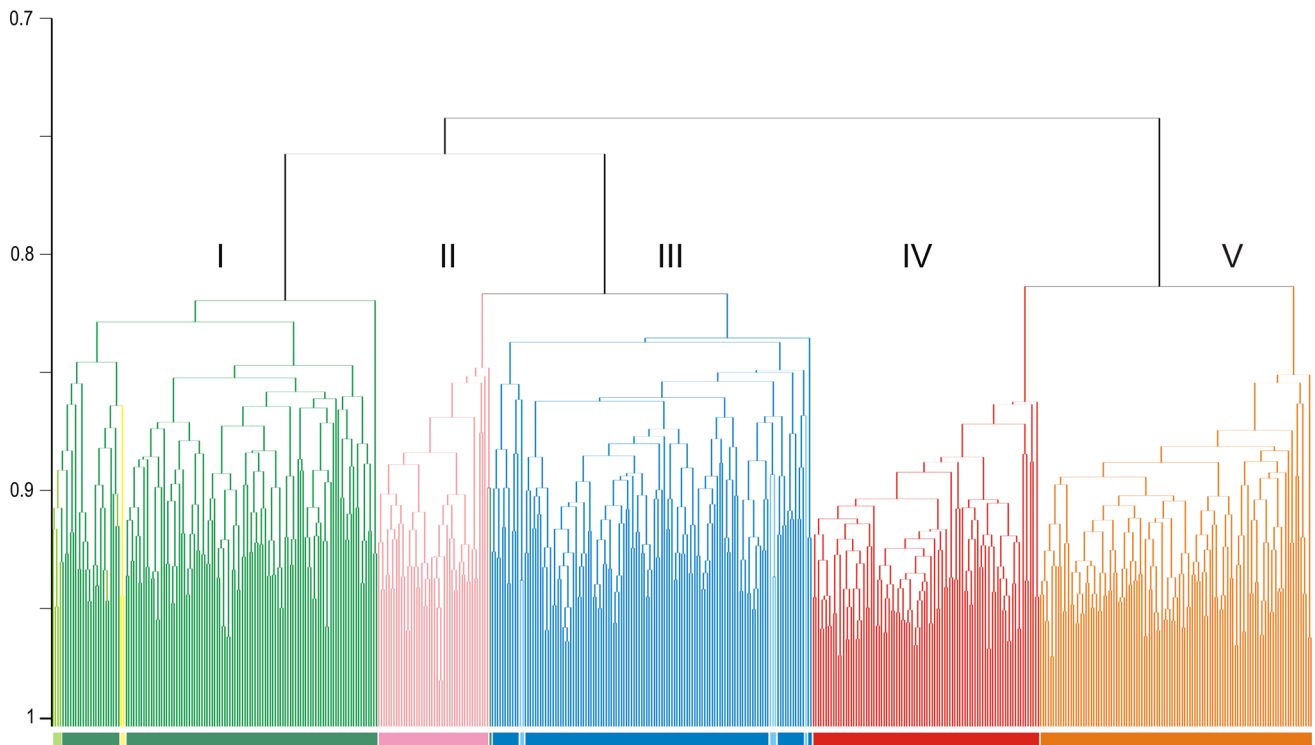


Fig. 2 Cluster analysis (UPGMA method of classification and Gower's general similarity coefficient) performed on 26 quantitative and qualitative characters. Main clusters (from the left): I *Stipa kirghisorum* (*S. kirghisorum* green, *S. ikonnikovii* light green, *S.*

nikitinae yellow), II *S. macroglossa* subsp. *kazachstanica* (pink), III *S. macroglossa* subsp. *macroglossa* (*S. macroglossa* var. *pubescens* light blue), IV *S. turkestanica* subsp. *trichoides* (red), V *S. turkestanica* subsp. *turkestanica* (orange)

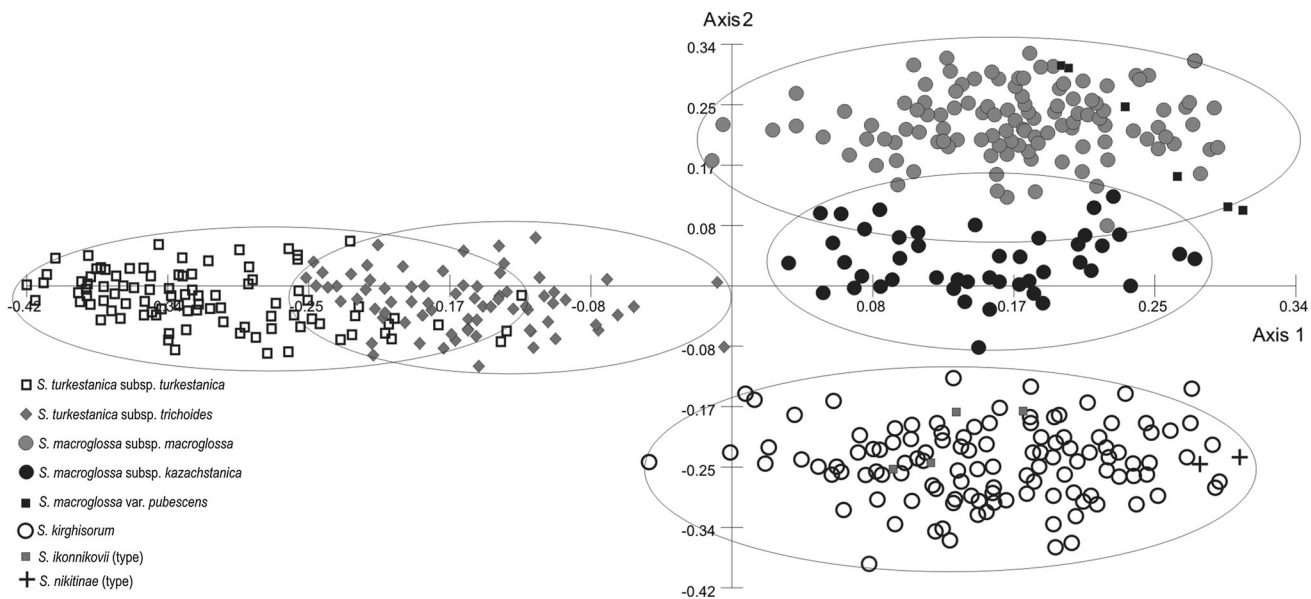


Fig. 3 Principal coordinate analysis (PCoA) performed on 26 quantitative and qualitative characters

the two subspecies of *S. turkestanica*, subsp. *turkestanica* and subsp. *trichoides*. Specimens of these subspecies differ from each other in LigV, AwnL, SL, Col₁L, and CalL (Table 5, Online Resource 2, 3).

