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## Taxonomic Revision of the Eurasian *Stipa* Subsections *Stipa* and *Tirsae* (Poaceae)

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**Abstract**—A comprehensive taxonomic revision of *Stipa* subsects. *Stipa* and *Tirsae* is presented. We analyzed the pattern of morphological variation of the taxa included in both subsections through the study of 1353 vouchers from 27 herbaria. Variation in floral and leaf morphology was further explored to reevaluate taxon limits in 165 specimens using univariate analyses (Anova, Tukey test and,  $\chi^2$  test), and multivariate tests (principal components analysis and discriminant analysis). We found that one species of subsect. *Tirsae* plus three species and five subspecies of subsect. *Stipa* can be distinguished based on morphological characters. For each taxon, we present a dichotomous key, a list of synonyms, detailed morphometric descriptions, illustrations, and distribution maps. In addition, neotypes are proposed for *S. pulcherrima* var. *mollis* (subsection *Stipa*) and *S. aperta* (subsection *Stipa*), and a lectotype is proposed for *S. cerariorum* (subsection *Tirsae*). Likewise, two new combinations are proposed: *Stipa* subsection *Tirsae* (Martinovský) R. Gonzalo, and *Stipa turkestanica* subspecies *macroglossa* (P.A Smirn.) R. Gonzalo.

**Keywords**—Asia, Europe, multivariate analyses, *Stipa pennata*, *Stipa tirsae*, taxonomy.

The Poaceae is among the largest plant families of angiosperms, including around 800 genera and 11,000–13,000 species (Soreng et al. 2007), distributed in 12 subfamilies and 42 tribes (Barker et al. 2001). Of the 12 subfamilies currently recognized, the *Pooideae*, with ca. 3,300 species is one of the largest and most important economically (Barker et al. 2001). Indeed, important crops such as barley (*Hordeum vulgare*), rye (*Secale cereale*), and oats (*Avena sativa*) are all members of the *Pooideae* (Barker et al. 2001). This subfamily includes 13 tribes (Barker et al. 2001), of which *Stipeae* represents a basal lineage group, whose origin is placed after the separation of *Brachyelytreae*. Ohwi, *Lygeae* J. Presl, and *Nardeae* W.D.J. Koch (Barker et al. 2001; Davis and Soreng 2007; Soreng et al. 2007). *Stipeae* grasses are important components of the vegetation and often the dominant grass of xeric habitats from lowlands up to the alpine belt (Freitag 1985). These grasses have traditionally been employed in the production of paper (*S. tenacissima* L.), but are especially important and appreciated as pasture plants for their high regeneration ability, resistance against grazing, and nutritional properties. Tribe *Stipeae* is a well-defined monophyletic group (Peñailillo 1996; Hsiao et al. 1999; Jacobs et al. 2000, 2007), with approximately 21 genera (Romaschenko et al. 2010) and 400–600 species, distributed in all continents, except for Antarctica (Barkworth et al. 2008; Romaschenko et al. 2007, 2010; Cialdella et al. 2010). The tribe is characterized by a single-flowered spikelet, glumes equalling or longer than the lemma, an apical awn, and two or three lodicules (Clayton and Renvoize 1986). In addition, small chromosomes with a base number of  $X = 10-12$  are also diagnostic (Tzvelev 1976; Freitag 1985; Romaschenko et al. 2007, 2010).

Even though the limits of tribe *Stipeae* are well defined, the circumscription of genera within this tribe has been controversial during the past decades. The major area of uncertainty is associated with the circumscription of *Stipa* (Jacobs et al. 2007). Traditionally, the genus has been broadly circumscribed (Spegazzini 1901, 1925; Hitchcock 1925, 1951), encompassing most of the currently accepted genera in the tribe, except for *Oryzopsis* Michx., *Piptochaetium* J. Presl, *Nassella* E. Desv. and *Aciachne* Benth. This traditional circumscription included ca. 300–400 species of temperate and subtropical regions in both hemispheres (Clayton and Renvoize 1986; Tzvelev 1976; Bor

1970; Cope 1982; Moraldo 1986; Freitag 1985; Watson and Dallwitz 1992). However, recent morphological, anatomical and molecular studies have substantially changed generic boundaries in the tribe (Peñailillo 1996; Jacobs and Everett 1996; Vázquez and Barkworth 2004; Barkworth et al. 2008; Romaschenko et al. 2007, 2010; Cialdella et al. 2010). In particular, the circumscription of *Nassella* has been significantly expanded, and the genus now includes ca. 116 species, representing the second largest genus in the tribe (Barkworth et al. 2008). In addition, older genera have been resurrected (*Jarava* Ruiz and Pav., *Macrochloa* Kunth), and new ones have been described, such as *Hesperostipa* (M. K. 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.

The current circumscription of *Stipa* includes approximately 140 species (Barkworth et al. 2008) geographically confined to Asia, Europe and North Africa (Romaschenko et al. 2007; Barkworth et al. 2008). Under this circumscription, the genus is characterized by 1-flowered spikelets, and anthecia that are disarticulated above the glumes, leaving a sharp-pointed callus attached at its base. The lemma is often very long and narrow, terete, indurate, and strongly convolute, terminating in a prominent awn. The callus, lemma and palea are known as antheicum. The awn is unigeniculate or bigeniculate and usually twisted below the first bend. The portion below the bend is referred to as the column, while the portion above the bend is referred to as the seta.

*Stipa* includes some of the most complicated taxonomic problems in Poaceae, with species often exhibiting great plasticity in morphological characters. The lack of stable morphological structures and the difficulty in establishing clear morphological boundaries between taxa, has resulted in complicated infrageneric classifications, with the creation of a high number of taxa at the specific and infraspecific ranks (Smirnow 1925, 1926, 1928, 1929, 1938, 1970; Martinovský 1982; Klokov and Osychnyuk 1976; Moraldo 1986; Vázquez and Gutiérrez 2011). These problems have been extensively noted in the literature (Tzvelev 1974, 1976; Scholz 1985; Freitag 1985; Strid 1991).

The infrageneric classification of *Stipa* suffered many changes during its taxonomic history. Dumortier (1823) was

the first author to provide an infrageneric classification, with two sections based on awn features: (1) sect. *Eriostipa* Dumort., with “*Arista plumosa vel pubescent*,” including *S. pennata* L.; and (2) sect. *Leiostipa* Dumort., with “*Arista glabra*,” including *S. capillata* L. Most European and Asian species were subsequently included in sect. *Eustipa* Trin. & Rupr. (Endlicher 1836–1841; Steudel 1854). The first comprehensive infrageneric classification of *Stipa* was published by Roshevitz (1934), who recognized seven series based on awn morphology: (1) ser. *Pennatae* Roshev: including all species with glabrous or scabrous column and a plumose seta, including *S. pennata*, the type species of the genus; (2) ser. *Sibiricae* Roshev, with pointed glumes, shorter lemma than glumes, and short awns (<2 cm); (3) ser. *Brevigeniculatae* Roshev, with unigeniculate awns, and columns that are 1/10–1/8 as long as the setas; (4) ser. *Barbatae* Roshev, with awns that are hairy all along its length; (5) ser. *Tortiles* Roshev, with hairy columns and glabrous or scabrous setas; (6) ser. *Pseudocapillatae* Roshev, with hairy columns, hairs up to 7 mm long, and scabrous or shortly hairy setas; and (7) ser. *Capillatae* Roshev, with awns that are scabrous at the edges. Roshevitz’s classification has been the starting point of all subsequent taxonomic studies in the genus.

During the second half of the last century, many researchers tried to clarify the infrageneric taxonomy of *Stipa* (Bor 1970; Tzvelev 1974, 1976; Martinovský 1977, 1982; Moraldo 1986; Vázquez and Gutiérrez 2011; see Table 1). However, the taxonomic placement of the individual species and the limits of the sections have remained problematic. For example, sections *Aristella* (Trin.) Hackel and *Lasigrostis* (Link) Hackel are currently included under *Achnatherum* P. Beauv. (Tzvelev 1976), whereas section *Orthoraphium* (Nees) Hackel and ser. *Gigantea* Martinovský are retained at generic rank (Tzvelev 2000; Wu and Phillips 2006; Vázquez and Barkworth 2004). *Stipa gaubae* Bor has been indistinctly placed under section *Barbatae* A. Junge (Freitag 1985, under section *Smirnovia* Tzvelev (Vázquez and Gutiérrez 2011), or in its own section, *Subsmirnovia* Tzvelev (Tzvelev 1993; Gonzalo et al. 2011). Species with completely pilose awns are included in sect. *Barbatae* (Klokov and Osychnyuk 1976; Tzvelev 1976), or in sect. *Stipa* of ser. *Barbatae* (Bor 1970; Moraldo 1986).

The current circumscription of the type section *Stipa* sect. *Stipa*, includes approximately 60 species from North Africa, Europe and Asia (Vázquez and Gutiérrez 2011), that are characterized by a caespitose habit, long acuminate glumes, terete lemmas with longitudinal rows of hairs, bigeniculate awns, glabrous or minutely scabrous (rarely hairy) columns, plumose setas with hairs longer than (3-)4 mm long, and ovary with 2 styles (Tzvelev 1976; Vázquez and Devesa 1996).

The various taxonomic treatments of the European taxa made by Martinovský (1966, 1967, 1970, 1976, 1977, 1980, and 1982) have remained as landmarks in the taxonomic history of *Stipa* sect. *Stipa*. Martinovský described several new taxa and divided *Stipa* sect. *Stipa* into five series and five subseries (Table 1), a concept followed and extended by other European taxonomists (Klokov and Osychnyuk 1976; Moraldo 1986; Vázquez and Gutiérrez 2011). Series *Lessingiana* Martinovský includes the widespread *S. lessingiana* Trin. & Rupr., characterized by a completely pubescent lemma and short ligules in the basal leaves. This taxon is currently separated in the monotypic sect. *Subbarbatae* Tzvelev. series *Pulcherrimae* Martinovský by the lack of a dorsal row of the lemma or a lemma that is shorter than the subdorsal row

TABLE 1. Infrageneric classification of *Stipa* s.s. In bold the infrageneric groups currently included in Sect. *Stipa* s.s.

ROSEHITZ (1934), Former USSR only	BOR (1970), Iran only	TZVELEV (1974, 1976, 1993), former USSR and Caucasus only	MARTINOVSKÝ (1966, 1967, 1970, 1976), Europe only	FEITAG (1985), S and SW Asia only	KLOKOV AND OSYCHNYUK (1976), Ukraine only	MORALDO (1986), Italy only	VÁZQUEZ AND GUTIÉRREZ (2011), seta plumose species only
<b>Sect. Stipa</b>	<b>Sect. Stipa</b>	<b>Sect. Stipa</b>	<b>Sect. Stipa</b>	<b>Sect. Stipa</b>	<b>Sect. Stipa</b>	<b>Sect. Stipa</b>	<b>Sect. Stipa</b>
Ser. <i>Sibiricae</i>	Ser. <i>Inaequiglumis</i>	Sect. <i>Subbarbatae</i>	Ser. <i>Pulcherrimae</i>	Sect. <i>Aristella</i>	Ser. <i>Dasyphyllae</i>	Ser. <i>Pulcherrima</i>	Ser. <i>Stipa</i>
Ser. <i>Brevigeniculatae</i>	Ser. <i>Sibiricae</i>	Sect. <i>Achnatheropsis</i>	Ser. <i>Subser. Ericanalis</i>	Sect. <i>Orthoraphium</i>	Ser. <i>Atlanticae</i>	Ser. <i>Eriocaulis</i>	Ser. <i>Stipa</i>
Ser. <i>Barbatae</i>	Ser. <i>Brevigeniculatae</i>	Sect. <i>Barbatae</i>	Sect. <i>Subser. Atlanticae</i>	Sect. <i>Ptilagrostis</i>	Ser. <i>Eriocaulis</i>	Ser. <i>Subser. Atlanticae</i>	Ser. <i>Stipa</i>
Ser. <i>Tortiles</i>	Ser. <i>Barbatae</i>	Sect. <i>Leiostipa</i>	Sect. <i>Subser. Epilosae</i>	Sect. <i>Achnatheropsis</i>	Ser. <i>Pulcherrimae</i>	Ser. <i>Epilosae</i>	Ser. <i>Stipa</i>
Ser. <i>Capillatae</i>	Ser. <i>Penninatae</i>	Sect. <i>Pseudoptilagrostis</i>	Sect. <i>Subser. Syreschtschikovianae</i>	Sect. <i>Pseudoptilagrostis</i>	Ser. <i>Poëticae</i>	Ser. <i>Siculae</i>	Ser. <i>Stipa</i>
Ser. <i>Pseudocapillatae</i>	Ser. <i>Capillatae</i>	Sect. <i>Regelia</i>	Sect. <i>Subser. Tirsae</i>	Sect. <i>Stipella</i>	Ser. <i>Rubentes</i>	Ser. <i>Barbitae</i>	Ser. <i>Stipa</i>
	Ser. <i>Capillatae</i>	Sect. <i>Smirnovia</i>	Ser. <i>Subser. Dasyphyllae</i>	Sect. <i>Lasiogrostis</i>	Ser. <i>Peniticlerae</i>	Ser. <i>Tirsae</i>	Ser. <i>Stipa</i>
	Ser. <i>Pseudocapillatae</i>	Sect. <i>Stipella</i>	Ser. <i>Subser. Peniticlerae</i>	Sect. <i>Barbitae</i>	Ser. <i>Stenophyllae</i>	Sect. <i>Subser. Syreschtschikovianae</i>	Ser. <i>Stipa</i>
	Sect. <i>Lasigrostis</i>	Sect. <i>Smirnovia</i>	Ser. <i>Subser. Peniticlerae</i>	Ser. <i>Barbitae</i>	Sect. <i>Parastipa</i>	Ser. <i>Leiostipa</i>	Ser. <i>Stipa</i>
	Sect. <i>Ptilagrostis</i>	Sect. <i>Stipella</i>	Ser. <i>Subser. Peniticlerae</i>	Ser. <i>Barbitae</i>	Ser. <i>Paradoxa</i>	Ser. <i>Capillatae</i>	Ser. <i>Stipa</i>
			Ser. <i>Subser. Lessingiana</i>	Ser. <i>Barbitae</i>	Ser. <i>Anomalae</i>	Ser. <i>Bromoides</i>	Ser. <i>Stipa</i>
			Sect. <i>Leiostipa</i>	Ser. <i>Barbitae</i>	Sect. <i>Leiostipa</i>	Ser. <i>Capenses</i>	Ser. <i>Stipa</i>
			Ser. <i>Lessingiana</i>	Ser. <i>Barbitae</i>	Sect. <i>Barbitae</i>	Ser. <i>Gigantae</i>	Ser. <i>Stipa</i>

(rarely slightly shorter), in combination with the ventral row of hairs reaching the top (rarely ending 1–2 mm below the apex). Martinovský (1966, 1967, 1977) divided series *Pulcherrimae* into 4 subseries: (1) subseries *Syresitschikovianae* Martinovský; (2) subseries *Atlanticae* (pubescent); (3) subseries *Epilosae* (scabrous, tuberculate or papillose); and, (4) subseries *Eriocaulis* (scabrous ribs and shortly pubescent furrows). While subseries *Syresitschikovianae* Martinovský includes the species with hairy columns, the other remaining three subseries are distinguished by the ornamentation of the adaxial surface of the basal leaf. Series *Dasyphyllae* Martinovský only differs from series *Pulcherrima* in the pubescent abaxial surface of the basal leaf.

Series *Penicelliferae* (subsect. *Stipa*) and series *Tirsae* (subsect. *Tirsae*), reviewed in this paper, include plants native to the temperate zones of Europe, Asia and Caucasus that are characterized by having the ventral row of hairs ending 2–5 mm below the lemma apex, and the dorsal row quite longer than the subdorsal ones. Martinovský (1976) recognized three species for series *Penicelliferae*: *S. joannis* Céla. (type), *S. borysthennica* Klokov ex Prokud., and *S. styriaca* Martinovský. Currently, *S. joannis* is considered a synonym of *S. pennata* (Tzvelev 1976; Connert 1982; Vázquez and Devesa 1996), the type species of the genus (Hitchcock 1925). As a result, ser. *Penicelliferae* is treated as a synonymy of subsect. *Stipa*. Sub-section *Stipa*, the type subsection, is also characterized by an apical tassel of hairs at the apex of the basal leaves, although this trait is sometimes absent (e.g. *S. kirghisorum*, *S. pennata* subsp. *sabulosa*). *Stipa pennata* subsp. *pennata* and *Stipa pennata* subsp. *sabulosa*, and two additional species from Asia (*S. kirghisorum* P.A. Smirn. and *S. turkestanica* Hack.), clearly fit within subsect. *Stipa*. On the other hand, series *Tirsae* only includes *S. tirsae* Steven, a species that is closely related and morphologically very similar to *S. pennata*. However, *S. tirsae* clearly differs in the ligule length, the basal leaf apex and the ornamentation of the abaxial leaf surface. We consider these features sufficient for the recognition of subsect. *Tirsae*.

Even though *Stipa* sect. *Stipa* has been profusely studied (Smirnow 1925; Klokov and Osychnyuk 1976; Tzvelev 1976; Martinovský 1982; Moraldo 1986), these revisions only cover particular geographical areas of the section. In addition, the species level taxonomy of the group remains confusing, with complicated species limits (*S. capillata*, *S. arabica* Trin. & Rupr., *S. capensis*). The present study includes a taxonomic revision of members of subsect. *Stipa* and *Tirsae*, as part of a comprehensive treatment of *Stipa* sect. *Stipa*. Specifically, our study aims to (i) reevaluate the status of individual species in the tribe through the examination of herbarium specimens from the whole area of distribution of representatives of the group; (ii) conduct a broad analysis of the morphological traits used to support the taxonomic circumscription of individual taxa; and (iii) supply detailed maps and illustrations for each taxon. Seven taxa are recognized: three species and three subspecies for subsect. *Stipa*, plus one species for sect. *Tirsae*.

#### MATERIALS AND METHODS

**Morphological Sampling and Characters**—The current revision is based on the study of 1,353 herbarium specimens of *Stipa* subsections *Stipa* and *Tirsae* (Appendix 1) from the following herbaria: B, BR, C, COI, E, FI, G, GH, GOET, H, HBG, JE, K, L, LD, LE, M, MA, MEL, NY, PR, S, U, UPS, W, WAG, and WU.

For the morphometric analyses, 165 specimens were used as operational taxonomic units (OTUs), selected to represent as far as possible,

the entire geographical range and the morphological variability within each taxon. Specimens were distributed as follows: *S. pennata* subsp. *pennata* (37); *S. pennata* subsp. *sabulosa* (26); *S. kirghisorum* (27); *S. tirsae* (25); *S. turkestanica* subsp. *turkestanica* (18); *S. turkestanica* subsp. *trichoides* (15); *S. turkestanica* subsp. *macroglossa* (17).

Initially, 68 morphological characters were recorded, including those previously used in the taxonomy of *Stipa* (Roshevitz 1934; Tzvelev 1976; Martinovský 1980; Freitag 1985; Vázquez and Devesa 1996; Gonzalo et al. 2011), as well as others used in the taxonomy of grasses. Species from both of these sections have cleistogamous spikelets; therefore, the size of the structures enclosed by the floret was determined by the size of the lemma. Characters with missing data and those that were either constant or too variable were excluded, reducing the number of characters analyzed to 33 (Appendix 2). Of these, 17 were quantitative, 4 were ratio derivate, and 12 were qualitative; characters were scored as binary or multistate (Table 2).

**Numerical and Statistical Analyses**—Quantitative characters were analyzed by mean value, range, standard deviation and significance using the SPSS 17.0 statistical package for Windows (SPSS Inc., Chicago, Illinois). Prior to the statistical analyses, every pair of characters in the dataset was subjected either to either a Pearson or a Kendall's Tau correlation depending on their quantitative or qualitative status (Molina et al. 2008). Variables with high correlation ( $> 0.75$ ) were eliminated to avoid redundant information. Quantitative data were also subjected to a Shapiro-Wilk test for normality and to the Levene test of homogeneity. Non-normal data and data with heterogeneous variance were standardized and Log 10 transformed, to meet the assumption of normality required.

A principal component analysis (PCA) based on a correlation matrix was used to evaluate the morphological variation between specimens (Pimentel et al. 2007). Only those axes corresponding to components with eigenvalues greater than 1.0 were extracted. A Kaser-Meyer-Olkin (KMO) test and the Bartlett's test of sphericity were performed to assess the suitability of the selected data for the analysis (Almeida-Pinheiro de Carvalho et al. 2004). The varimax rotation was used to maximize the variance of each factor.

The relationships between the different taxa were investigated using classification discriminant analyses (DA, cross validation). This method requires an a priori assignment of OTUs to groups allowing an evaluation of whether the recognized groups are statistically definable entities or whether there is too much variation within groups to allow classification (Sneath and Sokal 1973; Legendre and Legendre 1998; Saint-Laurent et al. 2000). For cross validation, 25% of the specimens studied were randomly excluded from the dataset and the discriminant functions were calculated for the remaining specimens. To represent the variability of the most discriminant characters within taxa, box-plots were prepared (Fig. 1). These plots contain medians and percentiles and were obtained using the STATISTICA package.

One-way analysis of variance ANOVA and the Tukey's Post Hoc test were carried out for each quantitative character to assess the divergence among species, among subspecies within species, and to determine the importance of each quantitative character. Qualitative characters were studied through  $\chi^2$ . Statistical analyses were performed with SPSS vers. 17.0 (SPSS Inc., Chicago, Illinois).