The results of the one-way ANOVA revealed significant differences in all of the characters examined (Table 4). The results of the post hoc tests and Tukey's HSD test for variables with normal distribution and multiple

Table 4 Results of the principal component analysis (PCA) for the specimens of the *Stipa turkestanica* group as OTUs—total variance and 22 morphological characters showing the highest factor loadings on the first three principal components; results of one-way ANOVA ($p < 0.05$): F and p values for characters with normal distribution

Character	Principal component analysis—factor loadings			ANOVA— F value	p value
	PC1	PC2	PC3		
AC	0.791	−0.122	0.209	228.39	<0.05
AL	0.901	0.193	−0.211	366.89	<0.05
AwnL	0.811	0.368	−0.101	371.34	<0.05
CaL	0.632	0.607	0.001	300.06	<0.05
CvH	0.581	0.569	0.221	166.79	<0.05
CdH	0.272	0.712	0.295	141.43	<0.05
Col ₁ L	0.286	0.830	−0.217	326.28	<0.05
CRL	0.670	−0.467	0.164	204.51	<0.05
CRW	0.674	−0.361	0.125	133.14	<0.05
DDL	0.672	−0.368	−0.292	186.13	<0.05
DVL	0.368	−0.521	−0.215	75.04	<0.05
LG	0.856	−0.315	−0.066	431.87	<0.05
LHB	−0.348	−0.492	0.131	142.19	<0.05
LHD	0.252	0.124	0.605	11.04	<0.05
LHV	0.125	0.220	0.518	11.45	<0.05
LigC	−0.088	−0.324	0.485	69.41	<0.05
LigV	−0.133	−0.772	0.306	468.53	<0.05
SHL	0.302	−0.096	0.299	28.81	<0.05
SL	0.925	−0.051	−0.175	399.90	<0.05
SL/CL	0.552	−0.731	−0.032	351.87	<0.05
UG	0.861	−0.310	−0.053	445.81	<0.05
WVS	0.493	0.265	0.294	70.01	<0.05
Total variance (in %)	34.9	21.2	7.5		

High value of factor loadings (>0.6) and F are given in bold. For character abbreviations, see Table 2

comparisons of average ranks for variables with non-normal distribution are presented in Online Resource 3.

Adaxial surface of leaves of the vegetative shoots: patterns of hairiness

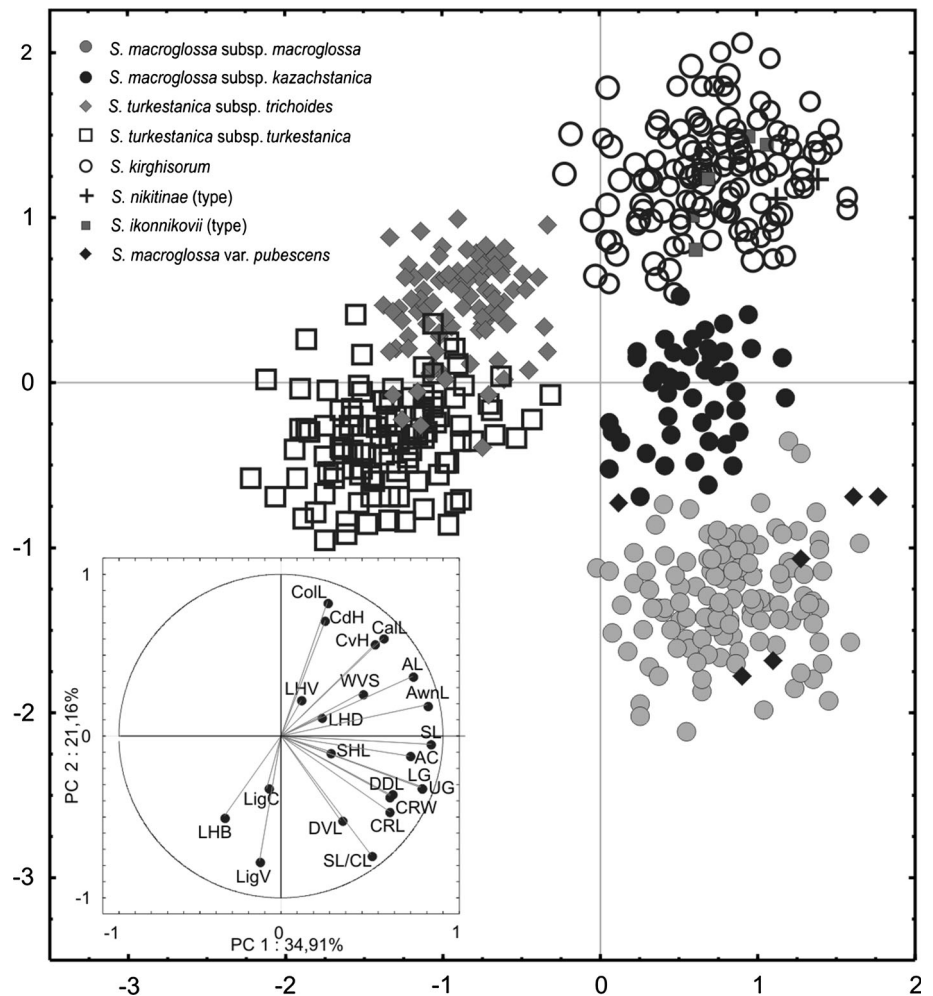
The adaxial surface of leaves of the vegetative shoots is ribbed and covered by hairs (Fig. 5). Density and length of hairs differs in particular taxa of the *Stipa turkestanica* group; however, patterns of hairiness are consistent. Generally, three types of hairiness can be distinguished here: (a) shortly pilose, with prickles and/or short hairs 0.05–0.1 mm long, (b) pilose, with short hairs 0.15–0.30 mm in length, and (c) pilose with mixture of short and long hairs 0.1 and 0.2–0.5 mm (Fig. 5). The first type contains specimens of *S. macroglossa* subsp. *kazachstanica* and *S. kirghisorum* (Fig. 5d, e), which have a pattern of hairiness unlike all the other members of the studied group. The second type comprises specimens of the three taxa: *S. turkestanica* subsp. *turkestanica*, *S. turkestanica* subsp. *trichoides*, *S. macroglossa* subsp. *macroglossa*, with the adaxial surface of leaves covered by short hairs. The third type contains specimens of *S.*

kirghisorum, in which hairs on the adaxial surface of leaves distinctly differ in length; however, density and distribution of longer and shorter hairs is variable. This concerns in particular the long hairs, which were sometimes located along the marginal ribs or distributed across the entire adaxial leaf surface (Fig. 5).

Lemma micromorphology

The general patterns of the lemma micromorphology are typical of the genus *Stipa* (cf. Barkworth and Everett 1987; Romaschenko et al. 2012; Nobis 2013; Nobis et al. 2013, 2014b, 2015) and are relatively uniform in all of the studied taxa. Fundamental (long) cells are elongated to rectangular in *S. turkestanica* s. lato and *S. kirghisorum*, whereas rectangular to more or less square in shape in both subspecies of *S. macroglossa* (Fig. 6). Side walls of long cells in all of the studied taxa are raised, thickened and undulate with sinuous Ω - to V-shaped curves. Silica bodies are reniform to oblong or ovate, while cork cells were either sporadic or completely absent. Hooks are common and generally morphologically similar in all four taxa, whereas prickles are very sparse and uniform, occurring

Fig. 4 Principal component analysis (PCA) performed on 22 quantitative characters. Diagram in the lower left corner shows projection of the variables on the factor plane (PC1 × PC2). For character abbreviations see Table 2