Morphological data were used to elaborate detailed morphological descriptions for each taxon. Additional data on the habitat, distribution, and chromosome numbers were based on the literature and information supplied in collection labels. Distribution data derived from herbarium specimens were used to build detailed distribution maps, with the program ArcView GIS v. 3.2.

Transversal sections of the basal leaves were obtained with a Bright Starlet 2212 Cryostatand, stained with Fasga mixture (Tolivia and Tolivia 1987), and photographed using optical microscopy. Ideograms of these sections were drawn by J. L. Castillo.

#### RESULTS

**Morphology—HABIT**—All species of *Stipa* subsects. *Stipa* and *Tirsae* are perennial and herbaceous grasses. Species are generally xerophilous, exhibiting intravaginal growth, with many vegetative shoots and few generative shoots, resulting in a “rossulate perennial,” as defined by Freitag (1985).

**VEGETATIVE BODY**—The culms are erect, 2–4 noded and almost completely covered by the culm leaf-sheaths. In both subsections, nodes are glabrous, whereas the ornamentation of the

TABLE 2. Main qualitative characters in *Stipa* subsections, *Stipa* and *Tirsae*.

	<i>S. pennata</i> subsp. <i>pennata</i>	<i>S. pennata</i> subsp. <i>strobilosa</i>	<i>S. kirghisorum</i>	<i>S. turkestanica</i> subsp. <i>turkestanica</i>	<i>S. turkestanica</i> subsp. <i>trichoides</i>	<i>S. turkestanica</i> subsp. <i>macroglossa</i>	<i>S. tirsae</i>
Leaf abaxial ornamentation	Glabrous or minutely scabrous	Glabrous or minutely scabrous	Distinctly scabrous	Distinctly scabrous	Distinctly scabrous	Distinctly scabrous	Sparingly stiff hairs
Leaf adaxial ornamentation	Scabrous, papillose or pubescent	Scabrous or papillose	Scabrous, papillose or pubescent	Pubescent, minutely pubescent or papillose	Pubescent, minutely pubescent or papillose	Pubescent, minutely pubescent or papillose	Usually papillose or scabrous
Leaf-blades apex	Usually with an apical tassel of hairs	With an apical tassel of hairs or glabrous	Glabrous	Usually glabrous	Usually glabrous	Usually glabrous	Delicate tip
Ligule margin	Ciliolate or glabrous	Ciliolate or glabrous	Ciliolate or ciliate	Usually glabrous	Usually glabrous	Usually glabrous	Ciliolate
Ligule tip	Ciliolate or glabrous	Ciliolate or glabrous	Ciliolate or ciliate	Ciliolate or glabrous	Usually ciliate	Usually ciliate	Ciliolate
Upper sheaths ornamentation	Glabrous, papillose or scabrous	Glabrous, papillose or scabrous	Glabrous, papillose or scabrous	Usually papillose or glabrous	Usually papillose or glabrous	Usually scabrous or papillose	Scabrous, papillose and with stiff hairs
Culm ornamentation	Glabrous or scabrous	Glabrous or scabrous	Glabrous, scabrous or pubescent	Glabrous or pubescent	Glabrous or pubescent	Glabrous or pubescent	Pubescent
Panicles	Exserted or partially enclosed	Exserted or partially enclosed	Exserted or partially enclosed	Exserted or partially enclosed	Exserted or partially enclosed	Exserted or partially enclosed	Enclosed or partially enclosed
Panicle basal internode surface	Glabrous or scabrous	Glabrous or scabrous	Glabrous or scabrous	Usually pubescent	Scabrous or pubescent	Usually scabrous	Pubescent
Dorsal and subdorsal row	Fused	Fused	Distinct	Distinct	Distinct	Distinct	Fused
Callus shape	Slightly curved	Straight	Slightly curved	Slightly curved	Slightly curved	Slightly curved	
Awns column surface	Glabrous (rarely pilose)	Glabrous	Usually glabrous	Glabrous or tuberculate	Glabrous or tuberculate	Glabrous (rarely pilose)	Glabrous

internode surface is highly variable even within the same species: normally glabrous in both subspecies of *S. pennata*, densely pubescent in *S. tirsae* and scabrous or pubescent in *S. turkestanica* and *S. kirghisorum*.

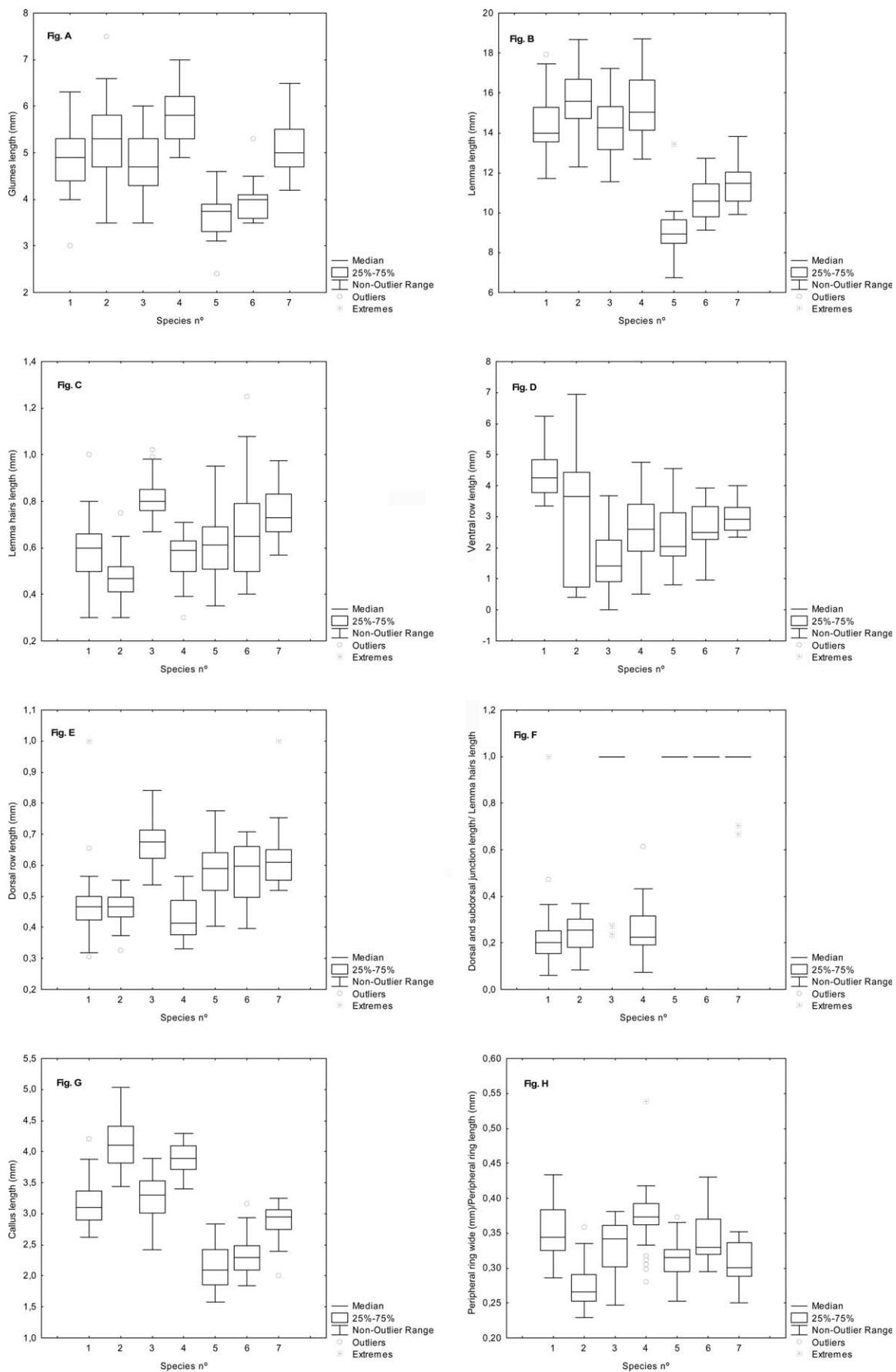
**LEAVES**—The ornamentation, shape, and size of ligules, leaf-sheaths, and leaf-blades are variable in the same plant, depending on whether it is the basal leaf or the culm leaf. There is also variation along the length of the leaves and its age.

**LEAF SHEATHS**—Leaf-sheaths are glabrous, scabrous with prickles or with stiff hairs, papillose or pubescent. The leaf-sheaths of the basal leaves may be glabrous or ciliate, while the culm leaf-sheaths usually exhibit glabrous margins.

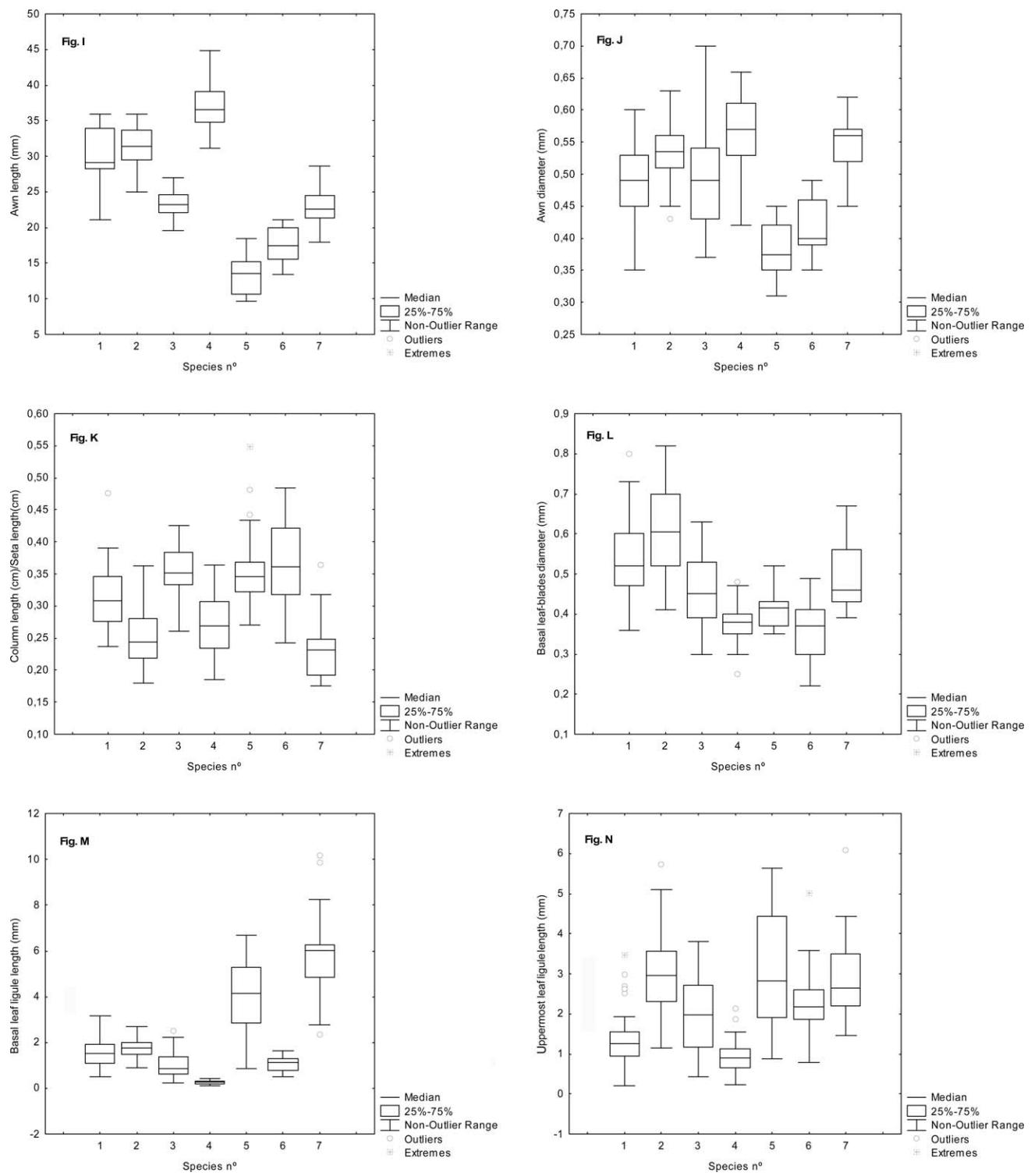
**LEAF BLADES**—All the taxa are more or less xerophilous, having convolute or involute leaf-blades, being extremely thin in *S. tirsae* (up to 0.3 mm in diameter). The ornamentation of both sides of the leaf-blades has been traditionally used as a distinctive character for taxon delimitation (Martinovský 1982; Moraldo 1986; Klokov and Osychnyuk 1976). However, leaf-blade features have been considered less important than spikelet morphology for the taxonomy of species with large distributions (i.e. *S. caucasica* Schmalh, *S. pennata*, and *S. capillata* L.) due to the high variability of this trait. The exception is *S. tirsae*, in which leaf-blade ornamentation is stable, showing the abaxial surface covered by scattered stiff hairs, whereas the adaxial surface may be scabrous, papillose, or, less commonly, with scattered hairs. In all species from subsect. *Stipa*, the abaxial surface is distinctly scabrous, with the exception of both subspecies of *S. pennata*, which may be either glabrous or minutely scabrous. The adaxial surface is extremely variable within the same taxon and may be scabrous, minutely pubescent, papillose, pubescent or with scattered hairs. Leaf-blade apices contain remarkable features, ending in a very delicate and long setaceous tip in *S. tirsae*, or in a fragile apical tassel of hairs in the young leaves of *S. pennata* and occasionally in *S. turkestanica*. However, tassels are deciduous and sometimes missing, or not developed.

The histology of the leaf-blade of members of sect. *Stipa* has been profusely studied (Martinovský 1970, 1977, 1980; Connert 1982; Devesa 1992). Representatives of *Stipa* subsections *Stipa* and *Tirsae* are C3-grasses (XyMS+), with leaf-blades bearing adaxial ribs or “nodular” in transverse section (Watson and Dallwitz 1992) and mesophyll with non-radiate chlorenchyma. The abaxial surface of leaf-blades has a regular outline, whereas the adaxial surface is divided into conspicuous ribs of unequal size, separated by deep and narrow furrows with V or U shapes (see figures in the Taxonomic Treatment). The number of ribs ranges from five to 11, in relation to the width of the leaf-blades. Rib apices may be rounded or quadrangular. Bulliform cells are displayed in discrete fan-shaped groups of three to five cells at the base of the furrows and are usually small and inconspicuous.

Vascular bundles are more or less embedded in the middle of the mesophyll, and its number is correlated with the number of ribs. Two different kinds of vascular bundles are found, typically alternating with one another. Each rib corresponds to one vascular bundle of the “basic type” (Metcalfe 1960), accompanied by sclerenchyma girders that reach both sides of the leaf blades or only the abaxial side of the leaf blade when the ribs are less developed. Usually, each furrow displays a small bundle without girders that alternates with the ribs. The xerophilous nature of the species of these two sections is reflected in the continuous subepidermal layers



Figs. 1A–N. Box plots of the most discriminant variables. Numbers refer to the following taxa: 1. *S. pennata* subsp. *pennata*; 2. *S. pennata* subsp. *sabulosa*; 3. *S. kirghisorum*; 4. *S. tirsa*; 5. *S. turkestanica* subsp. *turkestanica*; 6. *S. turkestanica* subsp. *trichoides*; 7. *S. turkestanica* subsp. *macroglossa*.



FIGS. 1A–N. Continued.

of sclerenchyma that connect the abaxial girders to each other. Species from strongly xeric habitats exhibit much more developed girders and layers. Thus, populations of *S. pennata* and *S. tirsa* from more mesophytic habitats have layers that are two cells tall, whereas *S. kirghisorum* and *S. turkestanica*, from more xerophytic habitats have layers that are five to six cells tall. This layer is discontinuous and narrow at the adaxial surface, often interrupted at the furrows.

**LIGULES**—The shape and size are quite variable in the culm leaves but uniform in the basal leaves, constituting useful characters for species delimitation. *Stipa tirsa* has short (up to 0.5 mm long) and truncate basal ligules. On the other hand, *S. turkestanica* subsp. *turkestanica* and subsp. *macroglossa* have longer, (1.85)2.76–6.7(10.2) mm, and lanceolate ligules.

**INFLORESCENCES**—Inflorescences are paniculate, contracted with few erect or almost erect branches and spikelets.

The panicle is more or less enclosed by the upper leaf-sheaths in *S. tirsia*, but exserted or partially enclosed at the base (depending on the stage of development) on members of subsect. *Stipa*. An inconspicuous character is the ornamentation of the first internode of the panicle. The first internode is more or less pubescent in *S. tirsia* and *S. kirghisorum*, usually glabrous in *S. pennata*, but scabrous or more rarely pilose in *S. turkestanica*.

**GLUMES**—Glumes are subequal and always long acuminate. The number of nerves usually ranges from three to seven. The mid nerve usually extends up to the tip, while the lateral nerves occur in pairs and never reach the tip. The glumes are glabrous with the midrib always ciliate in *S. tirsia*, and indistinctly ciliate in species of subsect. *Stipa*. The tips of the glumes are very delicate and easily damaged.

**ANTHECIUM**—Each unit including lemma, palea, and callus was here treated as an antheicum. For convenience, the awn was not included in the length of the antheicum (Freitag 1985). The antheicum is coriaceous, with overlapping margins and enclosing both flower and caryopsis. All the structures that are enclosed in the antheicum (stamens, lodicules, and ovary) are difficult to observe in herbarium specimens.

**LEMMA**—The lemma is glabrous or at most papillose near the apex and with seven rows of appressed to almost erect hairs. The ventral rows of hairs normally do not reach the apex. Occasionally, in a few specimens of *S. pennata*, *S. kirghisorum* and *S. tirsia*, the ventral rows almost reach the top. *Stipa turkestanica* and *S. kirghisorum* have seven distinct rows of hairs, whereas *S. tirsia* and *S. pennata* present dorsal and subdorsal rows of hairs that are slightly fused at the base. In all species, the dorsal row is always longer or at most equals the length of the subdorsal ones. The apex of the lemma is sometimes extended into short lobules surpassing the awn insertion. However, these lobules lack taxonomic value, because they can vary even within a single species. In floristic treatments of *Stipa*, the antheicum length has often been measured as lemma (Roshevitz 1934; Tzvelev 1976; Martinovský 1982; Moraldo 1986).

**CALLUS**—The callus has a cylindrical shape and is usually hidden by the hairs, with a lowermost part acute, pungent, oblique, and curved, composed by the scar and surrounded by the peripheral ring (Freitag 1985). *Stipa pennata* subsp. *sabulosa* is the only taxon of the subsection that shows a straight callus, with a very narrow peripheral ring (with a low width/length ratio). The callus is covered by straight and antrorse hairs, with the ventral hairs longer than the dorsal ones.

**PALEA**—The palea is enclosed by the lemma, and their lengths are relatively similar. A row of hairs between the two veins appears indistinctly in the different taxa.

**LODICULE**—The number of lodicules is three, one contiguous to the palea (ventral) and the other two (dorsal) flanking the dorsal side of the mature caryopsis. The dorsal lodicules are lanceolate, whereas the ventral lodicle is lanceolate or linear-lanceolate and slightly longer or shorter than the dorsal one. Lodicules are usually glabrous, only rarely presenting scattered hairs at the apex.

**AWN**—The awn is divided in two parts, column and seta (also called bristle). The column is the basal part of the awn and is bent twice and twisted in subsect. *Stipa* and *Tirsae*. The seta is plumose, with hairs longer than 4 mm and flexuous, except in some specimens of *S. turkestanica*, in which the awns may be falcate. Scattered throughout the area

of distribution of the species, some individuals show a distinct indumentum covering the column. Such forms were described as different subspecies or species. However, more convincing is the interpretation of Scholz (1985) upheld by Freitag (1985), who considered those specimens temporary aberrant forms or mutants.

**STAMENS**—There are three equal stamens per antheicum, whose sizes vary in proportion to the lemma length. The absence or presence of hairs at the apex is variable within species and therefore, of little value for the species level taxonomy of the group.

**OVARY AND CARYOPSIS**—Ovaries are similar in all species, glabrous, with two styles. The mature caryopsis is fusiform, with a linear hilum that almost reaches the top, and whose size varies in proportion to the lemma length.

**Morphometric Analyses**—Box plots showing the variability of the most discriminant characters are presented in Figs. 1A–N. The most distinctive discrete characters were combined with selected qualitative characters and used as basis for the species and subspecies keys. Descriptive statistic and box plots show that species are clearly differentiated in some characters, whereas the subspecies overlap for most of the characters studied. Floral characters such as lemma length, subdorsal and dorsal junction length ( $D_S$ )/lemma length, awn length and callus length are especially important for the differentiation of *S. turkestanica* and *S. kirghisorum* (Figs. 1B, F, G, I). Vegetative characters such as the basal leaf ligule length (Fig. 1M) are important for the differentiation of *S. tirsia*, *S. turkestanica* subsp. *turkestanica* and subsp. *macroglossa*, whereas the basal leaf diameter characterizes *S. tirsia* (Fig. 1L).

A high Pearson correlation was found in the distance between palea length, column length, and seta length. Consequently, only 27 characters were used for further analyses. One additional character ( $D_S$ /lemma length) was excluded in the DA 2, because it was constant within *S. turkestanica* and *S. kirghisorum*.