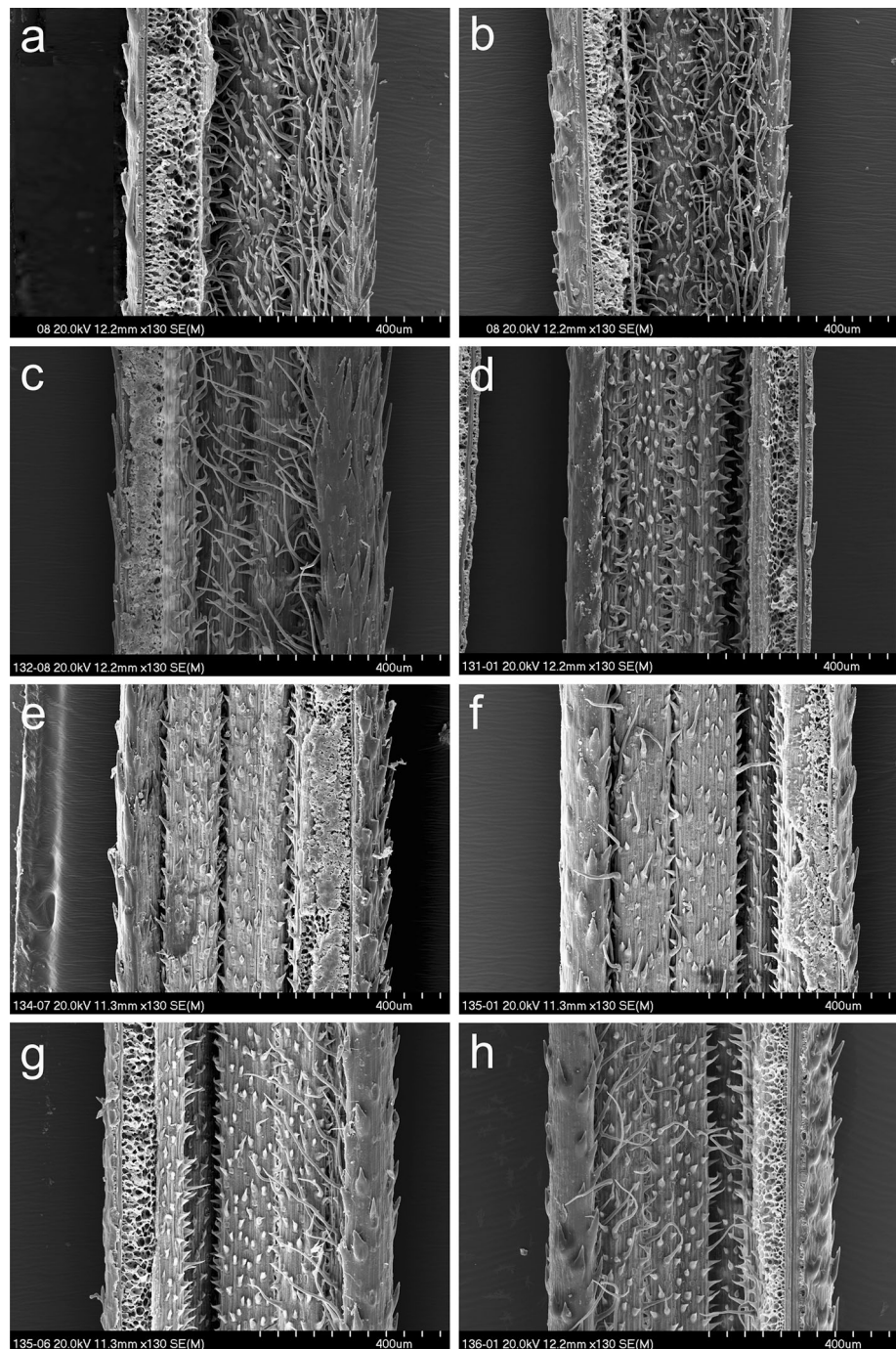
almost exclusively in the upper part of the lemma (near the apex), sometimes being completely absent. The lemma apex is glabrous or, sometimes possess macrohairs forming a tuft of short hairs up to 0.3 mm long occurring solely on the margins of the ventral part of the lemma. On the abaxial lemma surface, macrohairs are organized in seven lines which always end below the top of lemma in all of the studied taxa (Table 5, Online Resource 2). Exceptionally, e.g., in *S. turkestanica* subsp. *turkestanica* (specimens from Iran collected by *J. Soják*, PR), subdorsal and subventral lines of hairs are undeveloped and, consequently, 5 or 3 lines are visible.

Discussion

The result of morphometric analyses enabled the delimitation of three well-separated sub-groups within the *Stipa turkestanica* group, namely '*S. turkestanica*', '*S. macroglossa*' and '*S. kirghisorum*'. Because of morphological similarity of *S. trichoides* and *S. turkestanica*, Tzvelev

(1974) reduced the former to the subspecies of the later. Whereas Freitag (1985), based on the original description, went further treating *S. trichoides* as a synonym of *S. turkestanica*. He mentioned the fact that, in the description of *S. trichoides*, Smirnov (1925) differentiates his new species from *S. turkestanica* by glabrous, rather than scabrous awn column. On the other hand, Hackel (1906) stated in the diagnosis that *S. turkestanica* has a relatively short awn with a glabrous or scabrous column. Unfortunately, he gave no information on the length of the ligules at the vegetative leaves. A detailed examination of type collections of *S. turkestanica* at W and MW has shown that its ligules are much longer than in *S. trichoides*. Both of these taxa were well defined on the basis of their distribution range (see below); however, in the countries such as Tajikistan, where they co-occur, their delimitation was difficult and they were sometimes misidentified. Generally, the two taxa may be distinguished using the length of ligules at the vegetative leaves, which are (0.5–)1.6–2.8(–3.7) mm long in subsp. *trichoides* and (2.6–)4.5–8.2(–11.5) mm long in subsp. *turkestanica*; the length of awn, (145–)163–196(–225) mm long

Fig. 5 Patterns of hairiness on the adaxial surface of blades of vegetative shoots in the *Stipa turkestanica* group: *S. turkestanica* subsp. *turkestanica* (a), *S. turkestanica* subsp. *trichoides* (b), *S. macroglossa* subsp. *macroglossa* (c), *S. macroglossa* subsp. *kazachstanica* (d), *S. kirghisorum* (e–h)



in subsp. *trichoides* and (88–)118–158(–184) mm long in subsp. *turkestanica* (Table 5, Online Resource 2); and the surface of column, which is smooth in subsp. *trichoides* and scabrous, rarely slightly scabrous to smooth in subsp. *turkestanica*.

The specimens of *S. turkestanica* subsp. *trichoides* collected from high elevations in the Alai Mts are smaller and more gracile than specimens from lower elevations, e.g., the Zeravshan Mts and resembles *S. turkestanica* subsp.

turkestanica. These similarities can be explained by phenotypic plasticity associated with climatic conditions. Such plasticity is also observed in most vascular plants that have a large altitudinal range. In contrast, some specimens of *S. turkestanica* subsp. *turkestanica* collected in the southwestern Pamirs (4 June 2011, *M. Nobis*, KRA) are relatively tall and, apart from the scabrous column of the awns and longer ligules at the vegetative shoots, they are very similar to specimens of *S. turkestanica* subsp. *trichoides*

Table 5 Main differential characters of the taxa belonging to the *Stipa turkestanica* group

Taxon	<i>Stipa turkestanica</i> subsp. <i>turkestanica</i>	<i>Stipa turkestanica</i> subsp. <i>trichoides</i>	<i>Stipa macroglossa</i> subsp. <i>macroglossa</i>	<i>Stipa macroglossa</i> subsp. <i>kazachstanica</i>	<i>Stipa kirghisorum</i>
<i>Character</i>					
Culm length (cm)	(16–)31–50(–61)	(20–)39–59(–75)	(17–)36–51(–65)	(23–)26–43(–58)	(27–)38–59(–78)
Width of blades of vegetative shoots (mm)	(0.3–)0.4–0.5(–0.6)	(0.30–)0.35–0.45(–0.55)	(0.35–)0.40–0.55(–0.70)	(0.4–)0.5–0.6	(0.4–)0.5–0.6(–0.7)
Adaxial surface of blades of vegetative shoots	Covered by (0.15–)0.2–0.3(–0.35) mm long hairs	Covered by (0.15–)0.17–0.25(–0.30) mm long hairs	Covered by (0.15–)0.2–0.3(–0.4) mm long hairs	Covered by 0.1 mm long hairs	Covered by shorter than 0.1 mm long hairs sometimes with admixture of 0.2–0.5 mm long hairs
Abaxial surface of blades of vegetative shoots	Strongly scabrous	Scabrous covered by short hairs and spinules	Scabrous	Slightly scabrous or scabrous	Scabrous to strongly scabrous
Ligules of the vegetative shoots length (mm)	(2.6–)4.5–8.2(–11.5)	(0.5–)1.6–2.8(–3.7)	(2.6–)4.5–7.8(–10.3)	(2.9–)4.0–6.5(–8.5)	(0.3–)0.7–1.6(–3.0)
Lower glume length (mm)	(25–)34–41(–51)	(29–)34–41(–45)	(48–)56–64(–76)	(42–)49–57(–61)	(37–)46–55(–68)
Antherium length (mm)	(9.5–)10.8–12.1(–13.5)	(10.6–)11.9–13.1(–13.8)	(12.2–)13.1–14.5(–16.0)	(11.3–)12.4–13.4(–13.9)	(13.1–)14.5–16.0(–17.8)
Callus length (mm)	(1.4–)1.8–2.1(–2.5)	(1.8–)2.1–2.5(–2.9)	(1.7–)2.1–2.5(–3.0)	(2.2–)2.6–3.0(–3.4)	(2.3–)2.7–3.2(–3.8)
Ventral line of hairs on lemma	Terminated (1.2–)1.8–2.6(–4.1) mm below the top	Terminated (1.1–)2.0–3.0(–4.3) mm below the top	Terminated (2.0–)3.1–3.8(–5.4) mm below the top	Terminated (2.0–)2.2–3.0(–3.8) mm below the top	Terminated (0.5–)1.4–3.1(–4.6) mm below the top
Dorsal line of hairs on lemma	Terminated (2.1–)3.1–4.2(–5.6) mm below the top	Terminated (2.9–)3.8–4.7(–6.2) mm below the top	Terminated (4.3–)5.5–6.8(–9.1) mm below the top	Terminated (3.1–)3.6–4.5(–6.4) mm below the top	Terminated (2.5–)4.3–5.6(–6.6) mm below the top
Awn length (mm)	(88–)118–158(–184)	(145–)163–196(–225)	(175–)210–270(–337)	(179–)205–234(–256)	(185–)230–285(–342)
Column length (mm)	(23–)33–43(–53)	(26–)47–60(–72)	(26–)34–42(–53)	(32–)40–48(–56)	(44–)61–75(–87)
Character of column	Scabrous or rarely glabrous	Smooth	Smooth	Smooth, rarely very slightly scabrous	Smooth
Lower segment of column (up to the first bent) length (mm)	(14–)21–27(–34)	(18–)32–43(–54)	(14–)21–27(–35)	(20–)25–34(–40)	(27–)44–56(–71)
Column width, near its base (mm)	(0.3–)0.35–0.4(–0.45)	(0.30–)0.35–0.40(–0.50)	(0.4–)0.5–0.6(–0.7)	(0.35–)0.5–0.6(–0.7)	(0.40–)0.45–0.60(–0.65)
Seta length (mm)	(64–)85–117(–136)	(82–)116–138(–170)	(139–)174–220(–292)	(140–)164–191(–210)	(137–)162–210(–279)
Hairs on seta length (mm)	(2.3–)3.5–4.5(–5.5)	(3.2–)3.9–5.3(–6.0)	(3.3–)4.2–5.5(–6.7)	(3.8–)4.5–5.5(–6.7)	(2.9–)3.6–4.8(–6.5)
Ratio length of seta/length of column	(2.0–)2.3–3.0(–4.1)	(1.2–)2.1–2.7(–4.4)	(3.5–)4.6–5.7(–8.6)	(3.1–)3.6–4.6(–5.7)	(1.7–)2.4–3.2(–4.4)
Ratio length of seta/length of lower segment of column	(2.9–)3.7–4.9(–6.5)	(1.5–)2.9–4.0(–6.1)	(5.3–)7.2–9.5(–15.1)	(4.0–)5.2–7.3(–10.0)	(2.0–)3.1–4.5(–6.3)
Shape of long cells of the lemma epidermis	Elongated to rectangular	Elongated to rectangular	Rectangular to square	Rectangular to square	Elongated to rectangular

from the western Pamir Alai Mts (Nobis 2013). In our numerical analysis, both subspecies are well distinguished from the other members of the studied group; however, they are always grouped together. Given the several characters that separate the two taxa (Table 5, Online Resource 2), as well as their geographic isolation, we concur with Tzvelev (1974) that they should be treated on the subspecies level. *Stipa turkestanica* subsp. *turkestanica* is a more southeastern taxon of higher mountain elevations in Central Asia, occurring mainly in eastern Tajikistan, Afghanistan, Pakistan, northeastern India and in a handful of sites in Iran. *Stipa turkestanica* subsp. *trichoides* is more a northwestern taxon, occurring in Kyrgyzstan, Tajikistan, Uzbekistan, Turkmenistan, northern Iran and Afghanistan at generally lower elevations than *S. turkestanica* subsp. *turkestanica* (Ovchinnikov and Chukavina 1957; Pazij 1968; Bor 1970; Tzvelev 1976; Freitag 1985; Gonzalo et al. 2013).

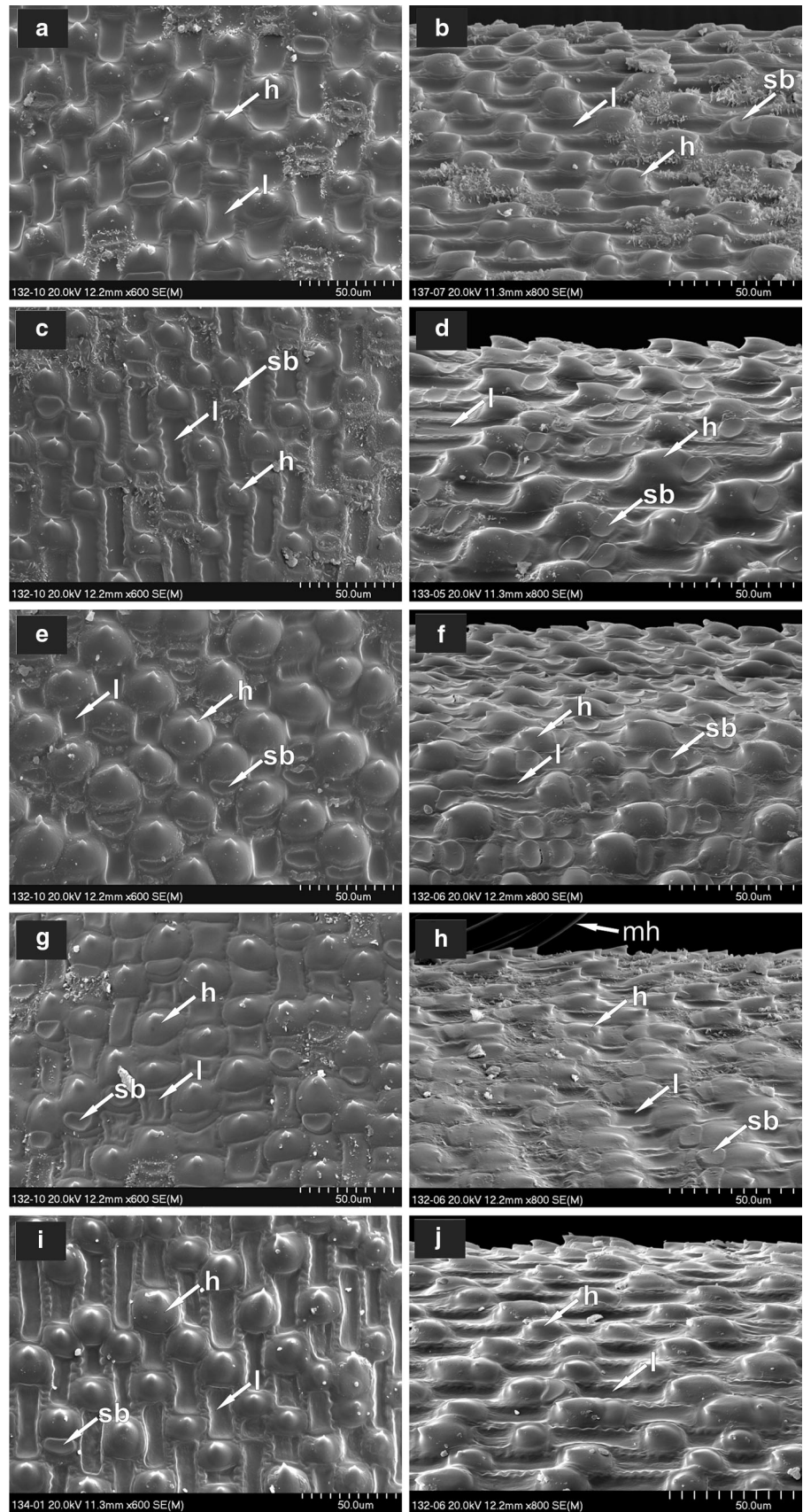
Kotukhov (1994) described *Stipa kazachstanica* from the Altai Mts. However, because of high similarity to *S. macroglossa*, it has recently been reduced to subspecies of the latter (Nobis 2013). *Stipa macroglossa* subsp. *kazachstanica* differs from the type subspecies in having somewhat shorter antheridium, seta, as well as in adaxial surface of blades of the vegetative shoots, which are covered by very short hairs, rather than solely by a mixture of short and long hairs (Fig. 5). These taxa were grouped close to each other in all of the analyses performed. Because of very short indument of the adaxial surface of leaves, *S. macroglossa* subsp. *kazachstanica* is slightly similar to *S. kirghisorum* (Fig. 5). However, they differ in the length of antheridium, awn, column, ligules at the vegetative shoots and the length of long cells on abaxial surface of lemma (Fig. 6; Table 5, Online Resource 2). It is also possible that hybrids of *S. macroglossa* subsp. *kazachstanica* and *S. kirghisorum* can occur in areas where the two last taxa co-occur, such as in the eastern Tian-Shan and Altai Mts. The specimens collected by V. Goloskokov (3 July 1952, LE) in Kungei-Alatau, in the Kara-bulak valley, may be hybrids, with intermediate characters including the length of awn column, seta, and ligules at vegetative shoots (which are 1–3.5 mm in length). Gonzalo et al. (2013) recognized *S. macroglossa* as a subspecies of *S. turkestanica*. However, based on the morphological and geographical evidence, we do not share this opinion. Moreover, Gonzalo et al. (2013) treat *S. kazachstanica* as conspecific with *S. turkestanica* subsp. *turkestanica*. However, it is also hard to agree with that, since the OTUs of the former taxon were grouped with OTUs of *S. macroglossa* subsp. *macroglossa* with a remarkable distance from the OTUs of *S.*