In the PCA performed for all taxa, the KMO analysis rendered a value of 0.83, indicating that our sample was adequate for multivariate analyses. The first three components accounted for 63% of the total variance observed. The first principal component (Axis 1) accounted for 39% of the total variance and had high contributing loading values from glume length, lemma length, callus length, awn length and diameter, basal leaf-blade diameter, basal leaf ligule length,  $D_S$ /lemma length, column length/sea length (COL/SET), and plant height. The second component (Axis 2) had high contributing loadings from awn length, lemma hair length, basal leaf ligule length, and  $D_S$ /lemma length. Finally, the third component (Axis 3) had high contributing loadings from peripheral ring width/peripheral ring length (PRW/PRL), basal leaf-blade diameter, basal leaf ligule length, COL/SET, and uppermost leaf ligule length.

In the scatterplot against the first two components, specimens are arranged in very loose and slightly overlapping groups (Fig. 2). Component 1 provides separation of *S. turkestanica* subsp. *turkestanica* and *trichoides*, mostly based on the smaller size of its floral characters. However, two OTUs of subsp. *turkestanica* and subsp. *trichoides* are intermingled with those of subsp. *macroglossa*. The remaining taxa, with larger spikelets, are depicted on the centre or right side of the scatterplot. The specimens belonging to *S. tirsia*, *S. pennata* subsp. *pennata* and subsp. *sabulosa* are highly

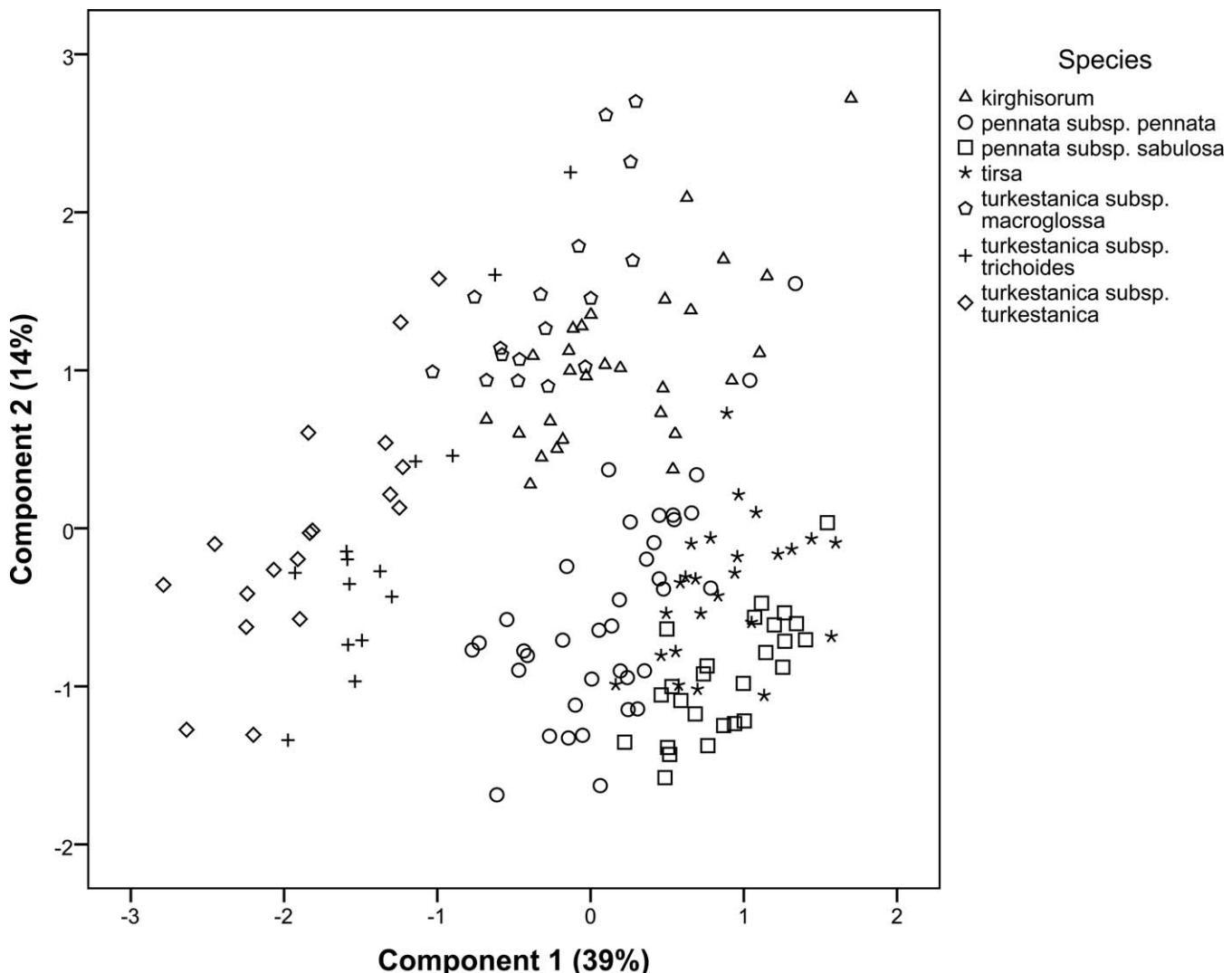


FIG. 2. Plot of the first two components of the principal component analysis (PCA).

intermingled and occur on the lower right corner. Component 2 provides a separation for specimens of *S. turkestanica* subsp. *macroglossa*, which are more or less confined to the middle portion of the upper quadrant. Specimens of *S. kirghisorum*, although rather dispersed, are placed in the upper quadrant, partially overlapping with *S. turkestanica* subsp. *macroglossa* and *S. pennata* subsp. *pennata*, holding an intermediate position between both taxa.

In the scatterplot against the first and third components (Fig. 3), samples of *S. turkestanica* subsp. *turkestanica* and subsp. *trichoides* are more clearly segregated at the left quadrant, whereas the remaining taxa form a single cluster.

In view of the results obtained from the PCA, two DAs were carried out. The two subspecies of *S. pennata* and *S. tirsa* (group I) plus *S. kirghisorum* were analyzed in DA 1. The 2-D scatterplot of root 1 against root 2 (Fig. 4) reveals a more or less clear separation of the OTUs of *S. kirghisorum* from the remaining OTUs along the first component, whereas *S. tirsa* was completely separated along the second axis. Specimens of *S. pennata* subsp. *pennata* and subsp. *sabulosa* are continuously distributed in the scatterplot, with no differentiation observed. One specimen of *S. pennata* subsp. *pennata* is

also intermingled between specimens of *S. kirghisorum*. Characters such as lemma hair length, D\_S/lemma length, callus length, basal leaf blade diameter, awn length and diameter were especially important for axis 1, whereas callus length, PRW/PRL, D\_S/lemma length, basal leaf ligule length, basal leaf blade diameter, and ventral row length were important in the second one (Table 3). However, subspecies *pennata* and *sabulosa* are partially separated along the third axis (Fig. 5). Callus length, ventral row length, uppermost leaf ligule length, and PRW/PRL are the traits with the highest contribution for the third component (Table 3). The cross-validation method classified 91.9%, 96.2%, 96.3%, and 100% of *S. pennata* subsp. *pennata*, subsp. *sabulosa*, *S. kirghisorum* and *S. tirsa*, respectively. *Stipa pennata* subsp. *pennata* presented one OTU that was misclassified as subsp. *sabulosa*, and two OTUs that were misclassified as *S. kirghisorum*. In addition, *S. pennata* subsp. *sabulosa* and *S. kirghisorum* presented one OTU each that was misclassified as *S. pennata* subsp. *pennata*. Willk's Lambda values of the three discriminant functions were 0.009, 0.027, and 0.299 respectively, indicating the greater morphological differences of the taxa studied.

The three subspecies of *Stipa turkestanica* and *S. kirghisorum* were analyzed in DA 2 (Fig. 6). The 2-D scatterplot reveals an

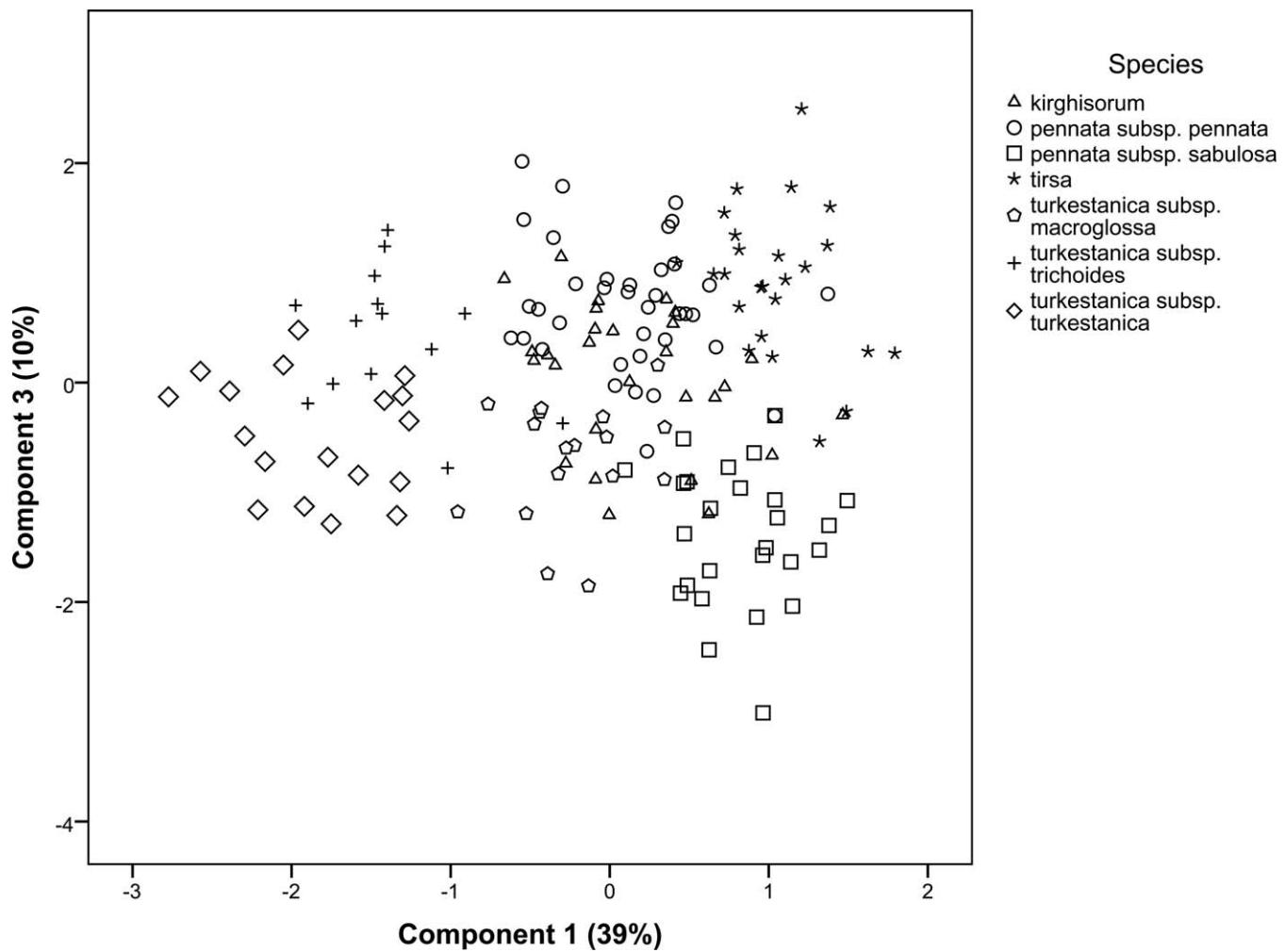


FIG. 3. Plot of the first and third components of the principal component analysis (PCA).

almost complete separation of all individuals of *S. kirghisorum* from the remaining samples along the first axis, whereas specimens of *S. turkestanica* subsp. *trichoides* and subsp. *turkestanica* slightly overlap their margins, with two specimens of subsp. *turkestanica* being intermingled between those of subsp. *trichoides*. Lemma length, awn length, and basal leaf ligule length represent the highest loading for the first axis. The second axis is responsible for the complete separation of *S. macroglossa*. However, one sample of *S. turkestanica* subsp. *macroglossa* clearly clustered with the other two subspecies of *S. turkestanica*. COL/SET, basal leaf ligule length, awn length, and basal leaf-blade diameter represent the highest loadings for the second axes. The percentages of well-classified OTUs were 100% for *S. kirghisorum* and *S. turkestanica* subsp. *trichoides*, but 88% for subspecies *macroglossa* and *turkestanica*. Subspecies *turkestanica* has two OTUs misclassified as subsp. *trichoides*, whereas subsp. *macroglossa* has one OTU misclassified as subsp. *turkestanica* and another one as *S. kirghisorum*. Wilk's Lambda values for the first and second discriminant functions were 0.025–0.200, indicating the greater morphological differences of the taxa studied.

ANOVA (Tukey, post hoc test,  $p < 0.01$ ) and  $\chi^2$  tests detected significant differences in most of the characters studied when comparing individuals of the four species

studied. The characters that best separate the species are the lemma length, lemma hair length, callus length, awn length, basal leaf ligule length, D\_S/lemma length, leaf-blade apex, and basal leaf abaxial ornamentation. However, subspecies are mainly differentiated by quantitative characters rather than qualitative. Among the three subspecies of *S. turkestanica*, ligule margin was the only significant qualitative character (Table 2), while awn length represents an example of significant quantitative character. In addition, specimens of subsp. *macroglossa* present significantly longer glumes, callus, and basal leaf-blade diameter and shorter COL/SET than the other two subspecies, whereas subsp. *turkestanica* has significantly smaller lemma; specimens of subsp. *trichoides* have shorter ligules on the basal leaf and are intermediate in length between the other two subspecies in all traits examined. The two subspecies of *S. pennata* are quite similar, only differing in callus features (PRW/PRL and callus length), lemma length, and the ventral row length.

A comparison between *S. kirghisorum*, *S. pennata* subsp. *pennata*, and *S. turkestanica* subsp. *macroglossa* indicates that these taxa significantly differ in COL/SET and ventral row length. Moreover, five traits (awn length, lemma hairs length, dorsal row length, ratio D\_S /lemma length, and panicle basal internode surface) statistically separate *S. kirghisorum* from *S. pennata* subsp. *pennata*, while three traits (lemma

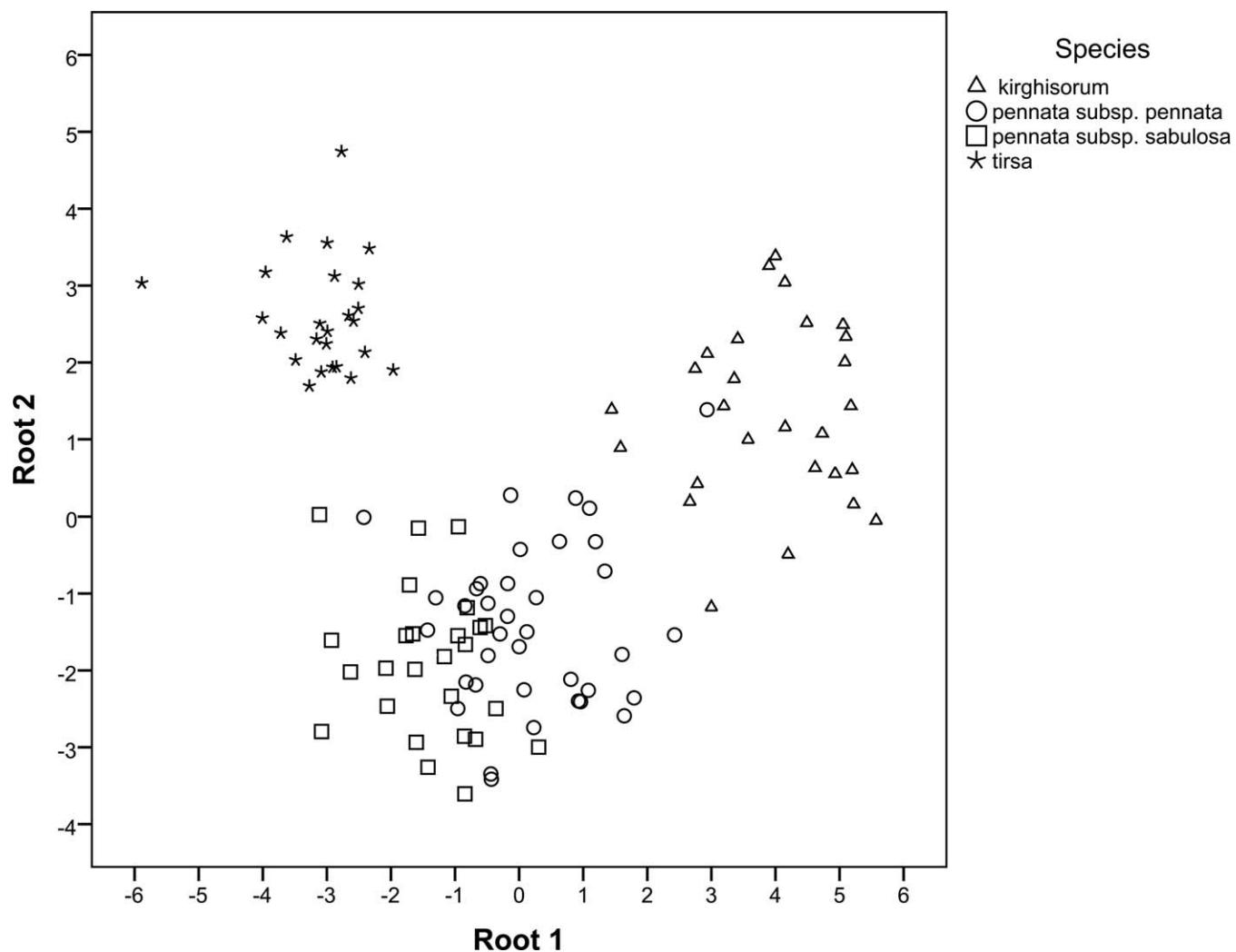


FIG. 4. Plot of the first two roots of the discriminant analysis for *S. pennata*, *S. kirghisorum*, and *S. tirsia*.

TABLE 3. Factor loadings of the 13 characters for the first three principal components of the PCA and the standardized coefficient obtained in the DA 1 and 2. (-) Variables not used by the analysis. In bold, morphological characters showing the highest factor loadings and standardized coefficient.

	PCA			DA 1			DA 2	
	Axes 1	Axes 2	Axes 3	Root 1	Root 2	Root 3	Root 1	Root 2
Glume length (cm)	<b>0.734</b>	0.002	0.141	-	-	-	-	-
Lemma length (mm)	<b>0.833</b>	-0.205	0.047	-	-	-	<b>0.620</b>	-0.066
Callus length (mm)	<b>0.882</b>	-0.198	-0.078	<b>-0.364</b>	<b>0.322</b>	<b>0.698</b>	-	-
Peripheral ring width/Peripheral ring length (PRW/PRL)	-0.052	0.038	<b>0.85</b>	0.017	<b>0.411</b>	<b>-0.306</b>	-	-
Awn length (mm)	<b>0.827</b>	<b>-0.318</b>	0.297	<b>-0.523</b>	0.118	-0.105	<b>0.405</b>	<b>0.895</b>
Lemma hairs length (mm)	-0.027	<b>0.835</b>	0.077	<b>0.723</b>	0.192	-0.147	-	-
Awn diameter (mm)	<b>0.762</b>	0.187	0.045	<b>-0.315</b>	-0.226	0.101	-	-
Basal leaf-blade diameter (mm)	<b>0.362</b>	-0.073	<b>-0.333</b>	<b>0.300</b>	<b>-0.372</b>	0.233	0.262	<b>0.310</b>
Basal leaf ligule length (mm)	<b>-0.356</b>	<b>0.343</b>	<b>-0.393</b>	0.211	<b>-0.500</b>	-0.079	<b>-0.536</b>	<b>0.537</b>
Dorsal and subdorsal rows joining length/lemma length	<b>-0.646</b>	<b>0.572</b>	-0.193	<b>0.427</b>	<b>0.406</b>	0.031	-	-
Ventral row length (mm)	0.065	-0.296	0.256	-0.214	<b>-0.362</b>	<b>-0.500</b>	-	-
Dorsal length/Lemma length	-0.184	0.071	-0.228	-	-	-	-	-
Columns length/seta length (COL/SET)	<b>0.725</b>	-0.253	<b>0.478</b>	-	-	-	0.210	<b>-0.559</b>
Plant height (cm)	<b>0.580</b>	-0.171	-0.250	-	-	-	-	-
Uppermost leaf ligule length (mm)	-0.221	0.186	<b>-0.699</b>	0.056	-0.280	<b>0.320</b>	-	-
Percent of total variance explained	39	14	10	52	29	19	67	31

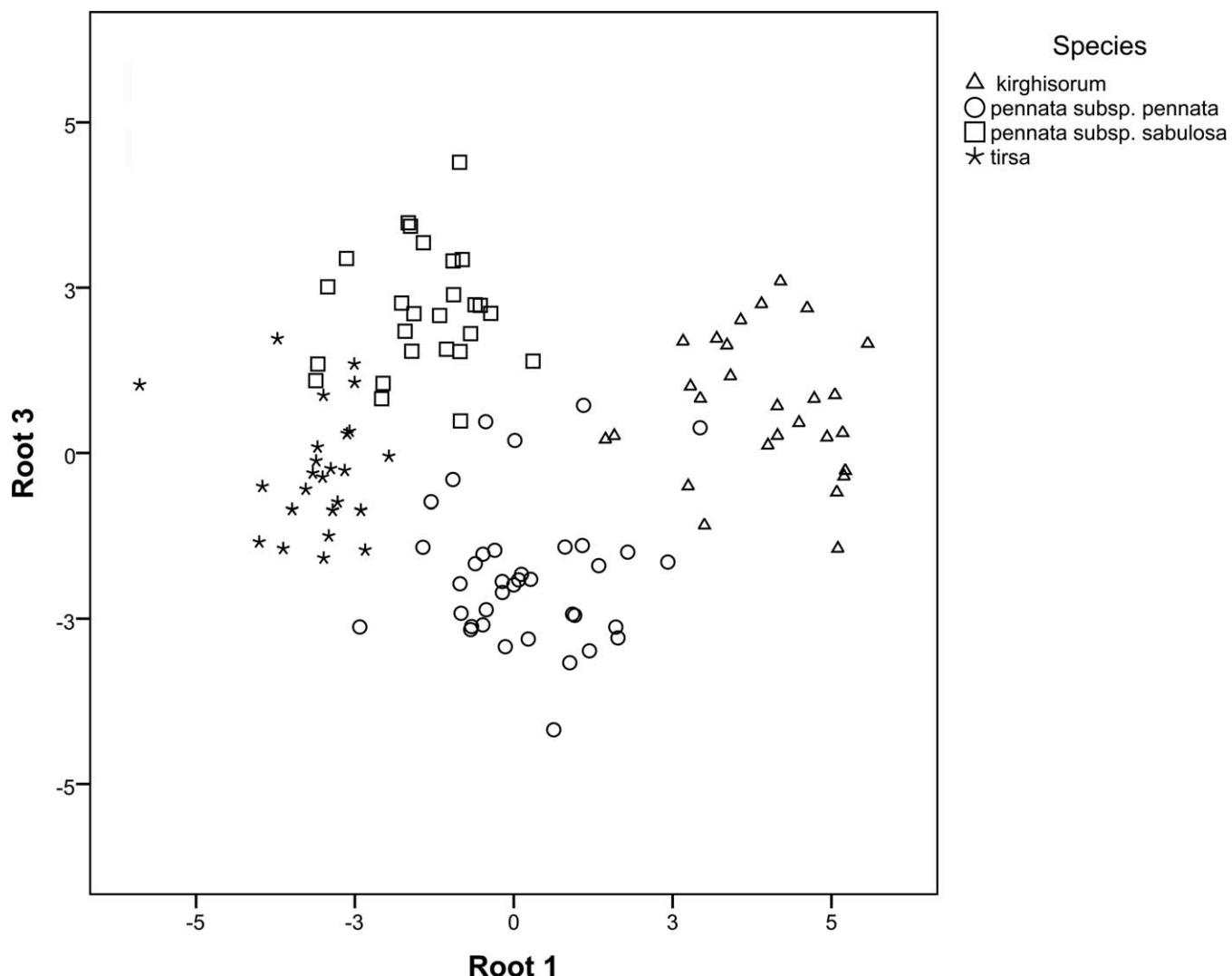


FIG. 5. Plot of the first and third root of the discriminant analysis for *S. pennata*, *S. kirghisorum*, and *S. tirsa*.

length, callus length, and ligule length) separate it from *S. turkestanica* subsp. *macroglossa*.