turkestanica subsp. *turkestanica* in all our analyses (Figs. 2, 3, 4, 5, 6; Table 5). *Stipa macroglossa* subsp. *kazachstanica* differs from both mentioned above taxa, more or less significantly, by 17 and 21 characters, respectively (Online Resource 3). Apart from the morphological characters distinguishing *S. macroglossa* subsp. *macroglossa* from *S. macroglossa* subsp. *kazachstanica* (Figs. 2, 3, 4, 5, 6), these two taxa differ also in their geographical distribution. The former is a more south-westerly, Central Asian taxon, occurring mainly in Kazakhstan, Kyrgyzstan, Uzbekistan, and Tajikistan (Lavrenenko and Nikolskaya 1965; Nobis et al. 2014c), whereas *S. macroglossa* subsp. *kazachstanica* is a more north-easterly, Central Asian taxon, occurring mainly in western Mongolia, western China, eastern Kazakhstan and eastern Kyrgyzstan (Nobis et al. 2014a).

Specimens of feather grasses with pubescent cauline sheaths are sometimes distinguished and given in different taxonomic ranks. In *Stipa lessingiana* Trin. & Rupr., for instance, they have been distinguished as var. *brauneri* (Pacz.) Roshev., or sometimes even at subspecies or species level [*S. lessingiana* subsp. *brauneri* Pacz. or *S. brauneri* (Pacz.) Klokov]. However, the pubescent specimens show no other difference from their glabrous relatives, nor do they occupy a distinct geographic range. Moreover, pubescent and glabrous plants may occur in the same population. For these reasons, the variety rank seems to be most appropriate for such specimens. Similar variation is observed also in *S. macroglossa* (Figs. 2, 3, Online Resource 2), where two varieties can be distinguished: var. *macroglossa*, with glabrous sheaths of cauline leaves, and var. *pubescens*, with shortly pubescent sheaths of cauline leaves. Such specimens were seen from Kazakhstan and Tajikistan (cf. Online Resource 1).

Together with *Stipa kazachstanica*, Kotukhov (1994) described *S. tzveleviana* Kotukhov from eastern Kazakhstan. It was recently synonymised with *S. turkestanica* subsp. *turkestanica* by Gonzalo et al. (2013). However, M. Nobis and P. Gudkova (submitted) based on field investigation and revision of herbarium materials consider *S. × tzveleviana* as a result of hybridisation between *S. orientalis* Trin. and *S. macroglossa* subsp. *kazachstanica*. A detailed examination of corresponding specimens revealed that it differs from *S. turkestanica* subsp. *turkestanica* in having shorter ligules at the vegetative shoots, poorly developed ring of hairs present at the top of antheridium and in scabrous column, which is covered by (0.05–)0.1–0.3 mm long spinules or hairs on its lower part and 0.2–0.5(–0.7) mm long on its upper part. In members of the *S. turkestanica* group, there is no ring of hairs at the apex and the column is either smooth or slightly scabrous

Fig. 6 Patterns of lemma micromorphology in the *Stipa turkestanica* group (superior and lateral view): *S. turkestanica* subsp. *turkestanica* (**a, b**), *S. turkestanica* subsp. *trichoides* (**c, d**), *S. macroglossa* subsp. *macroglossa* (**e, f**), *S. macroglossa* subsp. *kazachstanica* (**g, h**), *S. kirghisorum* (**i, j**). *h* hook, *l* long cell, *mh* macrohair, *sb* silica body



owing to short prickles. For these reasons, we did not include *S. × tzveleviana* in the numerical analyses.

In the mountains of Central Asia, *Stipa kirghisorum* often co-occurs with *S. macroglossa* and the two taxa have sometimes been misidentified in that region. Within *S. kirghisorum*, specimens with more purple lower part of the awn were distinguished as *S. kirghisorum* var. *violacea* (E.Nikit.) Tzvelev, and recently it was renamed by Tzvelev (2012) as *S. nikitinae* Tzvelev. The main difference between these two taxa is the color of column, which should be pale-green in *S. kirghisorum* and red-purple in *S. nikitinae*. During the revision of herbarium collections and field research, we observed specimens with a pale-green, red-purple, or dark purple awn column occurring frequently even within one population. We also noted that the color of column is influenced by local micro-climatic conditions. Local cooling, and even frosts, causes color changes not only in awns but also in glumes, sheaths or culms. The purple tint is often observed in various species of *Stipa*, such as *S. arabica* Trin. & Rupr., *S. hohenackeriana* Trin. & Rupr., *S. orientalis* and *S. turkestanica*. For this reason, it is hard to believe that specimens of *S. kirghisorum* with red-purple awns merit taxonomic recognition.