#### DISCUSSION

Multivariate techniques used in the present study did not yield the same level of resolution in different groups of specimens. In the PCA performed for the seven taxa analyzed, no clear pattern could be discerned, although some discrete groups appeared to be recognizable. Beyond that, the 2-D scatterplot did not provide a conclusive segregation for the different taxa studied. It should be noted that PCA is characterized by a faithful representation of distances between the major groups but is notorious for falsifying distances between close neighbors (Sneath and Sokal 1973). This is why ordination of smaller and related groups was checked with DA. Discriminant analysis is widely employed in studies of closely related taxa (Pimentel et al. 2007; Viruel et al. 2010). Overall, all analyses support the recognition of four species and five subspecies that present a set of very homogeneous morphological characters. Except for *S. tirsa*, there is not a unique character that can be used to distinguish a particular taxon by itself. Instead, the combination of several

morphological characters, in combination with habitat and distributional information is what allows the recognition of these taxa.

Spikelets of *S. tirsa* are superficially similar to those of *S. pennata*, which has led some authors to consider *S. tirsa* as a variety of *S. pennata* (Čelakovský 1884). Our analyses demonstrate that the distinctness of *S. tirsa* from the remaining taxa of subsect. *Stipa* is clear and supported by multiple qualitative and quantitative characters (Table 2; Fig. 2). In particular, short ligules, thin basal leaf-blades, longer awns, setaceous apices of the basal leaves, and sparsely stiff hairs on the abaxial surface of the basal leaves allow the separation of *S. tirsa* from the remaining taxa of subsect. *Stipa*.

In contrast, the recognition of *S. kirghisorum* is not as clear. This species shows ranges of morphological variation that overlap with those of *S. pennata* subsp. *pennata* and *S. turkestanica* subsp. *macroglossa*, being only separated by a combination of traits. Some of the characters used by other authors for species identification performed well in our analyses. The most useful characters to separate *S. kirghisorum* and *S. turkestanica* subsp. *macroglossa* are the size of the basal ligule leaf (Pazij 1968; Bor 1970; Tzvelev 1976; Wu and Phillips 2006), which is (0.25)0.42–1.7(2.5) cm long in *S. kirghisorum* and

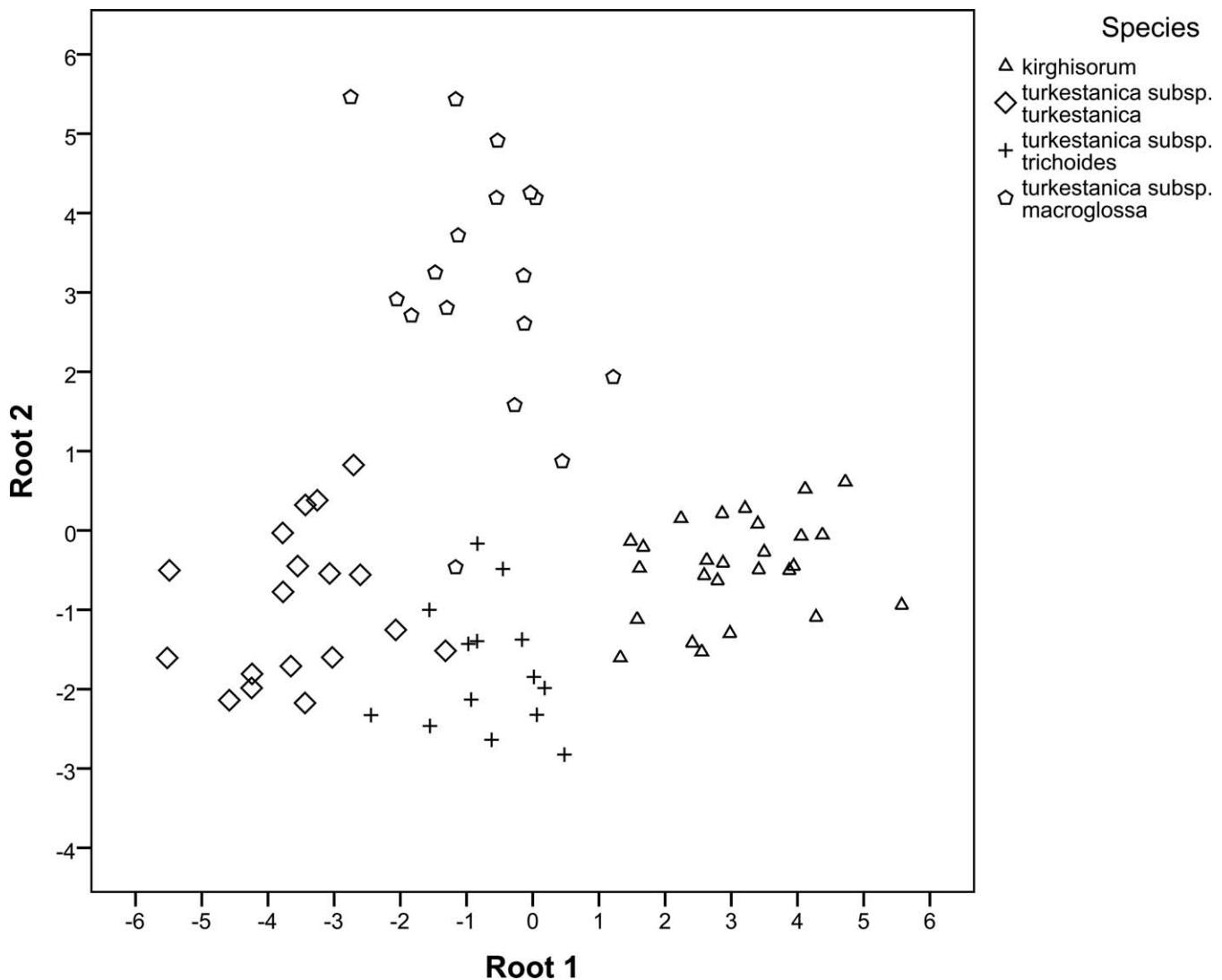


FIG. 6. Plot of the first two roots of the discriminant analysis for *S. turkestanica* and *S. kirghisorum*.

(2.3)2.8–9.8(10.2) in *S. turkestanica* subsp. *macroglossa*, and lemma size (Figs. 1C, M). Even though the size of the awn is similar, the ratio COL/SET is quite different, mainly due to the longer column of *S. kirghisorum*. The separation of *S. kirghisorum* and *S. pennata* subsp. *pennata* is, however, more problematic. Despite that, *Stipa kirghisorum* has been considered as a distinct species by all Asian taxonomists (Smirnow 1925; Pazij 1968; Tzvelev 1976, 2000), while *S. kirghisorum* was treated as a subspecies of *S. pennata* in a revision of *Stipa* from southwestern Asia (Freitag 1985). *Stipa kirghisorum* is morphologically similar to *S. pennata* subsp. *pennata*, and presents a slight overlap in the DA 1 (Fig. 4). A set of characters used to recognize these taxa previously such as the shorter awns, longer dorsal row, lemma with distinct rows of hairs, and distinctly scabrous surface of the basal leaf-blades (Smirnow 1925; Pazij 1968; Tzvelev 1976), as well as characters newly identified in the present study such as lemma hair length, dorsal row length, and pubescence of the panicle basal internode, support the recognition of *S. kirghisorum*. They also have different ecological preferences; *S. kirghisorum* is an alpine or subalpine taxon, whereas *S. pennata* is rarely found at high altitudes. Furthermore, the chromosome number of *S. kirghisorum* is  $2n = 32$  (Tzvelev 1976; Freitag

1985), whereas the chromosome number of *S. pennata* is  $2n = 44$  (Sheidai et al. 2006; Tzvelev 1976; Freitag 1985). We thus retain *S. kirghisorum* at specific rank. Nevertheless, the affinities of this taxon are not yet clear based only on morphological data and require molecular investigations in order to clarify its taxonomic position and relationships.

All analyses performed indicated that distinction between the two subspecies of *S. pennata* is rather difficult. *Stipa pennata* subsp. *sabulosa* was originally described as a variety of *S. pennata*, and later recognized as a subspecies by Lavrenko (1940) and Tzvelev (1976). Prokudin (1951), taking into account its habitat and morphological features, recognized it as a different species, circumscription that was followed by Tzvelev (2006) in his treatment for the Flora of Caucasus. Our analyses suggest that quantitative characters of the floret represent the only traits for a reliable identification of these subspecies. Other features previously used, such as the scabridness of the surface of the upper leaf-sheaths, are highly variable. However, DA 1 (Fig. 5) shows that *S. pennata* subsp. *sabulosa* presents slightly longer lemmas and callus, a peripheral ring that is somewhat straight and thin (low value PRW/ PRL), and a ventral row that is closer to the lemma apex. In addition, both subspecies

have different ecological preferences. Subspecies *sabulosa* inhabits sandy soils, whereas subsp. *pennata* is rarely found on sandy habitats. These morphological and ecological differences support the recognition of the two subspecies, as proposed by Lavrenko (1940) and Tzvelev (1976).

On the other hand, the separation of the three subspecies of *S. turkestanica* presents different problems. The specimens identified as subspecies *turkestanica* and *trichoides* are closely placed in the DA 2, but only a few of them appeared intermingled within each other. Traditionally, both subspecies have been either accepted as different species (Smirnow 1925; Ovczinnikov 1957; Pazij 1968) or *S. trichoides* has been treated as a subspecies of *S. turkestanica* (Tzvelev 1976). Delimitation of both taxa has been mostly based on features of the ligule of the basal leaf and the awn. Subspecies *turkestanica* displays longer ligules that are glabrous at the apex, and longer awns with a glabrous column. On the other hand, subsp. *trichoides* shows shorter ligules with ciliate apex and shorter awns, and frequently a glabrous column. More recently, Freitag (1985) considered that those characters were not diagnostic and treated subsp. *trichoides* as a synonym of *S. turkestanica*. We have found that both subspecies are not easily distinguished from each other because of the similarity of their spikelets. However, specimens with short ligules and ciliate apex consistently display longer

awns and lemma, whereas specimens with long ligules and glabrous apex have shorter awns and lemma. Our data suggests that *S. trichoides* is best treated as a subspecies of *S. turkestanica*.

Apart from the similarities between *S. turkestanica* subsp. *turkestanica* and *S. turkestanica* subsp. *trichoides*, *S. turkestanica* subsp. *macroglossa* is more easily diagnosed. This taxon is so morphologically distinct that it has even been treated as a separate species closely related to *S. pennata* in the past, from which it was distinguished by the longer ligules (Smirnow 1925). However, a detailed study of material available from its whole distribution range, suggests a closer relationship with *S. turkestanica*. *Stipa turkestanica* subsp. *macroglossa* presents the unusual long ligules of the basal blades-leaf present in *S. turkestanica* subsp. *turkestanica* (Fig. 1M). It differs mainly in the much longer reproductive parts, its ecological preferences, and geographical distribution. Subspecies *macroglossa* is restricted to lowlands and middle belts of mountains of the Tian Shan range, East and central Kazakhstan, whereas subsp. *turkestanica* is an alpine taxon, with northern limits in the Alai Mountains of Kyrgyzstan. Both taxa share similar qualitative characters (Table 2), differing only in qualitative features of the spikelets. For this reason, we here treat *S. turkestanica* subsp. *macroglossa* as a synonym of *S. turkestanica* subsp. *turkestanica*.

#### TAXONOMIC TREATMENT

#### KEY TO SPECIES AND SUBSPECIES

1. Ligules of basal leaves 0.1–0.4 mm long; abaxial surface of the basal leaves with sparsely stiff hairs and a long setaceous apex ..... 1. *S. tirsae*
1. Ligules of basal leaves (0.3)0.7–5.6(10.2) mm long; abaxial surface of the basal leaves glabrous or scabrous by prickles, with a glabrous apex or with an apical tassel of hairs ..... 2
2. Lemma subdorsal and dorsal rows distinct; abaxial surface of the basal leaf-blades distinctly scabrous; leaf-blade apex usually glabrous; awn (9.6)12–25(28) cm long ..... 3
2. Lemma subdorsal and dorsal rows fused at the base; abaxial surface of the basal leaf-blades glabrous or somewhat scabrous; leaf-blade apex usually with an apical tassel of hairs; awn (21)26–34(36) cm long ..... 6
3. Glumes (3.5)4–5.6(6.5) cm long; awn (18)20–26(28) cm long and (0.4)0.6–0.7 mm in diameter ..... 4
3. Glumes (2.3)3.2–4.4(5.3) cm long; awn (9.6)10.4–18.4(20) cm long and (0.3)0.4–0.5 mm in diameter ..... 5
  4. Anthecium (13.7)14.3–17.5(18.5) mm long; column (4.4)4.8–7(7.5) mm long; ligules (0.25)0.42–1.7(2.5) mm long ..... 4. *S. kirghisorum*
  4. Anthecium (11.9)12–14.6(14.8) mm long; column (1.7)2.3–3.8(3.9) mm long; ligules (2.3)2.8–9.8(10.2) mm long ..... 3c. *S. turkestanica* subsp. *macroglossa*
  5. Anthecium (8.3)9.6–11.9(12.2) mm long; awn (9.6)9.7–17(18.4) mm long; ligules of the basal leaves 1.6–5.8(6.7) mm long ..... 3a. *S. turkestanica* subsp. *turkestanica*
  5. Anthecium (11)11.5–14.4 mm long; awn (13.4)13.6–20.1(21.1) mm long; ligules of the basal leaves 0.5–1.4(1.5) mm long ..... 3b. *S. turkestanica* subsp. *trichoides*
  6. Callus (2.6)2.7–4 long; peripheral ring straight; peripheral ring width/ratio = (0.29)0.3–0.41(0.43) ..... 2a. *S. pennata* subsp. *pennata*
  6. Callus (3.8)3.9–5 long; peripheral ring curved; peripheral ring width/ratio = (0.23)0.24–0.32(0.36) ..... 2b. *S. pennata* subsp. *sabulosa*

#### I. *Stipa* subsection *Tirsae* (Martinovský) R. Gonzalo, stat. nov.

*Stipa* ser. *Tirsae* Martinovský, Preslia 48: 186. 1976.—TYPE: *Stipa tirsae* Steven

*Stipa* ser. *Stenophyllae* Klokov, Novosti Sist. Vyssh. Rast. 1975: 81. 1976.—TYPE: *S. stenophylla* (Czern. ex Lindem.) Trautv.

Herbs densely caespitose, perennial; branching intravaginal. Culms 3–4-noded, erect. Basal leaves convolute; abaxial surface with sparsely stiff hairs; adaxial surface somewhat scabrous, minutely pubescent and with scattered hairs; ligules truncate, to 0.4 mm long. Panicles contracted, 3–4 noded, the first internode pubescent; branches erect or almost erect and with long hairs. Glumes equal or subequal,

lanceolate, long acuminate, 3–7 nerved and with the central nerve usually ciliate. Anthecium coriaceous, fusiform or laterally compressed; lemma with 7 rows of hairs, the ventral rows of hairs ending 4.5 mm below the top of the lemma, the dorsal row and the subdorsal row slightly fused at the base, with the dorsal row longer or equalling in length the subdorsal row; callus acute, slightly curved, villous, scar elliptic, peripheral ring dorsally flattened and protruding. Palea lanceolate, two nerved and ± the lemma length; lodicules 3, equal or subequal, acute, membranous, lanceolate or linear-lanceolate. Awn bigeniculate; column glabrous; seta flexuous and plumose with hairs longer than 3.5 mm. Ovary glabrous, styles 2.

**Notes**—Subsection *Tirsae* includes only *S. tirsae*, a species widely distributed in Europe, Caucasus, South-western Russia, Northwest Kazakhstan and western Siberia. *Stipa tirsae* is morphologically closely related to species of subsect. *Stipa*. However, it has unique features, such as the presence of a setaceous apex on the basal leaves, very short ligules, and the abaxial surface of the basal leaves with sparsely stiff hairs. Martinovský (1976) considered these features sufficient to recognize series *Tirsae*, which is here treated as a subsection.

1. *STIPA TIRSA* Steven, Bull. Soc. Imp. Naturalistes Moscou 30(2): 115. 1857; *S. pennata* var. *tirsae* (Steven) L. F. Čelak., Sitzungsber. Königl. Böhm. Ges. Wiss. Prag. Math.-Naturwiss. Cl. 1884: 58. 1884.—TYPE: UKRAINE. Kaltschik, camp. Maeotic, Graff s.n. (lectotype: H!, selected by Martinovský & Skalický 1969).

*Stipa cerariorum* Pančić, Fl. Knevez. Srbje: 738. 1874; *S. pennata* subsp. *cerariorum* (Pančić) K. Richt., Pl. Eur. 1: 32. 1890.—TYPE: SERBIA. Brestovac. Pančić s.n. (lectotype: W 1916 19486!, designated here).

*Stipa pennata* var. *stenophylla* Czern. ex Lindem., Fl. Cherson 2: 283. 1882; *S. stenophylla* (Czern. ex Lindem.) Trautv., Trudy Imp. S.-Peterburgsk. Bot. Sada 9: 351. 1884.—TYPE: UKRAINE. Charkov region, steppe near Rogan, 29 Jun 1853, Czernajaev s.n. (holotype: LE!).

*Stipa schmiditii* Woronow ex Grossh., Fl. Kavk. 1: 66. 1928.—TYPE: GEORGIA. Jalno Mts near Tiflis, 30 Jul 1919, Schischkin s.n. (lectotype: LE!, designated by Tzvelev 1976).

*Stipa tirsae* subsp. *albanica* Martinovský, Preslia 44: 22. 1972.—TYPE: ALBANIA. Septentrionali in monte Paštak 22 Jul 1918 Doerfler s.n. (holotype: LD!; isotypes: WU!, SI!).