Throughout the distribution range of *Stipa kirghisorum*, we observed striking variation in the indument of the leaf adaxial surface as well as in the length of ventral line of hairs on lemma. The adaxial surface can be covered by short hairs (up to 0.1 mm) and/or by mixture of short and long hairs, while ventral line of hairs on lemma may terminate (0.4–)1.4–3.1(–4.6) mm below the top of lemma. Tzvelev (1977) described *Stipa ikonnikovii* from the Pamir Mts, and distinguished it from *S. kirghisorum* by a longer ventral line of hairs on lemma, reaching almost to the top, i.e., terminating (0.3–)0.4–1.2(–1.5) mm below the top, and longer hairs on the adaxial surface of the vegetative leaves. The first taxon is known almost exclusively from the Badakhshan region in the Pamir Mts. However, apart from these characters, the examined specimens of *S. ikonnikovii* do not differ from those of *S. kirghisorum* in any of 25 characters studied. It is worth noting that other taxa from the genus *Stipa* also express significant variability in hairiness of adaxial surface of vegetative leaves. The variation in the indumentum of the adaxial surface of the lamina is given strong weight by some authors, including even the rank of species (e.g., Martinovský 1980), while other authors consider this kind of variation rather of less important (e.g., Freitag 1985; Nobis 2012; Gonzalo et al. 2013; Gudkova et al. 2013). For the time being, we include *S. ikonnikovii* into synonymy of *S. kirghisorum*, but the importance of this character requires further study, including population level.

Taxonomic treatment

Identification key

- 1a. The longest ligules at the vegetative shoots up to 3.7 mm long 2
- 1b. The longest ligules at the vegetative shoots over 4 mm long 3
- 2a. Anthercium (13.1–)14.5–16.0(–17.8) mm long, awn (185–)230–285(–342) mm long, column (0.40–)0.45–0.60(–0.65) mm wide, leaves on vegetative shoots (0.4–)0.5–0.6(–0.7) mm wide, outside distinctly scabrous *S. kirghisorum*
- 2b. Anthercium (10.6–)11.9–13.1(–13.8) mm long, awn (145–)163–196(–225) mm long, column (0.3–)0.35–0.4(–0.5) mm wide, leaves on vegetative shoots (0.30–)0.35–0.45(–0.55) mm wide, outside covered by short hairs and spinules *Stipa turkestanica* subsp. *trichoides*
- 3a. Seta (139–)164–220(–292) mm long, (3.1–)4.0–6.0(–8.6) times longer than column, lower glume (42–)49–64(–76) mm long 4
- 3b. Seta (64–)85–117(–136) mm long, (2.0–)2.3–3.0(–4.1) times longer than column, lower glume (25–)34–41(–51) mm long *Stipa turkestanica* subsp. *turkestanica*
- 4a. Hairs on the adaxial surface of the vegetative leaves more than 0.1 mm long, anthercium (12.2–)13.1–14.5(–16.0) mm long, dorsal line of hairs extending to 1/2 lemma length and terminating (4.3–)5.5–6.8(–9.1) mm below the top *S. macroglossa* subsp. *macroglossa*
- 4b. Hairs on the adaxial surface of the vegetative leaves up to 0.1 mm long, anthercium (11.3–)12.4–13.4(–13.9) mm long, dorsal line of hairs extending to 2/3 lemma length and terminating (3.1–)3.6–4.5(–6.4) mm below the top *S. macroglossa* subsp. *kazachstanica*

Taxonomic synopsis

1. *Stipa turkestanica* Hack., Trudy Imper. S.-Petersb. Bot. Obsch. 26: 59. 1906. Described from: “Schugnan. Dschidak in valle fl. Badamdara, 27. VII. 1904 (B. A. Fedtschenko!)”; —TYPE: “*Stipa turkestanica* Hack., Shugnan: stoyanka Dzhidaka, 27 Iyul 1904, B. A. Fedtschenko s.n.” (holotype: W-Hackel No. 19184!; isotypes: 2 sheets MW!).

1.1. *Stipa turkestanica* subsp. *turkestanica*

Description: Leaves of vegetative shoots: ligules (2.6–)4.5–8.2(–11.5) mm long; blades (0.3–)0.4–0.5(–0.6) mm in diameter, abaxial surface strongly scabrous, adaxial surface

covered by (0.15–)0.2–0.3(–0.35) mm long hairs. Cauline leaves: ligules of middle leaves (1.5–)3–5.5(–7.5) mm long; leaf sheaths smooth to scabrous or shortly hairy scabrous. Glumes subequal, the lower (25–)34–41(–51) mm long, the upper (22–)31–39(–49) mm long. Antherium (9.5–)10.8–12.1(–13.5) mm long. Callus (1.4–)1.8–2.1(–2.5) mm long, with hairs on the ventral part (1.0–)1.2–1.6(–1.9) mm long and on dorsal part (0.7–)0.9–1.1(–1.3) mm long; peripheral ring of the callus base (0.6–)0.7–0.8(–1.0) mm long and (0.25–)0.3–0.35(–0.4) mm wide. Lemma with hairs (0.4–)0.5–0.7(–0.8) mm long on ventral part and (0.3–)0.5–0.8(–0.9) on dorsal part, arranged in 7 lines; ventral line of hairs terminating (1.2–)1.8–2.6(–4.1) mm below the top of lemma, dorsal line terminating (2.1–)3.1–4.2(–5.6) mm below the top. Awn (88–)118–158(–184) mm long; lower segment of column green, (14–)21–27(–34) mm long and (0.3–)0.35–0.4(–0.45) mm wide near the base, scabrous or rarely glabrous or almost so; upper segment of column (8–)11–16(–19) mm long, seta (64–)85–117(–136) mm long and (2.9–)3.7–4.9(–6.5) times longer than the lower segment of column, hairs on seta (2.3–)3.5–4.5(–5.5) mm long.

Habitat: Stony high mountain steppes, grasslands, screes and scrubs, mainly at exposures of SW-NW rarely S-SE or N-E and at altitudes of (1800–)2200–3500(–4060) m.

Distribution: Central-southwestern Asia: the Pamir, Hindu Kush, southern Karakorum, western Himalaya and Elburs Mts, in Tajikistan, Afghanistan, eastern Pakistan, northern India and Iran.

1.2. *Stipa turkestanica* subsp. *trichoides* (P.A.Smirn.) Tzvelev, Nov. Syst. Vyssh. Rast. 11: 17. 1974. ≡ *Stipa trichoides* P.A.Smirn., Repert. Spec. Nov. Regni Veg.: 21: 233. 1925. Described from: “Turkomania. Prope Ashabad, in m. Ludsha, 6500 pd. alt. lg. D. Litwinow.—Fergana. I. Alaicum, Langar, lg. B. Fedtschenko”; —TYPE: “Turkomania. Pr. Ashabad. In m. Ludsha, 6500, 9. VII 1898, D. Litwinow 2222” (lectotype **designated here**: LE!; isolecotypes: 3 sheets LE!, 1 sheet MW!).

Description: Leaves of vegetative shoots: ligules (0.5–)1.6–2.8(–3.7) mm long; blades (0.30–)0.35–0.45(–0.55) mm in diameter, outer surface scabrous covered by short hairs and spinules, adaxial surface of blades covered by (0.15–)0.17–0.25(–0.30) mm long hairs. Cauline leaves: ligules of middle leaves (0.5–)1.0–2.1(–4.1) mm long; leaf sheaths scabrous to shortly hairy scabrous. Glumes subequal, the lower (29–)34–41(–45) mm long, the upper (26–)32–38(–43) mm long. Antherium (10.6–)11.9–13.1(–13.8) mm long. Callus (1.8–)2.1–2.5(–2.9) mm long, with hairs on the ventral part (1.0–)1.2–1.6(–1.8) mm long and on dorsal part (0.6–)0.8–1.1(–1.3) mm long; peripheral ring of the callus base (0.6–)0.7–0.9(–1.0) mm long and (0.25–)0.30–0.35(–0.40) mm wide. Lemma with hairs (0.4–)

0.6–0.8(–1.0) mm long on ventral part and (0.4–)0.5–0.7(–0.8) on dorsal part, arranged in 7 lines; ventral line of hairs terminating (1.1–)2.0–3.0(–4.3) mm below the top of lemma, dorsal line terminating (2.9–)3.8–4.7(–6.2) mm below the top. Awn (145–)163–196(–225) mm long; lower segment of column green or rarely light-red, (18–)32–43(–54) mm long and (0.30–)0.35–0.40(–0.50) mm wide near the base, smooth; upper segment of column (8–)13–18(–22) mm long, seta (82–)116–138(–170) mm long and (1.5–)2.9–4.0(–6.1) times longer than the lower segment of column, hairs on seta (3.2–)3.9–5.3(–6.0) mm long.