Herbs 20–60 cm tall, perennial, caespitose; branching intravaginal. Culms 3–4 noded, nodes glabrous, violet; culm internode pubescent. Basal leaves 34–100 cm long, green, eventually pruinose; leaf-sheaths usually glabrous, margins glabrous (rarely ciliate); leaf-blades 28–57 cm long, (0.2)0.3–0.5 mm in diameter, convolute, abaxial surface distinctly scabrous by sparsely stiff hairs (0.03)0.09–0.25 mm long, adaxial surface somewhat scabrous, minutely pubescent and occasionally with scattered hairs, ending in a long setaceous apex; ligules 0.1–0.4 cm long, truncate, somewhat scabrous, ciliolate (rarely ciliate), cilia 0.01–0.08(0.29) mm long. Floriferous culm leaves 30–57 cm long; leaf-sheaths 24–50 cm long, somewhat scabrous with stiff hairs near the leaf-blades and the margins, and the remainder papillose, margins glabrous; leaf-blades 2.5–12 cm long, (0.19)0.2–0.32(0.36) mm in diameter, abaxial surface with sparsely stiff hairs, adaxial face papillose, minutely pubescent or pubescent, hairs (0.01)0.05–0.23(0.25) mm long; ligules (0.2)0.4–1.5(2.1) mm long, truncate, obtuse or rounded, somewhat scabrous or glabrous, margins glabrous or ciliolate, tip ciliolate (rarely glabrous), cilia (0.02)0.03–0.13(0.15) mm long. Panicles 6–37 cm long, contracted, enclosed or partially enclosed by the upper leaf-sheath, 3–4-noded; basal internodes (0.4)0.7–18(25) cm long, pubescent; branches (0.9)1.6–3.2(3.7) cm long, erect or almost erect, setulose, setae (0.34)0.39–1.22(1.29) mm long; basal nodes with (1)2 branches with 1 spikelets each. Glumes subequal, lanceolate, long acuminate, glabrous with the central nerve usually ciliate, cilia (0.1)0.3–1(1.6) mm long, green with margins and tip hyaline, the lower (4.9)5.3–6.7(7) cm long and 3–5 nerved, the upper (4.7)5–6.5(6.7) cm long and

5–7-nerved. Anthecium (16.7)17.2–19.2(19.7) mm long, (0.8) 0.9–1.3(1.4) mm wide, fusiform, coriaceous, pale or brown; lemma (12.7)13.3–15.5(16) mm long, near the apex glabrous, with 7 distinct rows of hairs or with the dorsal and subdorsal ones fused and the remainder rows free, the ventral row ending (0.5)1.1–4.18(4.76) mm below the top of the lemma, the dorsal row measuring  $\pm$  1/2–1/3 the length of the lemma, the remainder rows shorter or equaling the dorsal row, rows with appressed to almost erect hairs (0.3)0.4–0.7 mm long; callus 3.4–4.2(4.3) mm long, acute, curved or slightly straight, villous, hairs (1.3)1.5–2.1(2.5) mm long on the ventral face and (0.8)0.9–1.2(1.5) mm long on the dorsal face, scar elliptic, peripheral ring (0.6)0.7–0.9(1) mm long, 0.25–0.33(0.35) mm wide (ratio width/length= 0.3–0.4(0.5)); palea (12)12.9–14.9(15.7) mm long, lanceolate, margins and tip hyaline, dorsally 2-nerved, between the two nerves papillose or glabrous (rarely with a dorsal row of hairs up to 1/4 the length of the palea), margins and tip glabrous (rarely ciliate), brown or green; lodicules 3, equal or subequal, with the dorsal ones slightly longer or shorter than the ventral one, acute, lanceolate or linear-lanceolate, membranous, glabrous, dorsal lodicules (2)2.5–3.7(4.9) mm long, ventral lodicule (1.7)2.1–3.9(4) mm long. Awn (31)34–43(45) cm long, bigeniculate; column (5.2)6.3–9(9.3) cm long, base (0.42)0.48–0.64(0.66) mm in diameter, twisted, brown or brown and green, glabrous; geniculation (1.3)1.4–2.2(2.4) cm long, glabrous; seta (23.3)25.5–35.5(36.5) cm long, (ratio column length/seta length = (0.18)0.22–0.34(0.36)), flexuous, plumeous, hairs in lower part (4)4.4–6.2(6.7) mm long. Anthers (5.2)5.7–8.7(9.6) mm long, glabrous. Ovary glabrous, styles 2. Caryopsis (9.5)9.6–11.5(11.9) mm long, fusiform; embryo 1.5–2.6(2.7) mm long. Figure 7.

**Chromosome Number**— $2n = 44$  (Tzvelev 1976; Freitag 1985; Connert 1982).

**Distribution and Habitat**—This species inhabits stony and dry slopes, pastures, forest glades, mountain meadows, and steppes from sea level up to middle mountain belts, 0–2,300 m. It is roughly distributed from Central, North, South and East Europe to Southwest Siberia (Omsk, Kuban and Tyumen provinces). It also occurs scattered in Central and South France, North Italy, North Caucasus, Transcaucasia, Northeast Turkey, and in the Caspian Area of Kazakhstan (central Asia). *Stipa tirsae* has been also reported from Bulgaria (Dimitrov 2002: 357). Unfortunately, however, this specimen was unavailable to us during the present study. One sheet from Spain has been identified as *S. tirsae*: "Se cría en montes y colinas áridas cerca de Madrid, Aranjuez, Mancha y Reyno de Murcia, Lagasca, s.n. (MA)." Paunero (1960) recognized this species for Spain; however, considering its general distribution and the fact that no other specimens have been collected since Lagasca (Vázquez and Devesa 1996), this reference probably represents a labelling mistake (Fig. 8).

**Phenology**—Flowering specimens have been collected in May, June and July.

**Representative Specimens Examined**—ALBANIAKukés: Albania septentrionali in monte Pâstrik, 42°13' N 20°30' E, 22 Jul 1916–1918, Doerfler 866 (S, WU).

ARMENIA—Aragatsotn: Monte Aragat, Ghazaravan, road to Kari lake, 40°23' N 44°15' E, 30 Jun 2005, Medina et al. 2591 (MA). Gegharkunik: Krasnoselsko district, montes Areguni in vicinitate pagi Tokludza, 40°34' N 45°15' E, 31 Jul 1975, Vasak s.n. (MA, WAG).

AUSTRIA—Niederösterreich: Weinviertel, Mortz ner World. Sriolhorf, 48°23' N 16°40' E, 10 Jun /15 Jul 1962, Melzer s.n. (BR, GZU, W).

AZERBAIJAN—Nakhchivan: Prope pag. Bist, 39°8' N 45°52' E, 27 Jul 1931, Prilipko and Vichert s.n. (LD).

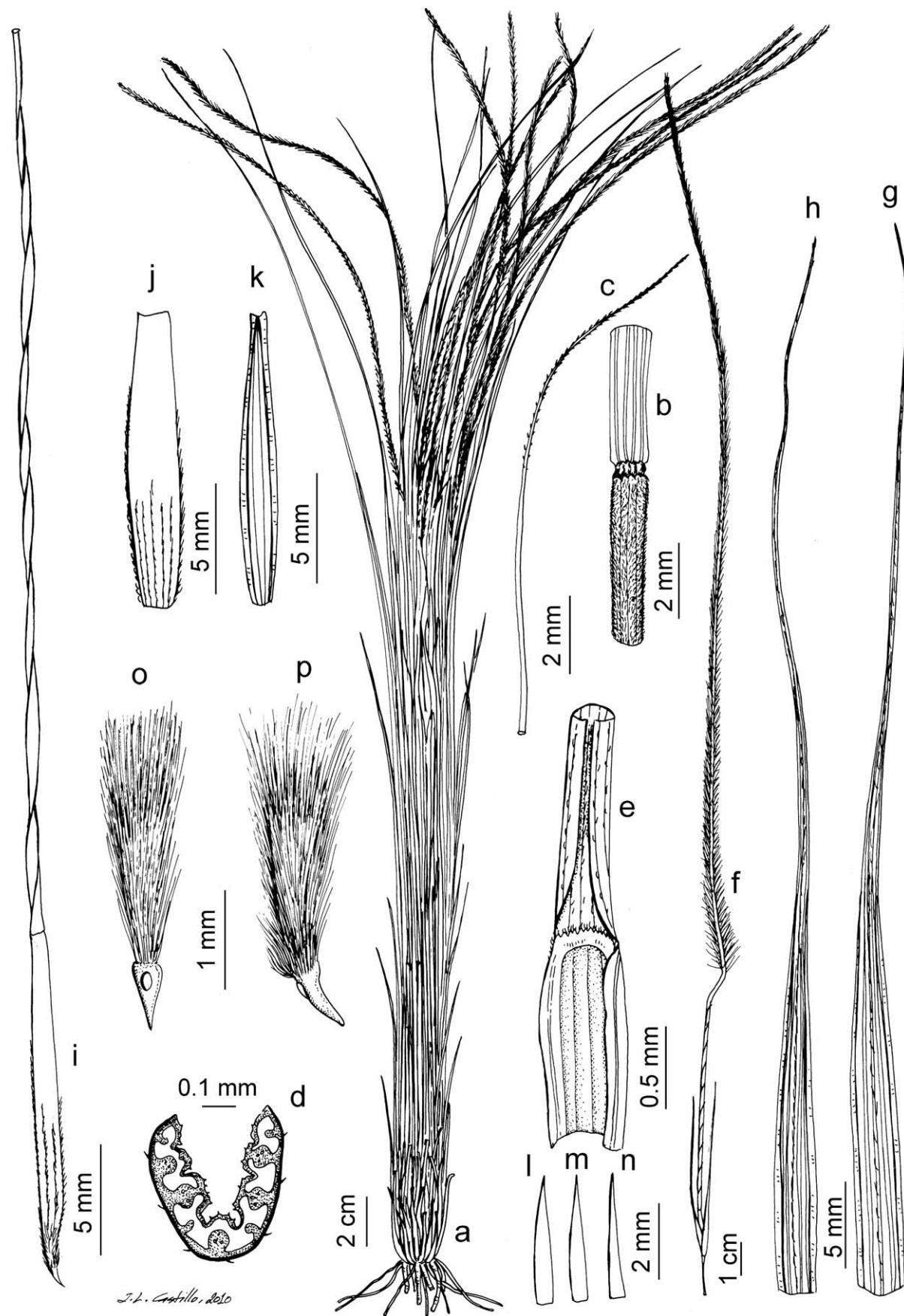
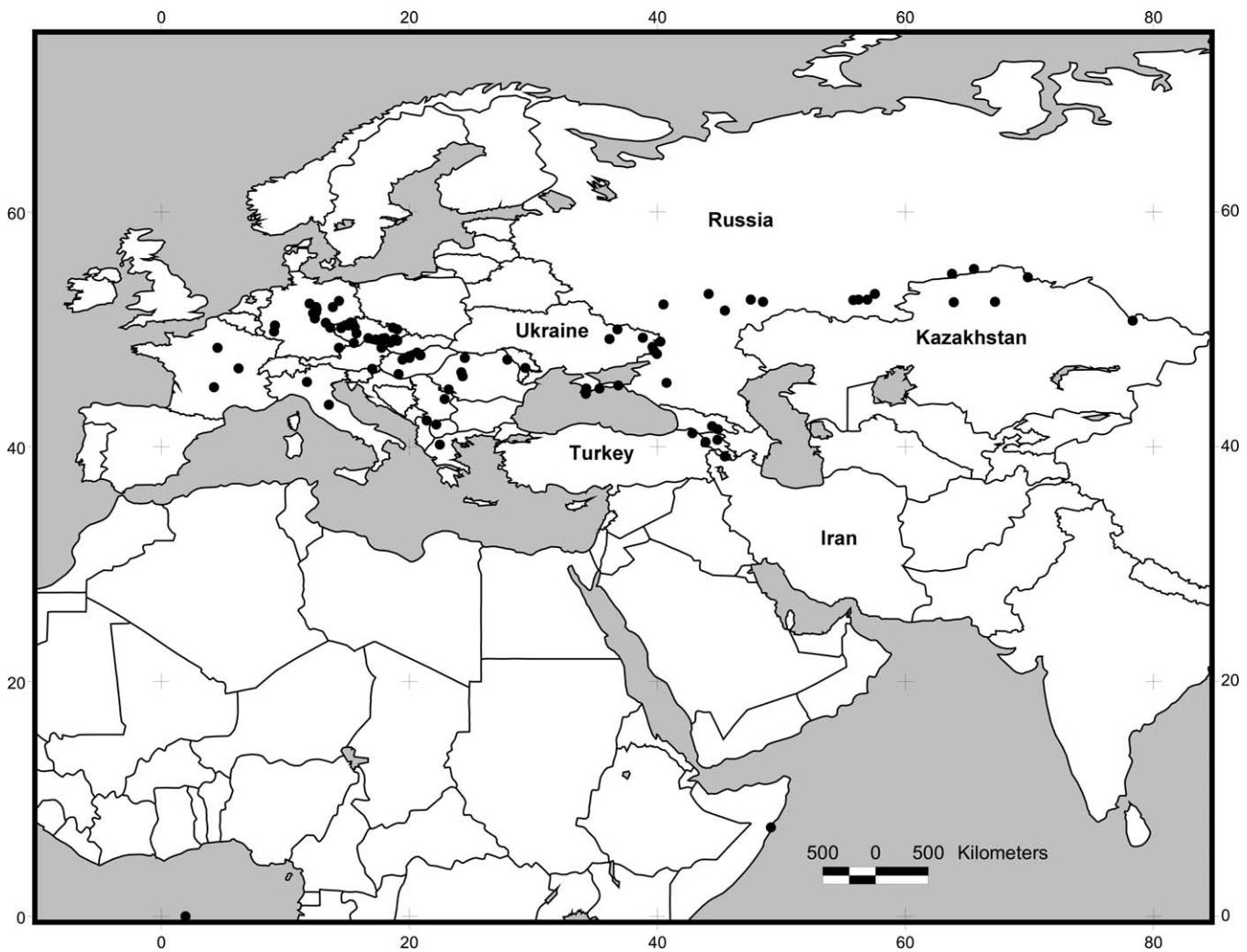


FIG. 7. *Stipa tirsa*. a. Habit. b. Culm node. c. Basal leaf apex. d. Transversal section of leaf-blades. e. Basal leaf ligule. f. Spikelet. g. Upper glume. h. Lower glume. i. Anthecium and column. j. Lemma. k. Palea. l, m. Ventral lodicules. n. Dorsal lodicule. o. Callus, ventral view. p. Callus, lateral view. [based on: Weber s.n. 20 May 1932 (MA 4987(2)).]

FIG. 8. Distribution map of *S. tirsia* (●).

CZECH REPUBLIK—Jihočeský kraj: Krumlov versus Rokytno, 48°49' N 14°19' E, 6 Jul 1926, *Podpěra s.n.* (JE). Jihomoravský Kraj: Montes Bílé Karpaty. Vyzkum prope vicum Tasov, 48°52' N 17°27' E, Jun 1935, *Weber s.n.* (BR, H, W); JIHMORAVSKÝ KRAJ: Vyškov: in declivibus stepposissimis collis Větrníky supra pagum Lysovice, 49°13' N 16°58' E, 17 Jun 1960, *bad handwriting s.n.* (LD); Umgebung von Moravský Krumlov, SW-Hang des Berges Krížová hora über dem rechten Ufer des Ro-kyná-Flusses, 49°3' N 16°29' E, 14 Jul 1986, *Pokorný & Strudl s.n.* (W). Karlovarský Kraj: Kobylé, 50°4' N 13°14' E, 30 Jun 28, *Colrube s.n.* (JE); Milejové louky, ad p. Hluk, district Uh. Ostroh, 50°8' N 12°17' E, 13 Jun 1926, *Otruba 165* (BR, H, S, WU). Moravskoslezský Kraj: Werte, Karpaten, Steppenabhänge C.M. Vrbka, 49°59' N 18°1' E, Jun 1934, *Laus s.n.* (MA); Werte, Karpaten, Kobyl slava, 50°8' N 17°38' E, Jul 1933, *Laus s.n.* (MA). Středoceský Kraj: Vetrníky bei Bucovice, 49°38' N 14°33' E, 5 Jul 1911, *Colrube s.n.* (JE); Rosendals, 50°10' N 14°23' E, Jul 1865, *Kugelberg s.n.* (S); Deblík, 50°35' N 14°3' S, Jun 1912, *Missbach s.n.* (S). Ústecký Kraj: Böhmen: Abhänge der Radobyl bei Leitmeritz, 50°32' N 14°8' E, 10 Jun 89, *Hora, P.* (S); Saaz, bei Trnowan auf der Anhöhe, 50°33' N 14°11' E, 20 Jul 1886, *Celakovský s.n.* (WU). Vysočina: Větrníky ad urbem Vyškov, 49°14' N 15°33' E, 13 Jun 1926, *Podpěra & Jirásek 165* (BR, H, S, U, W, WU); Mahren vid Mohelno, 49°7' N 16°11' E, 3 Jul 1936, *Anderberg s.n.* (UPS). Zlínský Kraj: Luhačovice, 49°6' N 17°46' E, 15 Jul 1928, *Regel s.n.* (G); Montes Bílé Karpaty, Hájová prope Lípov, 49°7' N 17°53' E, 11 Jun 1932, *Weber 384* (H, M, NY, W).

FRANCE—Auvergne: Tournemire. Sur le plateau de Larrac, 45°3' N 2°25' E, 7 Jun 1905, *Frame s.n.* (MA). Bourgogne: Saône et Loire, 46°40' N 4°30' E, 23 Jun 1948, *Bonnot s.n.* (L). Ile-de-France: Fontainebleau, 48°24' N 2°42' S, Jun 1844 (BR, MA).

GEORGIA—Kakheti: Sagaredjo District, Iori plateau, David Gareddi, 41°28' N 45°16' E, 16 May 2005, *Lachashvili 29* (W). Tbilisi: Jalno Mts near Tiflis, 41°43' N 44°47' E, 41.72544.790833, 30 Jul 1919, *Schischkin s.n.* (LE).

GERMANY—Rheinland-Pfalz: Bad Kreuznach; Nahetal, Martinstein, Flachsberg, 7°32' N 49°48' E, 9 Jul 1978, *Kalheber 78-464* (H); Near valley: Martinstein, 49°48' N 7°31', 21 Jun 1967, *Schumacher, A. s.n.* (H); Sachsen-Anhalt: Ostlich von Questenberg, 51°29' N 11°7' E, 13 May 1894, *Quelle s.n.* (JE); Halle: Lunz berg bie Lettin, 50°32' N 11°55' E, 20 Jun 1965, *Meyer & Lippold s.n.* (JE); Quedlinburg, Harslebener Berge zwischen Wsterhausen und Harsleben, 51°52' N 11°6' E, 20 Jun 1976, *Meyer & Manitz s.n.* (JE). Thüringen: Kyffhäuser, Fremkemburg, 51°23' N 11°5' E, 23 Jun 1960, *Bisse s.n.* (JE); Steigerthal. Harz, 51°21' N 10°52' E, Jun 1910, *Alpers s.n.* (S).

GREECE—West Macedonia: Nomos Grevena. Vurinos, Südhange entlang der Straße von Palaeoakastron nach Chromion. Zwischen Palaeoakastron und Exarkhos, 40°10' N 21°38' E, 25 Jun 1985, *Lippert 20891* (M).

HUNGARY—Baranya: Montis Kiskőhegy prope Szentendre, 46°9' N 18°6' E, 21 Jun 1939, *Borós s.n.* (S, W). Fejér: Pap Irtás prope Csákvár, 47°24' N 18°27' E, 28 Jun 1937, *Borós s.n.* (W). Heves: Motnis Sarhegy supra Gyöngyös, 47°47' N 19°58' E, 21 Jun 1902, *Degen 252* (JE, W, WU). Nógrád: In monte Hármashtárhely (Drei Hosserberg), 48°0' N 19°40' S, 7 Jun 1897, *Borbás, s.n.* (PR). Pest: Hármashtárhely ad urbem Budapest, *Simonkai 3990* (GH, H, JE, L, LU, PR, S, W, WU); In declivibus orientalibus, montis Harmus határhely supra Ó-Buda, 47°33' N 19°2' E, 1 Jun 1904, *Degen 352* (W); Budae-Pestini; in montibus Aquinci, 47°34' N 19°4' E, 4 Jun 1897, *Borbás s.n.* (W, WU); Izbég, 47°41' N 19°4' E, 20 May 1916, *Degen s.n.* (S); Montis Kis Szenús supra Pilis-Szentivan, 47°37' N 18°54' E, 21 May 1916, *Degen s.n.* (WAG).

ITALY—Lombardia: Rezzato (Brescia at sud), 45°31' N 10°19' E, 15 Jun 1984, *Moraldo s.n.* (Herb. Moraldo, digital image). Toscana: Alta valle Tiberina: intorno al torrente Sovare, 43°33' N 12°12' E, 20 Jun 1984, *Moraldo s.n.* (FI). Alta valle Tiberina: Monticello quoam 466 sotto Cammiano, 27 Jun 1937, *Zermetti s.n.* (W).

KAZAKHSTAN— Kostanay: Kustanayskiy. Fedorovskiy rayon. Steynoy, 52°17' N 65°21' E, 19 Jun 1930, *Kuznezow* 310 (NY).

Macedonia— Vardar: Monte Snha planina prope Drzilovo, 41°51' N 21°20' E, 27 Aug 1922, *Vandas* s.n. (PR).

MOLDOVA— Cimislia: Chimshiliyskiy District, Zlotyi village, 46°41' N 28°53' E, 11 Jun 1958, *Botezoni* s.n. (LE).

ROMANIA— Alba: Mühlbach, 45°58' N 23°34' E, 22 Jun 1906, *Barth* s.n. (B, JE, M, U, W). Cluj: Techintău ad Fâñatele Clujului, 47°32' N 23°46' E, 8 Jun 1927, *Nyárády* 1340 (BR, K, H, S); Cheia, pr. Cheile Turzii, 46°18' N 23°27' E, 14 Jul 1998, *Güemes & Bacchetta* 2510 (C, MA); Aud dem Berge Suškuluj bei Herkulesbad im banata, 44°52' N 22°24' S, 1 Jul 1902, *Richter* 313 (WAG).

RUSSIA— Astrakhanskaya Oblast: Prov. Tambow, in steppa Jamskaja prope pag. Streletzkaja, 47°19' N 47°22' E, 29 May 1929, *Smirnow* 4902a (H, W). Bashkortostan: Zilair District, between Tukatov and Shafeevskiy villages, 52°27' N 56°47' E, 14 Jul 1928, *Knorrung* 341 (JE); Region Bashkiria, district Abzelilov, Bakr-Uzyak village, 52°59' N 58°38' E, 8 Aug 1949, *Khokhryakov & Mazurenko* s.n. (W). Krasnodarskiy Kray: Kuban prov. Tamanskiy peninsula S shore of the liman Isokur opposit Steblivskoj, 45°11' N 36°48' E, 23 Jul 1926, *Schiffers* 2138 (S). Kurgan: Between Obryadovka and Kungurovka, 54°43' N 65°13' E, 19 Jul 1928, *Ivanova & Tonshina* 704 (LE); Lopatinskij District, Stepnaya village, 55°7' N 67°3' E, 21 Jul 1928, *Ivanova & Tonshina* 1193 (LE). Novosibirskaya Oblast: Turcia, inter opp. Sarykamish et pag. Promezhutocnoje, 50°44' N 80°34' E, 5 Jul 1914, *Litvinov* 4902b (C, H, K, JE, S, W). Omsk: Poltavskiy District, Poltavskoye village, 54°25' N 71°40' E, 22 May 1949, *Vandakurova* s.n. (LE). Penzenskaya: Kuchkino district near Poperchchnaya village. Privolzhskaya Vozvyshennost' Reserve (Volga upland reserve). Poperechenskaya Steppe, 53°0' N 44°30' E, 6 Jul 1951, *Bunyashina* s.n. (K). Rostov: Novotscherkassk, 47°52' N 40°5' E, 26 May 1910, *Jakoushev* s.n. (M); Millerovo, the 4st department of Millerovo sovhoz, 2.5 km to NE from the estate, S slope of ravine Medvezhya, 48°55' N 40°23' E, 4 Jul 1939, *Kuryushkin* s.n. (LE). Saratov: Ivantsevka reg., 10 Km N of Ivantsevka, near settlement Znamenskiy, 52°20' N 49°8' E, 7 Jul 1993, *Skvortsov* et al. s.n. (LE); Vicinity of Saratov, between Bol'shaya, Polivanovka and Fedorovka, 51°34' N 45°53' E, 16 Jun 1922, *Kazakova* s.n. (LE). Voronezh: Distr. Novochopersk, prope Kalinovka, 51°25' N 41°35' E, 17 Jun 1963, *Skvortsov* s.n. (M).

SERBIA— Serben, Ilić, s.n. (WU); Serbia Breslovac, Pančić s.n. (W). In apricis ad Breslovac Banja, 44°03' N 22°02' E, Pančić s.n. (W).

SLOVAKIA— Prešov Region: Vová Baria; in declivibus merdi. collis Kliča supra pag. Sr. Benedik, 49°14' N 21°33' E49.23333321.55, 3 Jul 1938, Krist s.n. (JE, LD). Trenčín Region: Montes Bile Karpaty, in declivibus collis Hájora, 49°0' N 18°0' E, 20 May 1932, Weber, s.n. (MA).

TURKEY— Ardahan: Osttürkei: Steppe am Cildir-Gölü, 41°7' N 43°8' E, 1 Jul 1991, Lang s.n. (M); Hucgel bei Atsihikler bei Smonk, 6 Jun 1896, Callier 219 (PR); Agri: Distr. Erzurum/Agri: Tahir-Pab, 20 Aug 1971, Volk 71/604 (M).

UKRAINE— Kharkiv: Charcovia, 49°9' N 36°3' E, 1853–1854, Czern. s.n. (MEL). Krym: Karadag. The NE slope of Legener mountain, 44°56' N 35°13' E, 10 Jul 1928, Chernova 209 (W); Mountain Ay-Petri, 44°29' N 34°3' E, 9 Aug 1948, Golubkova 1221 (LE); Luhansk: Elevatio Donetz, Provalje, prope st. viae ferreae Krasnaja mogila, 48°10' N 39°51' E, 26 Jun 1928, *Smirnow* 40 (H, JE, S); Distr. Starbelsk, 49°16' N 38°54' E, 10 Jun 1903, *Skvortsov*, s.n. (M); Distr. Meloviensis, reservatum "Striletzjkij step" dictum, 12 Jun 1957 48°28' N 39°44' E, *Dubovik* s.n. (NY).

**Notes**—The basal leaves of *S. tirsia* present a setaceous apex, very short ligules, and the abaxial surface of the basal leaves with sparsely stiff hairs, allowing this species to be distinguished from its closest relatives. Even though few narrow-leaved specimens of *S. zalesskii* Wilensky can be confused with *S. tirsia*, the ligules in *S. zalesskii* are always more developed and the basal leaves are scabrous by both prickles and long and erect-spreading stiff hairs, whereas prickles are missing in *S. tirsia*.

Martinovský (1972) described *Stipa tirsia* subsp. *albanica* from Paštrik and Djakovo in Albania, characterized by having the ventral rows reaching the apex of the lemma and the others longer than half the length of the lemma. A careful observation of the three type specimens in LD, S and WU revealed that the holotype (LD) presents the ventral rows ending 0.5 mm below the apex, while the others are longer than half the length of the lemma.

The isotypes deposited at the herbaria S and WU have ventral rows that end 1.5 mm below the apex and other rows that reach only up to the half of the length of the lemma. Likewise, other specimens with ventral rows ending ca. 1.5 mm below the top of the lemma apex have also been collected in Germany, Romania, and Czech Republic. Therefore, the relative length of the rows is variable, not supporting Martinovský's view of a separate subspecies.

## II. STIPA subsection STIPA L.—TYPE: *Stipa pennata* L.

*Stipa* ser. *Pennatae* Roshev in Komarov (ed.), Fl. URSS 2: 92. 1934.—TYPE: *Stipa pennata* L.

*Stipa* subser. *Penicilliferae* Martinovský, Oesterr. Bot. Z. 118: 172. 1970.—TYPE: *Stipa joannis* L. F. Čelak

*Stipa* ser. *Penicilliferae* Martinovský, Preslia 48: 187. 1976.—TYPE: *Stipa joannis* L.

*Stipa* ser. *Anomalae* Klokov, Novosti. Sist. Vyssh. Nizsh. Rast. 1975: 29. 1976.—TYPE: *Stipa anomala* P.A. Smirn.

Herbs densely caespitose, perennial; branching intravaginal. Culms 3–4 noded, erect. Basal leaves convolute; abaxial surface glabrous, distinctly scabrous or minutely scabrous; adaxial surface scabrous, minutely pubescent or with scattered hairs; ligules acute, obtuse or rounded. Panicle contracted, 3–4 noded, the first internode glabrous, scabrous (rarely pubescent or with sparsely hairs); branches erect or almost erect and sparsely setulose. Glumes equal or subequal, lanceolate, long acuminate, 3–7 nerved and with the central nerve sometimes ciliate. Antheicum coriaceous, fusiform or laterally compressed; lemma with 7 distinct rows of hairs, or with the dorsal and subdorsal rows of hairs slightly fused at the base, the ventral rows of hairs ending 7 mm below the top of the lemma, the dorsal row and the subdorsal row slightly fused at the base and with the dorsal row longer or at most equaling in length the subdorsal row; callus acute, curved or straight, villous, scar elliptic, peripheral ring dorsally flattened and protruding. Palea lanceolate, two nerved and ± the lemma length; lodicules 3, equal or subequal, acute, membranous, lanceolate or linear-lanceolate. Awn bigeniculate; column glabrous or scabrous (rarely pilose); seta flexuous and plumose, hairs longer than 3.5 mm. Ovary glabrous, styles 2.

2. STIPA PENNATA L. Sp. Pl.: 78. 1753. TYPE: Ind. loc.: "Habitat in Austria, Gallia" (lectotype: L 900.320–437 Herb A. van Royen, selected by Freitag, 1985, digital image!).

Herbs 21–76 cm high, perennial, caespitose; branching intravaginal. Culms 2–3 noded, nodes glabrous, violet; culm internodes usually glabrous. Basal leaves 15–83 cm long, green and occasionally pruinose; leaf-sheaths glabrous, papilloose, scabrous or pubescent, margins glabrous or ciliate; leaf-blades 8–66 cm long, (0.36)0.41–0.77(0.98) mm in diameter, usually convolute, abaxial surface glabrous or scabrous, adaxial surface scabrous, pilose or with scattered hairs (0.06)0.18–0.56(0.77) mm long, apex acute, glabrous, setulose or with an apical tassel of hairs 0.5–3 mm long; ligules (0.5)0.93–2.5(3.1) cm long, acute, obtuse or rounded, glabrous or scabrous (rarely pilose), margin glabrous or ciliolate (rarely ciliate), cilia (0.01)0.09–0.2 mm long. Floriferous culm leaves 22–51 cm long; leaf-sheaths 22–50 cm long, minutely scabrous, papilloose or glabrous, margins glabrous; leaf-blades (0.4)1–5.4(12) cm long, (0.1)0.15–0.39(0.49) mm in diameter,

abaxial surface glabrous, somewhat scabrous or sparsely aculeate, adaxial face scabrous, pilose or scabrous with scattered hairs (0.07)0.08–0.4(0.42) mm long; ligules (0.2)0.7–3.8(11.2) mm long, acute, obtuse, rarely truncate or bifid, glabrous, scabrous, sparsely aculeate or sparsely pilose, margins glabrous, ciliolate or ciliate, cilia (0.02)0.05–0.3(0.33) mm long. Panicles 13–52 cm long, contracted, enclosed or partially enclosed by the upper leaf-sheaths, 3–6(8) noded; basal internode (6.2)17–39(48) cm long, glabrous, scabrous (rarely pubescent); branches 1.4–5(6) cm long, erect or almost erect, glabrous, scabrous, setulose or sparsely setulose, setae 0.02–0.8(1.2) mm long; basal nodes with (1)2(3) branches with 1–2 spikelets each. Glumes subequal, lanceolate, long acuminate, glabrous, rarely ciliate on the central nerve, cilia 0.05–1 mm long, green with margins and tip hyaline, occasionally with purple stains, the lower (3.2)4.3–6(8) cm long and 3–5 nerved, the upper (3)4.1–6(7) cm long and 5–7 nerved. Anthecium (13.4)15.5–19(21) mm long, (0.6)0.8–1.2(1.4) mm wide, fusiform, coriaceous, pale, brown or green; lemma (10.8)12.3–15(16.1) mm long, near the apex glabrous, with 7 rows of appressed to almost erect hairs (0.3)0.4–0.7(1) mm long, the dorsal row and subdorsal ones fused at the base and the remainder rows free, the ventral row ending (2.5)3.6–6.2(7) mm below the top (rarely ending (0.4)0.5–1(1.2) mm below the top), the dorsal row measuring 1/2 as long as the lemma and quite longer than the subdorsal rows; callus (2.62)2.9–4.4(5) mm long, acute, curved or straight, villous, hairs (1.2)1.6–2.6(2.9) mm long on the ventral face and (0.7)0.8–1.5(1.6) mm long on the dorsal face, scar somewhat circulate to broadly elliptic, peripheral ring (0.65)0.74–0.98(1.05) mm long, (0.2)0.22–0.32(0.38) mm wide (ratio width/length = (0.23)0.25–0.4(0.43)); palea (9)11.9–14.3(15.5) mm long, lanceolate, membranous, margins and tip hyaline, dorsally 2-nerved, between the two nerves papillose or glabrous, margins glabrous and tip glabrous or ciliate, rarely with a dorsal row of hairs up to 1/3 the length of the palea, pale brown, brown or green; lodicules 3, equal or subequal, with the dorsal ones slightly longer or shorter than the ventral one, acute, lanceolate or linear lanceolate, membranous, glabrous (rarely ciliate at the apex), dorsal lodicules (1.5)1.7–3.3(3.7) mm long, ventral lodicule (1)1.6–3.4(3.7) mm long. Awn (21)26–34(36) cm long, bigeniculate; column (4.8)5.5–8(9.2) cm long, base (0.35)0.44–0.57(0.63) mm in diameter, twisted, brown, brown and green, and frequently with purple stains, glabrous (rarely pilose); geniculation (1.3)1.4–2.2(2.4) cm long, glabrous, scabrous, more rarely pilose; seta (16)19.8–28.1(29.4) cm long, (ratio column length/seta length = (0.18)0.22–0.34(0.47)), flexuous, plumose, hairs in lower part (4)4.6–6.1(7.9) mm long. Anthers (4.1)4.4–8(8.4) mm long, glabrous (rarely with scattered hairs), yellow or purple. Ovary glabrous, styles 2. Caryopsis (8.3)9–11.2(11.6) mm long, fusiform; embryo (1.3)1.5–2.2(2.7) mm long.

#### a. subsp. PENNATA L.

*Stipa aperta* Janka ex L. F. Čelak., Oesterr. Bot. Z. 33: 318. 1883; *S. pennata* [c] *aperta* Asch. & Graebn., Syn. Mitteleur. Fl. 2: 105. 1899.—TYPUS: CZECH REPUBLIC. Inter Mócs et Izombasselke. Trasnilvaniae centralis, 1 Jun 1869, *Janka s.n.* (neotype: W!, designated here).

*Stipa joannis* L. F. Čelak., Oesterr. Bot. Z. 34: 318. 1884; *S. pennata* [a] *joannis* (L. F. Čelak.) Beck, Fl. Nieder Österreich: 50. 1884; *S. pennata* [A] *joannis* (L. F. Čelak.)

Asch. & Graebn., Syn. Mitteleur. Fl. 2: 105. 1899; *S. pennata* subsp. *joannis* (L. F. Čelak.) Pacz., Zlaki Khers. Gub. 1913; *S. pennata* subsp. *joannis* (L. F. Čelak.) Hyl., Bot. Not. 1953: 354. 1953., comb. superfl.—TYPE: CZECH REPUBLIC. In dem romantischen St. Joanthale unweit Karkstein bei Prag wachst sie um die Felsenhöhle des hlg. Jvan, *Johannes s.n.* (type: original material not located).

*Stipa pulcherrima* var. *mollis* (Czern. ex Asch.) B. Fedtsch., Izv. Imp. Bot. Sada Petra Velikago. 14 (Suppl.): 48. 1915; *Stipa pennata* [III] *mollis* Czern. ex Asch. & Graebn., Syn. Mitteleur. Fl. 2: 107. 1899.—TYPE: UKRAINE. Charkow, *Czerniaw s.n.* (neotype: W 1916 26187!, selected here).

*Stipa lejophylla* P.A. Smirn. Uchen. Zap. Mosk. Univ. 2: 335. 1934; *S. pennata* subsp. *lejophylla* (P.A. Smirn.) Tzvelev, Novosti Sist. Vyssh. Rast. 11: 18. 1974.—TYPE: ARMENIA. Prope pag. Karadshoran, in vulcano Karny Janych, 9 Aug 1929, *Smirnow s.n.* (lectotype: MW, selected by Smirnow (1970); isolectotype: B!, JE, E!, H!, LE!, S!, WU!).

*Stipa danubialis* Dihoru & Roman, Rev. Roumaine Biol., Sér. Bot. 14: 26. 1969.—TYPE: ROMANIA. In saxosis lapidosis ad ripas Danubii inter pagos Gura Văii et Dudașul Schelii dictos, prope opp. Turnu-Severin (distr. Mehedinți), *Savulescu s.n.* (holotype: BUCA digital image!).

*Stipa styriaca* var. *melzerii* Martinovský, Oesterr. Bot. Z. 118: 179. 1970; *S. melzerii* (Martinovský) Klokov, Novosti Sist. Vyssh. Nizsh. Rast 1975: 67. 1976.—TYPE: AUSTRIA. Bei Pölshof nahe von Pöls auf trockenem Hang und an Felsen, 24 Jun 1964, *Melzer s.n.* (holotype: GZU!).

*Stipa styriaca* Martinovský, Oesterr. Bot. Z. 118: 179. 1970.—TYPE: AUSTRIA. Bei Pöls ob Judenberg auf der Südseite des Lausbichls, 24 Jun 1964, *Melzer s.n.* (holotype: GZU!).

*Stipa joannis* subsp. *balcanica* Martinovský, Oesterr. Bot. Z. 118: 181. 1970; *S. balcanica* (Martinovský) Kožuharov, Opred. Vissh. Rast. Bulg.: 786. 1992.—TYPE: MONTE NEGRO. In monte Ljut supra coeneb. Piva, Jul 1905, *Rohlena s.n.* (holotype: PRC digital image!).

*Stipa graniticola* Klokk., Novosti Sist. Vyssh. Rast. 1975: 68. 1976.—TYPE: UKRAINE. Village Semenovkaon Bug, 9 May 1909, *Pachoskii s.n.* (holotype: KW).

*Stipa disjuncta* Klokk., Novosti Sist. Vyssh. Rast. 1975: 75. 1976.—TYPE: UKRAINE. Dit. Sumensis, distr. Czervonensis, P. Studenok, 7 Jun 1954, *Klokov s.n.* (holotype: KW)

Herbs 21–76 cm high. Basal leaves 19–83 cm long. Leaf-blades abaxial surface glabrous, minutely scabrous or scabrous, adaxial surface scabrous, scabrous with sparsely long hairs or pilose, leaf-blades apex with an apical tassel of hairs almost at young leaves (rarely glabrous). Culms leaf-sheaths glabrous, papillose or minutely scabrous. Glumes 3–4.1–5.8(6.3) cm long. Anthecium (13.4)15–18(19) mm long; lemma (10.8)12.4–14.5(16) mm long, with seven rows of hairs, the dorsal and subdorsal row slightly fused at the base and the remainder rows free, the ventral one ending (3.4)3.5–5.7(6.3) mm long below the top of the lemma, the dorsal row ending (4.3)6.5–9(10) mm below the top and longer than the subdorsal ones. Callus (2.6)2.7–4 mm long (callus/lemma = (0.18)0.2–0.27(0.3)), villous, scar elliptic, curved, peripheral

ring (0.6)0.72–1 mm long, (0.2)0.25–0.36(0.38) mm wide (ratio width/length = (0.29)0.3–0.41(0.43)). Awn (21)26–34(36) cm long. Figure 9 m–v.

**Chromosome Number**— $2n = 44$  (Sheidai et al. 2006; Tzvelev 1976; Freitag 1985).

**Habitat and Distribution**—This taxon inhabits dry and stony slopes, pastures, mountain meadows, steppes, and open forest glades from lowlands up to middle mountain belts (rarely in alpine or subalpine communities), 100–4,000 m. This species is widely distributed from Western Europe to Central and West Siberia, being especially abundant in steppes and xeric habitats of Central and Western Europe, whereas it is rare in East Kazakhstan, Tajikistan, and Siberia. *Stipa pennata* subsp. *pennata* is also found in isolated areas of Xinjiang and West Mongolia. One specimen from Spain, collected in Sierra Nevada by Willkomm and preserved in MEL herbarium, has been identified as *S. pennata* subsp. *pennata*. However, not a single specimen identified as *S. pennata* was encountered during the study of hundreds of specimens from Sierra Nevada. Considering its area of distribution (Fig. 10), it looks quite unlikely that *S. pennata* actually grows in Spain. Therefore, Willkomm's record is likely a labelling mistake.

**Phenology**—Flowering specimens have been collected in May, June, July, and August.

**Representative Specimens Examined**—ALBANIA—Dibër: Corab. Albania, 41°46' N 20°32' E, Jul 1908, *Dimonie*, s.n. (W, WU).

ARMENIA—Ararat: Vedinskiy District, villages Azizkend and Dainag, the right shore of Vedi, 39°57' N 44°57' E, 27 May 1960, *Gabrielian et al. s.n.* (MA, MSB). Kotayk: Hrazdan distr., valley of river Hrazdan Bjni, SE above village, 44°39' N 40°27' E, 17 Jun 2004, *Fayvush et al. 04–0516* (W). Yerevan: Prope Karadshoran, in vulcano Karyjarych, 40°24' N 44°28' E, 9 Aug 1929, *Smirnow 101* (B, H, S, W, WU); Caucasus, distr. Razdan, clivi montis Ketandag in vicinitate pagi Charencavan., 40°30' N 44°40' E, 7 Jul 1975, *Vašak s.n.* (W).

AUSTRIA—Burgenland: Neusiedler See-Gebiet: Ober dem See (Oberseewald), etwa 3 km S St. Margarethen, 47°51' N 17°0' E, 28 May 1972, *Döbbeler 241* (M); Neusiedler-See, zwischen Weiden und Gols, 47°50' N 16°45' E, 17 May 1928, *Ronniger s.n.* (H); Steppe nördlich von Podersdorf am Neusiedlersee, 47°53' N 16°52' E, 29 May 1955, *Höpflinger s.n.* (C, W); Hornstein, Bges, 47°52' N 16°26' E, 20 May 1923, *Schneider s.n.* (W). Niederösterreich: Pfaffstätten, Baden, 48°1' N 16°14' E, Jun 1961, *Dulfer s.n.* (MA, W); Deustsh-Wagram, (Marchfeld, NO in einem mit Gras benachseinen Laubwald, 48°15' N 16°40' E, 3 May 1964, *Lang s.n.* (W); Rodan bei Perchtoldsdorf, 48°7' N 16°16' E, 16 May 1931, *Jurisic s.n.* (W); Perchtoldsdorf in Nied.Oesterreich, 48°7' N 16°16' E, n.d., *Keik s.n.* (C); Wien, Lobau, 47°50' N 16°50' E, 27 May 1936, *Ronniger s.n.* (W); Thaya bei Raabs, 48°85' N 15°5' E, 3 Jul 1877, *Krenberger s.n.* (WU); Kamptal unterhalb Gars, Zitternberg (7459/2), 48°35' N 15°14' E, 8 Jun 1982, *Pokorny & Strudl s.n.* (W). Steiermark: Grashange ander Stephaniehohe auf der Turkensekanze bei Wien, 46°29' N 14°34' E, 30 May 1898, *Handel-Mazzetti s.n.* (WU); Bei Pölsdorf nahe von Pöls auf trockenem Hang und an Felsen, 47°13' N 14°36' E, 24 Jun 1964, *Melzer s.n.* (JE, U); Kärnten, nahe der steirischen Grenze südöstlich des Neumarkter Sattels nordwestlich Althaus bei Mühlen aud dem Steilhang der Mülltheiten, 47°6' N 14°21' E, 18 Jun 1969, *Melzer s.n.* (W); Schanze 2. Alte Schanzen, 47°31' N 14°0' E, 5 Jun 2002, *Mrkvicka 13645* (W); Geisberg bei Rodaun, 46°58' N 15°42' E, IV-1904, *Witaszek s.n.* (WU).