Habitat: Stony mountain steppes, steppe grasslands and screes, mainly at exposures of NW-SW-S rarely at SE-NE, at altitudes of (1840–)2200–2600(–2900) m.

Distribution: Central Asia: the western Pamir Alai, western Tian-Shan and Kopet Dagh Mts, in Tajikistan, Kyrgyzstan, Uzbekistan, Afghanistan, Turkmenistan and northern Iran.

Notes: The original description of *Stipa trichoides* is based on D. Litvinov’s and B. Fedtschenko’s collections, without designation of the type (Smirnov 1925). Tzvelev (1976) treated one of the sheets with specimens of *S. trichoides* collected by D. Litvinov as a type (= holotype), and the other three as isotypes; however, we still do not know which sheet was treated as a holotype. Therefore, a lectotype, the specimen from the Litvinov’s collection selected and labeled by M. Nobis is designated here.

2. *Stipa macroglossa* P.A.Smirn., Bot. Mat. Gerb. Glavn. Bot. Sada RSFSR 5: 47. 1924. Described from: “Prov. Turgai. Mujun-kumy, ad fl. Ssary-ssu, H. Krascheninnikov”; —TYPE: “Turgaiskaya obl. i u. Kizil-dzhingilskaya volost, R. Sary-su v svoikh nizovyakh, Okrestnosti Muyun-kumov, Obnazhenie tretichnykh peschanikov, 1914.VI.01, H. Krascheninnikov 5203” (lectotype: LE!, selected by M. Nobis in Nobis et al. (2014a); isolecotypes: 3 sheets LE!).

2.1. *Stipa macroglossa* subsp. *macroglossa* ≡ *Stipa turkestanica* subsp. *macroglossa* (P.A.Smirn.) R.Gonzalo, Syst. Bot. 38: 370. 2013.

Description: Leaves of vegetative shoots: ligules (2.6–)4.5–7.8(–10.3) mm long; blades (0.35–)0.40–0.55(–0.70) mm in diameter, outer surface scabrous, adaxial surface of blades covered by hairs (0.15–)0.2–0.3(–0.4) mm long. Cauline leaves: ligules of middle leaves (1.0–)2.0–4.3(–6.5) mm long; leaf sheaths scabrous to shortly hairy scabrous. Glumes subequal, the lower (48–)56–64(–76) mm long, the upper (45–)53–62(–73) mm long. Antherium (12.2–)13.1–14.5(–16.0) mm long. Callus (1.7–)2.1–2.5(–3.0) mm long, with hairs on the ventral part (1.1–)1.4–1.7(–2.1) mm long and on dorsal part (0.5–)0.7–1.0(–1.2) mm long; peripheral ring of the callus base (0.9–)

1.0–1.1(–1.2) mm long and (0.35–)0.4–0.45(–0.5) mm wide. Lemma with hairs (0.3–)0.5–0.7(–1.0) mm long on ventral part and (0.4–)0.5–0.7(–1.0) on dorsal part, arranged in 7 lines; ventral line of hairs terminating (2.0–)3.1–3.8(–5.4) mm below the top of lemma, dorsal line terminating (4.3–)5.5–6.8(–9.1) mm below the top. Awn (175–)210–270(–337) mm long; lower segment of column green, (14–)21–27(–35) mm long and (0.4–)0.5–0.6(–0.7) mm wide near the base, smooth, upper segment of the column (9–)12–16(–19) mm long, seta (139–)174–220(–292) mm long and (5.3–)7.2–9.5(–15.1) times longer than the lower segment of column, hairs on seta (3.3–)4.2–5.5(–6.7) mm long.

2.1.2. *Stipa macroglossa* subsp. *macroglossa* var. *macroglossa*

Description: Cauline leaf sheaths slightly scabrous or scabrous. Awn (175–)210–258(–291) mm long, seta (139–)174–214(–247) mm long.

Habitat: Stony mountain steppes, steppe grasslands and screes, mainly at exposures of S–W, S or W rarely N–E or E and at altitudes of (1100–)1750–2400(–2800) m.

Distribution: Central Asia: the western Pamir Alai and western Tian-Shan Mts, in western Tajikistan, Kyrgyzstan, eastern Uzbekistan and southern Kazakhstan.

2.1.2. *Stipa macroglossa* subsp. *macroglossa* var. *pubescens* (P.A.Smirn.) M.Nobis, **comb. nov.** \equiv *Stipa macroglossa* f. *pubescens* P.A.Smirn., Bot. Mat. Gerb. Glavn. Bot. Sada RSFSR 5: 48, 1924. Described from: “Semirechinskaya obl., Przhevalskii u. Ur. Toguz-torau, terrasy prav. stor. r. Kugart. 9. VI. 1913. izr. pl. V. Sapozhnikov; Ur. Toguz-torau, R. Ataika vyshe s., vysokaya terrasa prav. stor. step. 6. VI. 1913. izr. pl. V. Sapozhnikov”; —TYPE: “Semirech. obl., Przhev. u. “Ur. Toguz-torau, terrasy prav. stor. r. Kugart., 9. iyunya 1913, V. Sapozhnikov 35” (lectotype **designated here:** LE!; isolectotype: LE!).

Description: Cauline leaf sheaths pubescent. Awn 248–315(–337) mm long, seta (210–)214–265(–292) mm long.

Habitat: Stony high mountain steppes, mainly at exposures of S–SW and at an altitude of ca. 2000 m.

Distribution: Central Asia: the western Pamir Alai and northern Tian-Shan Mts, in Tajikistan and Kazakhstan.

Notes: The original description of *Stipa macroglossa* f. *pubescens* (Smirnov 1924) is based on two Sapozhnikov’s collections from June 6th and 9th 1913. A year later, Smirnov (1925) referred to the collection gathered on June 9th (original: Prov. Semireczje. Distr. Prshewalsk, ad fl. Kurgat, lg. W. Saposhnikow) as the type but it consists of two sheets. Smirnov attached his revision label, ‘*Stipa macroglossa* m. f. *pubescens* m., 1924. I. det. P. A. Smirnow’, to both of them. The specimen on the sheet that contains two labels, one above the other, is designated here as the lectotype.

2.2. *Stipa macroglossa* subsp. *kazachstanica* (Kotukhov) M.Nobis, Plant Syst. Evol. 299: 1352. 2013. \equiv *Stipa kazachstanica* Kotukhov, Bot. Zhurn. 79: 104. 1994. Described from: “Saur-Tarbagatai, praemontia australi-occidentalia jugi Manrak, locus Sarybulak, clivulus schistosus australi-orientalis, 12 VI 1992, Yu. Kotukhov (LE)”; —TYPE: “*Stipa kazachstanica* Kotukhov (sect. *Stipa*), Saur = Tarbagatai, yugo-zap. peredgore khr. Manrak, uro-chishche Sarybulak, yugo-ost. shchebnistyi mikrosklon, 12 VI 1992, Yu. Kotukhov s.n.” (holotype: LE!; isotype: LE!).