AZERBAIJAN—Kalbajar: Khurdistan, Istisu inf., 39°56' N 45°57' E, 30 Jul 1934 (S).

BOSNIA AND HERZEGOVINA—Srpska Republika: Hercegovina, montis Bjelašica pl., 45°52' N 18°1' E, 19 Aug 1889, *Murbeck s.n.* (LD); Velez planina, 43°20' N 18°0' E, 30 Jul, *Sagorski s.n.* (JE).

BULGARIA—Blagoevgrad: M. Rilla, pr. lac Sedemjezeru, 42°8' N 23°33' E, 11 Aug 1939, *Lindberg s.n.* (H).

CHINA—Xinjiang: Mongolian Altai, to the west of the village Kok-Togai, riverhead of Cherny Irtysh River, 47°25' N 89°34' E, 6 Jun 1959, *Botanist of the expedition group 10381* (LE); Mongolian Altai. 20 km to the NW of Shara-Sume (on the river Kran), 48°34' N 87°30' E, 7 Jul 1959, *Junatov & Yuan I-fan 1104.1135* (LE).

CROATIA—Istarska Županija: Auf felsen b Vranja, 45°19' N 14°8' E, 8 Jun 1886, *Ničić s.n.* (WU).

CZECH REPUBLIC—Jihomoravský Kraj: Mahren vid Pausram, 48°56' N 16°37' E, 1 Jul 1936, *Anderberg s.n.* (UPS); Moravia australis: prope pagum Bořetice, 48°55' N 16°51' E, 24 May 1972, *Dvořák s.n.* (H); Vyškov: in declivibus stepposis collis Větrníky supra pagum Lysovice, 49°13' N 16°58' E, 17 Jun 1960, *bad handwriting* (M 0139271); Galgenberg bei Nikolsburg, 48°48' N 16°38' E, 22 May 1913, *Korb s.n.* (W); Göding, bei Rohatetz, 48°52' N 17°11' E, Jun 1936, *Laus, s.n.* (JE, LE, W); Weinberg bei Zaisa (Hardegg), 48°53' N 15°52' E, 12 Jun 1884, *Obořny s.n.* (W); Brnoad, m. Hády versus Velká Klajdovka, 49°12' N 16°42' E, 10 Jun 1932, *Šestka 765* (C, S, UPS, WU). Liberecký Kraj: Nachst Cervene Kolo bei Mt. Boleslav, 51°0' N 15°2' E, 9 May 1897, *Podpéra s.n.* (H, JE, WU); Prague: Umgebung Prag, Radolm, 50°5' N 14°28' E, 13 May 1927, *Asplund s.n.* (S); Praga, 50°5' N 14°28' E, May 1899, *Podpéra s.n.* (JE); Středočeský Kraj: Liptschitz, vid Moldan, 50°40' N 13°39' E, 11 May 30, *Cedercreutz s.n.* (H); Südböhmen auf Felsen in der Höhe von Poskala bei Příbram, 49°42' N 14°1' E, *Klášková s.n.* (LD); Flora Bohemia. pr. Belá p.-B., 50°30' N 14°48' E, Jun 1899, *Podpéra s.n.* (JE, W, WU); Karlstein, 49°56' N 14°11' E, May 1885, *Schiffner s.n.* (C); Pagi Zalov u Msenne, 50°10' N 14°23' E, 18 May 1926, *Vasak s.n.* (BR). Ústecký kraj: Deblik, 50°35' N 14°3' E, Jun 1912, *Missbach, s.n.* (S); Langenberg pr. Bečov, 50°27' N 13°43' E, Jun 1898, *Podpéra s.n.* (GH, S). Zlínský Kraj: Hádyberg bei Brüm, 49°6' N 18°2' E, May 1899, *Spitsnes s.n.* (JE).

FRANCE—Alsace: Colmar (Ht Rhin), 48°5' N 7°22' E, 3 Jul 1861, *Duval-Jouve s.n.* (G). Languedoc-Roussillon: Vallon de Lozere, 44°30' N 3°30' E, 22 Aug 1932, *Beauvard s.n.* (G). Provence-Alpes-Côte d'Azur: Lautaret, 45°2' N 6°24' E, 24 Jul 1934, *Beauvard s.n.* (G); Itatns Alpes route Lantanet-Briaçon, 44°54' N 6°37' E, 19 Jun 1960, *Charpin s.n.* (G); Beses Alpes vallen du Crachet près col Vars, 44°32' N 6°42' E, 9 Jul 1967, *Charpin s.n.* (G); Vallouise, Dauphine (Franhigh), 44°51' N 6°28' E, 2 Jul 1975, *Schahel s.n.* (L); Gondes, Vaucluse, 43°54' N 5°12' E, 21 May 1949, *Vautier s.n.* (G). Rhône-Alpes: Savoie, tussem Bonneval en l'Elcot langs de rechter oever van de Arc. Puinhelling, 45°30' N 6°25' E, 17 Jul 1960, *Stud. Biol. Rheno-Trai. in itinera* (U).

GEORGIA—Tiflis: Near the station Sakachavo, 41°43' N 43°28' E, 23 Jun 1918, *Kozlovskiy 1347* (H, LE, U).

GERMANY—Bayern: Untere Hochebene, um die Kiesgruben westlich von Sammern, 48°46' N 12°58' E, 11 Jun 1950, *Freiberg s.n.* (M); Oberpfaz. Osthang des Naabtales nordwestlich von Etterzhausen, 10 km westnordestlich von Regensburg; trockener Waldrand gegenüber Penk, 49°1' N 11°58' E, 18 May 1959, *Roessler 2465* (M); Unterfranken, Unterfir. Muschelkalkgebiet: Hohfeld plerbe nidóok. Thingersheim, 49°14' N 11°43' E, 13 Jun 1986, *Schuhwerk 86/140* (M); Kreuznach, 49°50' N 7°52' E, Jul 1877, *Geisenheyner s.n.* (JE); Legenfeld bei krems a./d. Donau Spiesberg, 50°7' N 11°12' E, Jun 1935, *Handel-Mazzetti s.n.* (WU); Flora Badensis Badberg bei Vbgtsberg, 48°15' N 12°5' E, 1865, *Lenz s.n.* (G), Baden-Württemberg: Mitterndorf gegen Moosbrunn nächst Wien auf trockenen Wiesenhäufig, 49°25' N 8°55' E, 1 Jun 1902, *Handel-Mazzetti s.n.* (WU). Brandenburg: Mittenwalde: Gr Machnower Weinberge, 52°17' N 13°27' E, 18 Jun 1882, *Gross s.n.* (S); Mark Brandenburg, Reitveiner Borge, 52°24' N 12°30' E, 14 Jun 1879, *Jachan 9* (JE); Kalbenstein bei Karlstarz a M., 54°45' N 9°46' E, 17 May 1924, *Oberneder s.n.* (BR, NY). Rheinland-Pfalz: Felsen dicht oberhalb Bahnhof Hatzendorf rechts der Chaussee nach Münstermaifeld, 50°15' N 7°22' E, 11 Jun 1950, *Freiberg 105/6* (M); Norfitforb bei Fischbach Birkenfeld, 49°44' N 7°24' E, 22 May 1897, *Ljift s.n.* (W); H. Thieme. Mainz, 50°0' N 8°16' E, 1843, *Schleiden s.n.* (JE); In Fulfun bei Oberstein, 49°42' N 7°19' E, 20 May 1897, *Hirth s.n.* (G); Nahetal, Bad Münster am Stein, Rotenfels, 49°49' N 7°51' E, 31 May 1987, *Krendl s.n.* (W); Environs de Bingen, 49°58' N 7°54' E, Jul 1879, *Muller s.n.* (BR). Sachsen-Anhalt: Abhänge zum Selktetal (Harz), 51°45' N 10°30' E, 10 Jun 1947, *Aach s.n.* (W); Steinkele bei Wendelstein, 51°17' N 11°28' E, Jun 1878, *Anhel s.n.* (JE); Mittelgebirge. Böhm. Leipa, 51°50' N 12°36' E, 26 Jun 95, *Gross s.n.* (UPS); Hohe Leeden bei Domburg, 51°52' N 11°19' E, 15 Jun 1899, *Haussknecht s.n.* (JE). Thüringen: Kyffhauser, Heinthalben, 51°23' N 11°5' E, 22 May 1953, *Branca s.n.* (JE); Fl. de Nassau Sternberg bei Bornhofen, 51°27' N 10°47' E, 25 May 1880, *Einsander s.n.* (JE); Keruberg bei Jena, 50°55' N 11°36' E, May 1953, *Groll s.n.* (JE); Mittelberg bei Auleben, 51°21' N 10°10' E, 1827, *John s.n.* (JE).

GREECE—West Macedonia: Vernon Oros, vom Vitsi nach Drosopigi, 40°39' N 21°22' E, 10 Jul 1978, *Krendl s.n.* (W).

HUNGARY—Békés: Jánosháza (Baes-Bodrag), 46°29' N 21°15' E, 14 Jun 1910, *Prodán s.n.* (S). Budapest: In Comitat Pest in Ungarn am Hámashatárhegy bei Ofen, 47°30' N 19°2' E, 6 Jun 1900, *Degen & Flatt 82* (BR, GH, H, JE, L, MA, W); Kasposztasmegeger bei Rakospalota, 47°34' N 19°8' E, 23 May 1933, *Korb s.n.* (W); Monor, in Steppenwäldern bei Csévharsasz, 47°18' N 19°26' E, 16 Jun 1975, *Lippold s.n.* (JE). Hajdú-Bihar: Hortobágy, 47°35' N 21°10' E, Jul 1936, *Timmermans s.n.* (L). Pest: Budaöns, Kakukk hepy, 47°36' N 18°56' E, 29 May 1963, *Bisse s.n.* (JE);

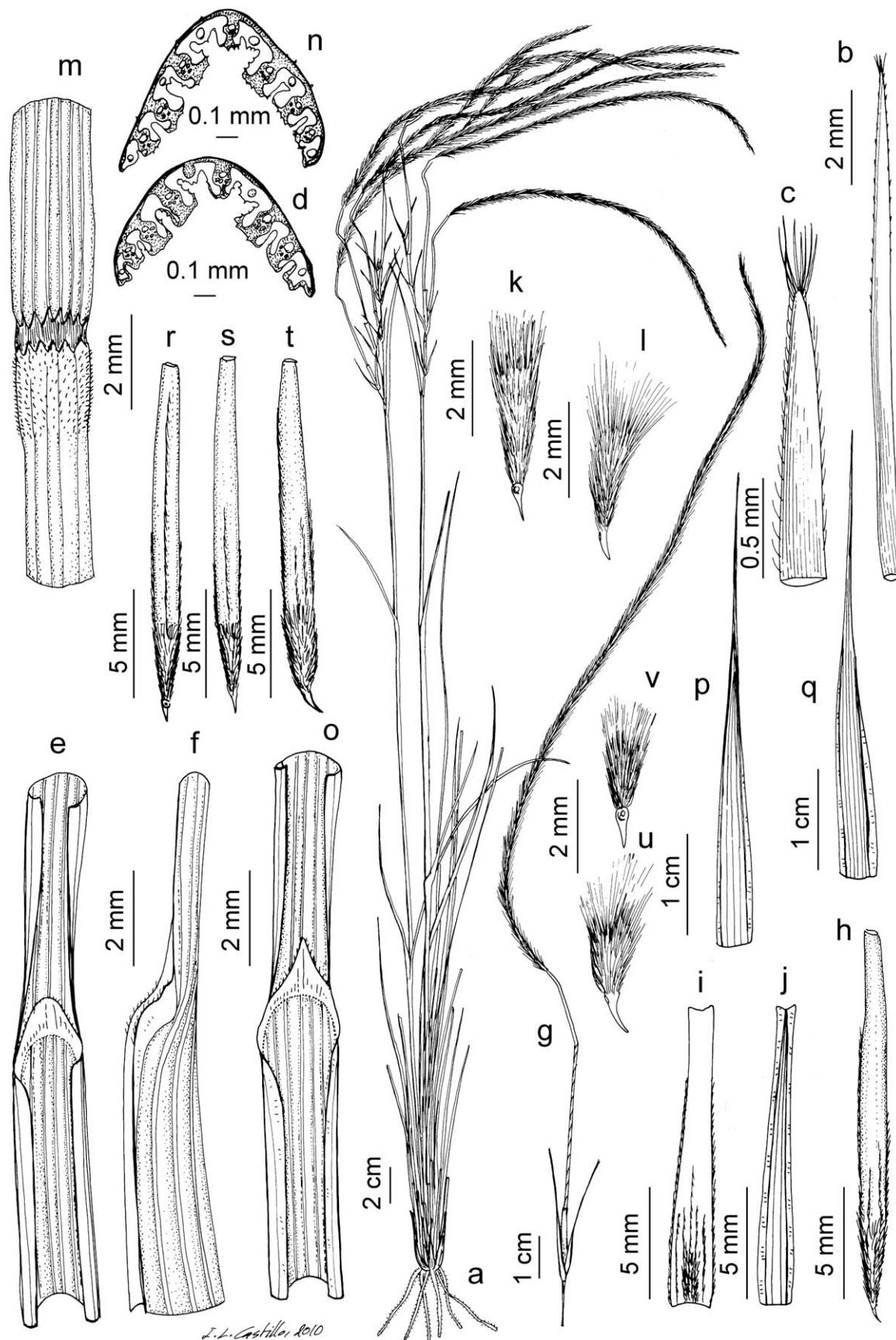


FIG. 9. *Stipa pennata* subsp. *sabulosa*. a. Habit. b. Basal leaf apex. c. Detail of the basal leaf apex. d. Transversal section of leaf-blades. e-f. Basal leaf ligule. g. Spikelet. h. Antheicum. i. Lemma. j. Palea. k. Callus, ventral view. l. Callus, lateral view. *Stipa pennata* subsp. *pennata*. m. Culm node. n. Transversal section of leaf-blades. o. Basal leaf ligule. p. Upper glume. q. Lower glume. r. Antheicum, ventral view. s. Antheicum, dorsal view. t. Antheicum, lateral view. u. Callus, ventral view. v. Callus, lateral view. [based on: a-l Hadinec 2 Jun 1990 (G 00080513); m-v Berger 19938 (MA 692669)]

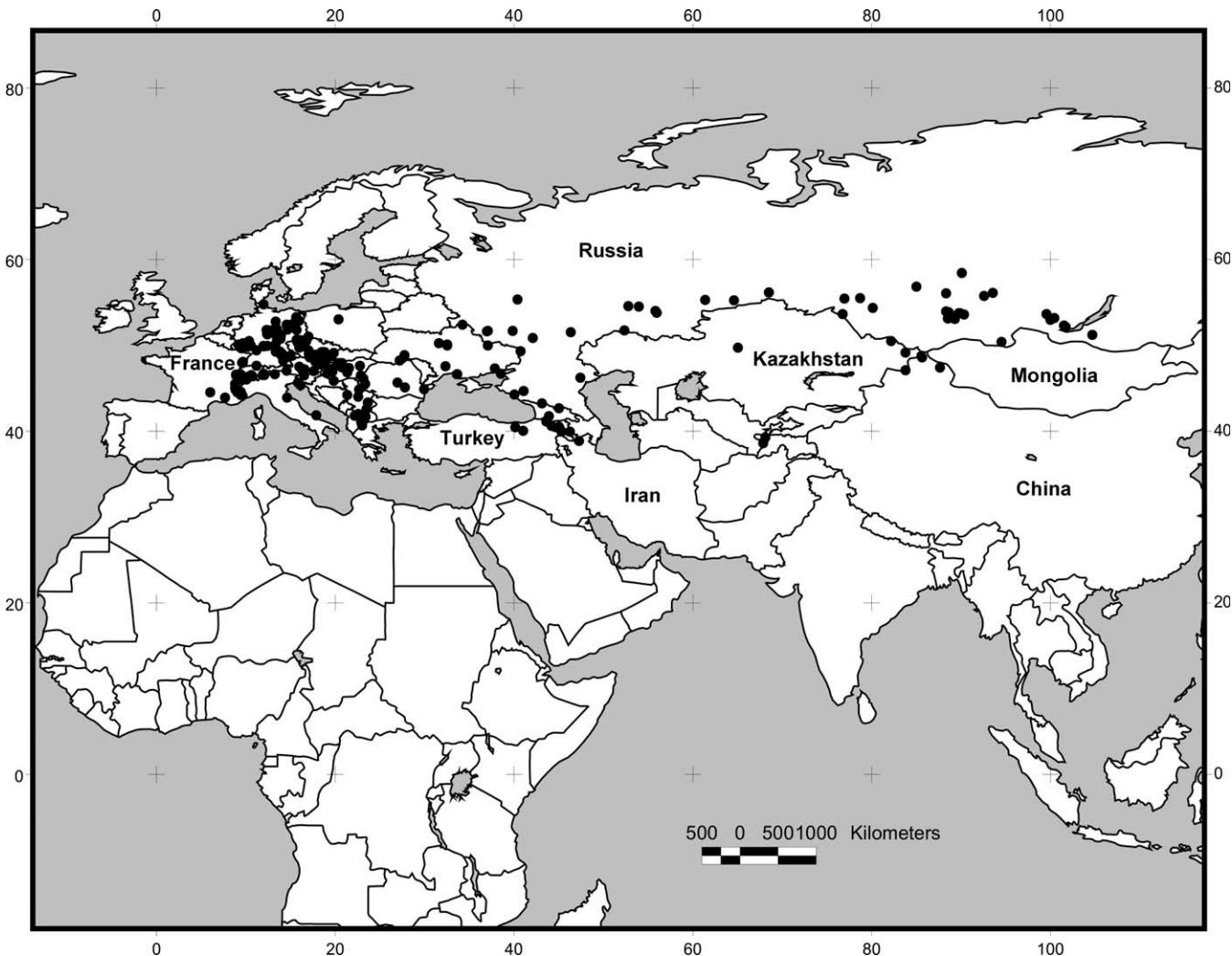


FIG. 10. Distribution map of *S. pennata* subsp. *pennata* (●).

Inter Monor et Pilis, 47°41' N 18°53' E, 31 May 1888, *Borbás s.n.* (JE); In monte "Nagy Koppán". In montibus "Börzsöny", 47°54' N 18°51' E, 14 May 1939, *Walger s.n.* (S, UPS); Farmos, 47°22' N 19°51' E, 6 Jun 1937, *Branco s.n.* (JE); Budaörs, *Csiki hegyek*, 47°27' N 18°58' E, 26 May 1963, *Schneide s.n.* (JE); Veszprém: Bakony, vallis Aszóvotgy infra Alsópere versus Hajméskér, 47°15' N 17°50' E, 29 May 1928, *Jávorka s.n.* (S); 100 m boven Balatonfürdö op. Z.O.-helling, 46°57' N 17°53' E, 19 May 1972, *Kramer 4962* (U). Zala: Keszhelyi-hegi. N Gyenesdiás am Kőmell, 46°46' N 17°17' E, 11 May 1975, *Krendl s.n.* (W). Virös-Benény Vesprimii, May 1900, *Borbás s.n.* (JE).

IRAN—Ažarbāyjān-e Sharqī: Montes Qareh Dagh, prope Aliabad 20 km SW Kaleybar, 38°52' N 47°2' E, 20 Jul 1971, *Lamont & Thermé 44360* (W).

ITALY—Apulia: Promontorio del Gargano, 41°50' N 16°0' E, 6 Jun 1990, *Licht 941 b* (B). Emilia-Romagna: Mte Colombo Val Gesso (FI) 43°55' N 12°33' E, 18 Jul 1961, *Bono s.n.* (FI). Friuli-Venecia Julia: Trieste, Monte Spacerto, 45°40' N 13°46' E, Jun 1869, *Marchesetti s.n.* (HBC). Piamonte: Valle Formazza-Riva sinistra del t. Hohsand tra Zum Stock e Grelschnode, 46°22' N 8°26' E, 29 Aug 1912, *Boggiani s.n.* (BR); Alpe marittime, Argentera, ob der Terme di Valdieri, gegen die Gias Lagarol, 44°12' N 7°16' E, 6 Jul 1982, *Burri & Krendl s.n.* (W). Valle de Aosta: Prov. Cuneo, Alpi Cozie Ander Straße von Casteldelfino im Valle Varaita zum Colle di Valante, 44°35' N 7°4' E, 13 Aug 1980, *Lipper & Merxmüller 17331* (M). Veneto: Oerh San Vigilio, 46°37' N 11°7' E, 23 Apr 1951, *Aach s.n.* (W).