Description: Leaves of vegetative shoots: ligules (2.9–)4.0–6.5(–8.5) mm long; blades (0.4–)0.5–0.6 mm in diameter, outer surface more or less scabrous, adaxial surface of blades covered by shorter than 0.1 mm long hairs. Cauline leaves: ligules of middle leaves (1.1–)2.3–4.0(–5.6) mm long; leaf sheaths scabrous to shortly hairy scabrous. Glumes subequal, the lower (42–)49–57(–61) mm long, the upper (40–)48–55(–59) mm long. Anthercium (11.3–)12.4–13.4(–13.9) mm long. Callus (2.2–)2.6–3.0(–3.4) mm long, with hairs on the ventral part (1.1–)1.5–1.9(–2.2) mm long and on dorsal part (0.7–)1.0–1.3(–1.4) mm long; peripheral ring of the callus base (0.8–)1.0(–1.2) mm long and 0.35–0.40(–0.45) mm wide. Lemma with hairs 0.5–0.7(–0.8) mm long on ventral part and (0.5–)0.7–0.8(–1.0) on dorsal part, arranged in 7 lines; ventral line of hairs terminating (2.0–)2.2–3.0(–3.8) mm below the top of lemma, dorsal line terminating (3.1–)3.6–4.5(–6.4) mm below the top. Awn (179–)205–234(–256) mm long; lower segment of column green, (20–)25–34(–40) mm long and (0.35–)0.5–0.6(–0.7) mm wide near the base, smooth, rarely very slightly scabrous; upper segment of column (8–)13–16(–18) mm long, seta (140–)164–191(–210) mm long and (4.0–)5.2–7.3(–10.0) times longer than the lower segment of column, hairs on seta (3.8–)4.5–5.5(–6.7) mm long.

Habitat: Stony mountain steppes, steppe grasslands and screes, mainly at exposures of S–W, N–NE–E and at altitudes of (1200–)1250–1750(–2000) m.

Distribution: Central Asia: the southern Altai, Tarbagatai and Tian-Shan Mts, in eastern Kyrgyzstan, eastern Kazakhstan and western China.

3. *Stipa kirghisorum* P.A.Smirn., Repert. Spec. Nov. Regni Veg. 21: 232–233. 1925. Described from: “Prov. Semipalatinsk, m. Bokaj lg. Kossinsky (typus!)”; —TYPE: “Semipalatinskaya obl., Bokai, sobral Kossinskii” (holotype MW!); “Semipalatinskaya obl., Semipalatinskii uezd, Chingiz, zapadnaya chast’ gory Karagian-koi-tas, krytoi kamenistyi sklon gory, 1 Jul 1914, C. Kossinsky 607” (epitype **designated here:** LE!).

\equiv *S. pennata* subsp. *kirghisorum* (P.A.Smirn.) Freitag, Notes: Roy. Bot. Gard. Edinburgh 42: 438. 1985.

= *Stipa nikitinae* Tzvelev, Novosti Sist. Vyssh. Rast. 43: 27. 2012. Described from: “Tsentr. Tian-Shan, sev. sklon khr. Kavyk-tau, pereval mezhd u Beiryuk i Kash-bel, 27 VII 1937 [sic!], no. 66, E. Mikhailova, L. Popova (LE)”. —TYPE: “Tsentralnyi Tian-shan, severnyi sklon khr. Kavak-tau, pereval mezhd u Beiryuk i Kash-bel, 1937.VII.28 [sic!], E. Mikhailova and L. Popova N. 66” (holotype: LE!).

≡ *Stipa violacea* E. Nikit., Tr. Biol. Inst. Kirg. Fil. AN SSSR 2: 68, 1947, nom. illeg.

≡ *S. kirghisorum* var. *violacea* Tzvelev, Novosti Sist. Vyssh. Rast.: 11: 18, 1974.

? = *Stipa ikonnikovii* Tzvelev, Spisok Rast. Gerb. Fl. S.S.S.R. Bot. Inst. Vsesoyuzn. Akad. Nauk 21: 49. 1977. —TYPE [citation and label]: “Badachshan, ad ripam dextram fl. Gunt, Czartym, in lapidosis, 5 VIII 1957, S. Ikonnikov, [G. Ladygina, L. Sidorov]” (holotype: LE!; isotypes: B!, JE!, MW!, TK!, KRAM!).

Description: Leaves of vegetative shoots: ligules (0.3–)0.7–1.6(–3.0) mm long; blades (0.4–)0.5–0.6(–0.7) mm in diameter, outer surface scabrous to strongly scabrous, adaxial surface of blades covered by shorter than 0.1 mm long hairs, sometimes with admixture of 0.2–0.5 mm long hairs, rarely covered by up to 0.3 mm long hairs. Cauline leaves: ligules of middle leaves (0.4–)1.5–3.6(–5.9) mm long; leaf sheaths scabrous to hairy scabrous. Glumes subequal, the lower (37–)46–55(–68) mm long, the upper (35–)44–53(–65) mm long. Anthecium (13.1–)14.5–16.0(–17.8) mm long. Callus (2.3–)2.7–3.2(–3.8) mm long, with hairs on the ventral part (1.5–)1.8–2.3(–2.7) mm long and on dorsal part (0.8–)1.1–1.6(–1.8) mm long; peripheral ring of the callus base (0.6–)0.8–0.9(–1.0) mm long and (0.3–)0.35–0.40(–0.45) mm wide. Lemma with hairs (0.4–)0.5–0.7(–1.0) mm long on ventral part and (0.4–)0.6–0.8(–1.1) on the dorsal, arranged in 7 lines; ventral line of hairs terminating (0.5–)1.4–3.1(–4.6) mm below the top of lemma, dorsal line terminating (2.5–)4.3–5.6(–6.6) mm below the top. Awn (185–)230–285(–342) mm long; lower segment of column green, light-red or red-purple, (27–)44–56(–71) mm long and (0.40–)0.45–0.60(–0.65) mm wide near the base, smooth; upper segment of column (12–)16–20(–25) mm long, seta (137–)162–210(–279) mm long and (2.0–)3.1–4.5(–6.3) times longer than the lower segment of column, hairs on seta (2.9–)3.6–4.8(–6.5) mm long.

Habitat: Stony mountain steppes, grasslands, screes, herb communities and scrubs often on calcareous rock, with different exposure, at altitudes of (900–)2000–3200(–4700) m.

Distribution: Widely distributed in Central Asia and Southern Siberia: southern parts of Asiatic Russia, Kazakhstan, Mongolia, western China, Kyrgyzstan, Uzbekistan, Tajikistan, Afghanistan, Pakistan and northern India.

Notes: The original material (holotype) of *Stipa kirghisorum* at MW is a fragmentary specimen, consisting of four awns with anthercia and few leaves of the vegetative shoots. The label of the holotype was partially preprinted from the original Kossinsky’s labels for plants collected during his expedition in Semipalatinsk province in 1914 (plants material is preserved in LE! and TK!). There is also a significant difference in the text on the label in MW and in LE and TK, and, what is more important, on any of four sheets from original Kossinsky’s collection, there is no a name ‘m. Bokaj’ as it is in protologue. Whereas on two labels (in LE and TK), there is the name Togai lake. In the original diagnosis of the species, there is also very general reference to the type of *S. kirghisorum*, without date and number of collection. On Smirnov’s revision label attached to the holotype at MW (*Stipa kirghisorum* m. 1924.I, det. P.A. Smirnov.), there is also his handwritten note, “Semipalatinskaya obl.” [oblast]. Thus, the holotype at MW is a small part of a collection taken possibly from a sheet preserved at LE. Because the holotype is not complete, a safe determination of the species is insufficient; therefore, a complete specimen from Kossinsky’s collection and labeled by P.A. Smirnov as *n. sp.* on 18 January 1924 is designated here as the epitype.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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