KAZAKHSTAN—Akmola: Atbasar District. Basin of Beleudy river, Dyusenbai river at the middle part, 49°43' N 65°45' E, 18 Jun 1914, *Krascheninnikov 5345* (S). East Kazakhstan: Ivanovsky range, in the region of Poperechnoe village. The valley of Belya uba river, 50°28' N 83°48' E, 25 Jun 1970, *Kotukhov s.n.* (UPS); Altaj merid. Jugum Narymense, prope

pag. Katon-karagaj, 49°10' N 85°30' E, 2 Jul 1930, *Smirnow 28* (H, JE, L, S, W); Saur range, the upper reaches of the Kizil-Kiya river, in the region of Kizil-Kiya winter camp, 47°4' N 85°30' E, 3 Jul 1991, *Kotukhov s.n.* (B, K, UPS); Altaj merid, ad fl. Sarymssak, prope pag. Katon-karagaj, 49°10' N 85°30' E, 2 Jul 1930, *Smirnow 4* (H, JE, L, S, W).

MACEDONIA—Polog: E-Hänge der Sar Planina oberhalb Tetovo, Kalkfelshänge oberhalb Popova Sapka, 42°0' N 20°58' E, 6 Aug 1976, *Podlech 28441* (M). Southeastern Republic Macedonia: Prilep, montis Drenska-planina, 41°23' N 22°13' E, 12 Jun 1918, *Bornmüller 5192* (JE). Vardar: N Pisoderion, auf der Bela Voda, 41°38' N 21°44' E, 5 Jul 1978, *Krendl s.n.* (W); Babuna Fl. Mukos-Dab, 41°40' N 21°48' E, May 1969, *Leute 50* (W); Baba Planina: Nordseite des Pelister bei Bitola, 41°1' N 21°20' E, 1 Jul 1968, *Roessler 6363* (M).

MONGOLIA—Zapadna Mongolia, Gora May Kapsagai kamo, 6 Jun 1914, *Sishkin s.n.* (NY).

POLAND—Kujawsko-Pomorski: Torun-Bielany, 45°53°2' N 18°36' E, 31 May 1975, *Gugnacko-Fiedor 195* (H, L, UPS).

ROMANIA—Arad: Inter Mócs und Szombathely, Transsilvania centralis, 46°8' N 21°31' E, 1 Jun 1869, *Janka s.n.* (PR, W, WU). Brașov: Distr. Brașov, 45°38' N 25°35' E, Jun 1965, *Morariu s.n.* (LD). Caraș Severin: Dorfes Kursovecz im Comitat Krassó-Söreny im Banat, 45°30' N 21°45' E, 25 Jun 1902, *Lajos 312* (C, GH, H, L, MA, W). Prahova: Tohani, distr. Prahoca-Romania, 45°4' N 26°26' E, 1 Jun 1969, *Negrean s.n.* (M, S). Tulcea: Babadagh, 44°54' N 28°43' E, 11 Jun 1973 (LD).

RUSSIA—Astrakhanskaya Oblast: Bagdo, 46°13' N 47°11' E, 28 May 1925, *Ilijn & Grigorjev 137* (S). Bashkortostan: Bashkir Republic (former Ufa Province). Belebeevskiy District. The island on the Kandry-Kul' lake, 54°30' N 54°4' E, 21 Jun 1926, *Fedchenko, B.F. et al. 201* (LE); Zalair District. 5 km SE from Mrakova village, 53°47' N 56°11' E, 3 Jul 1928, *Knorrung 178*

(LE). Buryatiya: Mukhor-Shibir'village, Ulan-tuya village, 51°14' N 107°35' E, 11 Jul 1965, *Peshkova & Tarasova* 2043 (LE); Ulan-Ude District, Nadeino village, Vyosaya mountain, 55°20' N 39°45' E, 14 Jul 1967, *Reschikov s.n.* (LE). Bryanskaya: Markovsk ad fluv. Sudost. ca 1 km N a pago, 52°24' N 33°15' E, 6–7 Jul 1979, *Skvorcov s.n.* (M). Chelyabinskaya Oblast': The Southern Ural, the vicinity of Miass town (former Miass plant). Ilmen Reserve, top of Savel'kul' mountain, 55°16' N 61°53' E, 16 Jun 1937, *Dervtz s.n.* (LE). Irkutskaya: Balagansk District, on islands of Angara river, Ubinskoye Lake, 52°17' N 104°14' E, 14 Jul 1909, *Ganeshin* 374 (LE); Balagansk District, Bazheevskoye village, 52°58' N 102°38' E, 16 Jun 1906, *Maljtsiev* 376 (C, GH, H, JE, L, LE, NY, S, W); Irkutskaya guberniya, 8 Jun 1907, *Maljtsiev* s.n. (M). Kabardino-Balkariya: Caucasus centralis: distr. Tiryauz, montis Elbrus, in vicinitate glacie Sheldia, 43°15' N 42°38' E, 29 Jul 1981, *Vasák s.n.* (W). Krasnodarskiy: Baraba. Between villages Taryshkina and Kochetovskiy, 44°15' N 39°23' E, 10 Jun 1912, *Krylov s.n.* (NY). Krasnoyarsky: Minusinsk Basin, Tigritskoye village, 53°35' N 92°24' E, 23 Jun 1959, *Golubeva et al. s.n.* (LE); Minusinsk Basin. Vicinity of village Tigritskoye, 53°35' N 92°24' E, 20 Jun 1959, *Golubeva et al. s.n.* (LE); Yenisei Province, Kanskij district. Steep slope to river Rybnaya near village V. Rybinskoye, 55°46' N 94°46' E, 3 Jun 1911, *Kuznetsov s.n.* (LE); Yenisei Province, Achinsk district, Podgornoye village, valley of Chulyum, 56°4' N 90°20' E, 8 Jul 1912, *Kucherovskaya s.n.* (LE); Minusinsk District, Between mountain Izyk Yerbinskiy and river Bei-Buluk, 53°58' N 90°18' E, 2 Aug 1910, *Smirnow* 54 (S). Kurganskaja: Kurgan District, Zvenigorodskiy District, Shemerov Village on river Alabuga, 55°14' N 65°18' E, 19 Jul 1928, *Ivanova & Tonshina* 836 (LE). Kurskaya: Streletskiy District, Central-Chernozem State Reserve, Streletska steppe, 51°36' N 36°8' E, 29 Jun 1965, *Novičkova s.n.* (H). Novosibirskaya: Chanovskiy District, close to railway station Karachi, 53°37' N 78°5' E, 28 Jun 1956, *Vagina & Kovachevich s.n.* (JE); Ordynsky District, Noviy Sharap village, 54°20' N 81°40' E, 19 Jun 1957, *Kulshnova & Buturlina s.n.* (S). Orenburg: Watershed of the rivers M. Churan and Tok, "N of Staroe Gumerovo village, 51° 45' N 52° 21' E, 7 Jun 1930, *Suhova* 18 (LE). Samara: Bugulma district, between fortresses Cheremshanskaya and Sheshminska (in about 2 km from each other), 54° 33' N 52° 48' E, 23 May 1889, *Korshinsky s.n.* (C). Saratow: Sapreta, 51° 32' N 46° 0' E, *Becker* (BR, JE, S, UPS, WU). Tomsk: Kainski district, Krasnovskiy, 56° 51' N 86° 47' E, 1912, *Kronotov s.n.* (LD); Kainsk district, prope pag. Pogorjelskaja, 55° 27' N 78° 18' E, 25 Jun 1930, *Poddjakova s.n.* (NY); Kainsk district. Ubinskoye Lake, 55° 30' N 80° 10' E, 8 Jun 1912, *Klopotov s.n.* (S). Tyumenksaya: Tobolsk Province. Ishimskiy District, NE of village Afonino, on Kuchumova gora, 56° 10' N 69° 25' E, 2 Jul 1895, *Gordyagin* 1260 (LE). Tuvinsky: Usinsky Region and the adjacent part of the Uryanskiye steppes, 58° 26' N 92° 10' E, 1907, *Shulga s.n.* (LE). Voronezh: Circa Voronezh, 51° 40' N 39° 12' E, *Grüner s.n.* (C).

SERBIA—Bajna Basta: Wess-Velez, 44°13' N 19°39' E, 10 Jul 11, *Schneider s.n.* (W). Bela Crvka: Banat, Deliblatska peščara inter Devojački bunari et Korn, 44°54' N 21°5' E, 29 Apr 1968, *Mayer s.n.* (M). Pančevo: Deliblát. Kincstári homokpuszta, 44°49' N 21°2' E, May 1909, *Ullépitsch s.n.* (U). Pirot: Sićovo, 43°20' N 22°5' E, 10 Jun 1932, *Ilić s.n.* (WU). Sumadija: Kragujevac (Bozatsch), 44°1' N 20°55' E, May 94, *Dimitrijin s.n.* (WU). Vranje: Monte Pljackavica, 42°35' N 21°54' E, 11 Jul 1896, *Adamovic s.n.* (W).

SLOVAKIA—Bratislavský: Pressburg, 48°9' N 17°7' E, May 1868, *Schneller s.n.* (BR, UPS); Nitriansky: Čachtice bei Nové Mesto nad Váhom, 48°43' N 17°47' E, 21 May 193, *Gailing s.n.* (JE); Sandflächen bei Čenkov, unweit Štúrov an der Donau, 47°56' N 18°31' E, 14 Jun 1962, *Schneider s.n.* (JE).

SWITZERLAND—Graubünden: Between Sur et Rona (grisons), 46°33' N 9°37' E, 13 Jul 1975, *Berghew s.n.* (BR); Eggerberg, 46°19' N 7°52' E, 4 Jun 1986, *Theurillata 4010* (BR, C, H, L, M, MA). Thurgau: Pfyn (Schweiz, Kanton Wallis) Pfinwald südwestlich Milliere, 47°35' N 8°57' E, 21 May 1965, *Berger* 2957 (BR, H, MA). Valais: Zmutt (bij Zermatt), 46°1' N 7°45' E, 23 Jul 1934, *Boom* 8695 (L); Branson (Schweiz, Kanton Wallis) bei Les Follatères, 46°35' N 6°30' E, 18 May 1957, *Berger* 16735 (BR, H, MA); Zermatt, 46°1' N 7°45' E, Jul 1955, *Duvigneaud s.n.* (BR); Hügel in Pfinwald bai Siders, 46°32' N 8°18' E, 8 May 1934, *Koch s.n.* (LD, MA, NY, S).

TAJIKISTAN—Sughd: Central part of Mountain Zeravshan. Basin of River Pasrut, left bank of river Izmat, 39°15' N 69°0' E, 18 Jul 1948, *Korotkova* 443 (M); Pamir, Hissarski khrebet, 20 km situ septentrionali ab appido Dushnabe, in valle flumiinis Varzob, 38°35' N 68°46' E, 23 May 1974, *Vasak s.n.* (M).

TURKEY—Erzurum: Askale-Bayburt 1 km s Kop Gecidi, 40°3' N 40°26' E, 14 Jul 1988, *Nydegger* 43755 (G); Gümüşhane: Armenia turcica Szanschak Gümüşchkhane. Karagoeldagh, 40°27' N 39°29' E, 31 Jul 1894, *Hackel* 7383 (BR, G, JE, W).

UKRAINE—Chernivets'ka Oblast: Kleine Karpathen: Auf dem Berge Kamena bei Blasenstein, 48°14' N 25°50' E, 23 May 1926, *Ronniger s.n.*

(H). Donetsk: Stalin region, Volodarsky District, village Nazarovka, reserve Kamennye Mogily 47°18' N 37°4' E, 1 Jun 1954, *Kuznetsova s.n.* (LE). Kharkivs'ka Oblast: Circa Charcovia, 50°0' N 31°27' E, 31 May 1854, *Czerniaëw s.n.* (MEL). Khersons'ka Oblast: Cherson, 46°38' N 32°36' E, Jun 1866, *Lindemann s.n.* (BR). Kyivs'ka Oblast: Kiev, 50°15' N 30°30' E, 25 May 1925, *Pisopliczka s.n.* (S). Luhansk: Voroshilovgrad Region, Melovskoy District, reserve Streletska steppe, 49°18' N 40°5' E, 26 May 1956, *Sarycheva s.n.* (LE). Mikolayiv: Semenovkaon Bug village, 47°32' N 31°16' E, 9 May 1909, *Pachoskii s.n.* (LE).

**b.** subsp. *SABULOSA* (Pacz.) Tzvelev, Novosti Sist. Vyssh. Rast. 10: 80. 1973; *S. pennata* f. *sabulosa* Pacz., Fl. Chers. 1: 112. 1914; *S. joannis* subsp. *sabulosa* (Pacz.) Lavr., Fl. URSS 2: 123. 1940; *Stipa borysthenica* Klokov ex Prokud. in E. Wulff, Fl. Kryma 1(4): 25. 1951; *S. sabulosa* (Pacz.) Sljussarenko, Trudy Nauchno-Issled. Inst. Biol. 37: 26. 1963. nom. illeg.—TYPE: UKRAINE. Kherson province, Alexandrovskii post, along Tyasmin, 18 Jul 1911, *Pachoskii s.n.* (lectotype: LE!, designated by Tzvelev, 1976)

*Stipa anomala* P.A. Smirn., Delect. Sem. Horti. Bot. Univ. Mosq. 15. 1930; *S. pennata* var. *anomala* (P.A. Smirn.) Novosti Sist. Vyssh. Rast. 11: 18. 1974.—TYPE: KAZAKHSTAN. Uralsk District, Teplov Region between the villages of Faduleev and Novenk, 16 Jun 1929, *Rubitsov* s.n. (holotype: LE!).

*Stipa joannis* subsp. *germanica* Endtm., Wiss. Z. Ernst-Moritz-Arndt-Univ. Greifswald, Math.-Naturwiss. Reihe 11: 148. 1976; *S. germanica* (Endtm.) Klokov, Novosti Sist. Vyssh. Nizsh. Rast. 1975: 67. 1976; *S. sabulosa* subsp. *germanica* (Endtm.) Martinovský & Rauschert, Preslia 48: 187. 1976; *S. borysthenica* subsp. *germanica* (Endtm.) Martinovský & Rauschert, Feddes Repert. 88: 320. 1977; *S. borysthenica* subsp. *germanica* (Endtm.) Dengler, Gleditschia 28: 20. 2000, comb. superfl.—TYPE: GERMANY. Geesower bei Gartz (oder) Geesower Hügel, Hügel 3, 11 Jun 1960, *Endtmann* s.n. (holotype: GFW; isotype: JE!).

*Stipa joannis* var. *marchica* Endtm., Wiss. Z. Ernst-Moritz-Arndt-Univ. Greifswald, Math.-Naturwiss. Reihe 11: 148. 1976; *S. borysthenica* var. *marchica* (Endtm.) Rauschert, Mitt. Florist. Kart. 4: 11. 1978.—TYPE: GERMANY. Naturschutzgebiet "Geesower Hügel" zwischen Gartz/Oder und Geeson /Kr. Angermünde, 18 Jun 1960, *Endtmann* s.n. (holotype: GFW; isotype: JE!).

Herbs 40–75 cm high. Basal leaves 15–55 cm long. Leaf-blades abaxial surface glabrous or minutely scabrous, adaxial surface scabrous, leaf-blades apex glabrous or with an apical tassel of hairs almost at young leaves. Culms leaf-sheaths, papillose or scabrous. Glumes (3.5)4.5–6(8) cm long. Antheicum (16)16.6–20(21) mm long; lemma (12.2)12.6–16 mm long, with seven rows of hairs, the dorsal and subdorsal row slightly fused at the base and the remainder rows distinct, the ventral one ending (0.5)3–5(6) mm long below the top, the dorsal row ending (7.2)7.3–9(10) mm below the top and longer than the subdorsal ones. Callus (3.8)3.9–5 mm long (callus/lemma = (0.26)0.27–0.33(0.35)), villous, scar elliptic, straight, peripheral ring (0.67)0.77–0.96(1) mm long, (0.2)0.21–0.26(0.28) mm wide (ratio width/length = (0.23)0.24–0.32(0.36)). Awn (25)29–35(36) cm long. Figure 9 a–l.

**Chromosome Number**—Unknown.

**Habitat and Distribution**—This taxon grows on sandy soils of slopes, steppes, riversides and forest glades, from seacoasts

up to lower mountain belts, 0–2000 m. Ranges from East and Central Europe to South-East Russia, also occurring in Kazakhstan (Aral Caspian, Balkhash area), and in South and central Siberia. Scarcely found in western Mongolia (Fig. 11).

**Phenology**—Flowering specimens have been collected in May, June, and July.

**Representative Specimens Examined**—**AUSTRIA**— Niederösterreich: Marchfeld, Weikendorfer Remise: Düne 0,4 km NE kt 152/Brunnfeld (7666/4), 48°33' N 16°79' E, 25 May 1986, *Strudl* 145 (W); Weinviertel, Falkenstein: 0,5 km NNE de Ruine, 48°43' N 16°46' E, 20 May 1985, *Pokorny & Strudl s.n.* (W); Weinviertel, Gollitsch bei Retz, SW Hang oberhalb des Steinbruch, 48°78' N 15°96' E, 31 May 1982, *Pokorny & Strudl s.n.* (W).

**BULGARIA**— Varna: 15 km W of Varna, NW of Poveljanovo, Pobiti camani place, 43°13' N 27°42' E, 2 Jun 1999, *Raus & Pina Gata* 35–1–13 (W); N of Nessebar, 42°37' N 27°43' E, 27 May 1999, *Raus & Pina Gata* 24–1–4 (W).

**CZECH REPUBLIC**— Jihomoravský Kraj: Göding, pr. Rohatetz, 48°52' N 17°11' E, Jun 1935, *Laus s.n.* (H); Hodonín district, inter opp. Bzenecet Rohatec, 48°55' N 17°16' E, 2 Jun 1990, *Hadinec s.n.* (G).

**GERMANY**— Bayern: Niederbayern: Felsen der Weltenburger Enge gegenüber dem Kloster Weltenburg, Landkreis Kelheim, 48°54' N 11°50' E, 2 Jun 1962, *Podlech* 8209 (M). Berlin: Berlin, 52°19' N 13°33' E, (MEL). Brandenburg: Potsdam, 52°24' N 13°2' E, *Oenicke s.n.* (H, S); Brabdburgo. N-Rand des "Höllengrund" arm W-Rand des, 52°27' N 13°58', 19 Jun 1964, *Endtmann s.n.* (JE); Geesower Hügel (nr 4; SW-Hang) S Geeson, Kr Angermünde, 53°2' N 14°0' E, 20 Jun 1962, *Endtmann s.n.* (JE); Gresower Hügel, nr 4 seeson / Kr. Angerm, 53°15' N 14°23' E, 15 Jun 1964, *Endtmann s.n.* (JE); 0,5 km NNW vornerk Bergthal von Altranfl, Kr. Freienwalde 10,

52°45' N 14°4' E, 18 Jul 1962, *Endtmann s.n.* (JE); Rhinow, am Litchberg, 52°45' N 12°20' E, Jul 1898, *Pralrow s.n.* (M); Missenvall de Co Machnower Weinberge, 52°17' N 13°27' E, 28 Jul 1881, *Scheppig s.n.* (M).

**HUNGARY**— Bács-Kiskun: S Teil des Alföld, Kiskunsag, ca. 6.5 km W Fülpöphaza, Szappen-Szek, 46°35' N 19°15' E, 8 May 2005, *Walter* 8175 (W); Kecskemét area, Fülpöphaza (20 km Wof Kecskemét), 44°47' N 19°5' E, 26 May 1987, *Bergqvist et al.* 5 (S). Budapest: Budapest, Csepel, Insel, 47°25' N 19°5' E, 19 May 1929, *Ronniger s.n.* (W); Pest: Montis Kis Szenús supra Pilis-Szentivan, 47°37' N 18°54' E, 21 May 1916, *Degen s.n.* (S); Pest Ongeveer 30 km oostelijk van Solt, nabij Fülpöphaza, district B'cs-Kiskun, 44°47' N 19°5' E, 30 May 1970, *Bodemk. exc.- Th. J. Visser* 141 (U).

**IRAN**— Āzārbāyjān-e Gharbī: Berdesin valley, 38°29' N 45°0' E, 20 May 1929, *Cowan & Darlington s.n.* (K).

**KAZAKHSTAN**— Akmola: Western Karabutak, 51°47' N 73°21' E, 3 Jul 1971, *Ikonnikov & Litvinova* 6747 (LE); Kurgalyino District, village Aryktý, 50°38' N 70°33' E, 29 May 1973, *Lovelius s.n.* (LE). Aktobe: Chelkar District, slope of Tyubel against the place of its falling to Ters-Butak, 58°2' N 48°18' E, 31 May 1927, *Spiridinow* 294 (NY); Turgai Region, Aktyubinsk, 52°55' N 62°22' E, 2 Jun 1904, *Yanishevsky s.n.* (K). East Kazakhstan: Semipalatinsk Province, Krasnooptyabr'skaya parish, right bank of river Chara, 49°57' N 80°44' E, 6 Jun 1928, *Enden* 102 (NY); Novoshul'binskiy District. Vicinity of village Bazhenovka, Irtysh floodplain, 50°23' N 80°59' E, 10 Jun 1973, *Prokofiev & Agafanov s.n.* (C); Valley of River Cherny Irtysh (Black Irtysh) near Alkabek on mountain "Chudesa", 48°1' N 85°34' E, 23 May 1961, *Grudzinskaya* (LE). Karagandy: Upper reaches of River Sary-su, valley of Dzhaksy-sary-su river. N Zhana-Arka, 48°41' N 71°37' E, 4 Jun 1937, *Pazij* 19 (LE); Left bank of the river Sary-su, near Dzhezkazgan-Zharyk railway-line, on 179 th km, 48°34' N 71°54' E, 22 Jun 1958, *Grubov* 21 (LE).

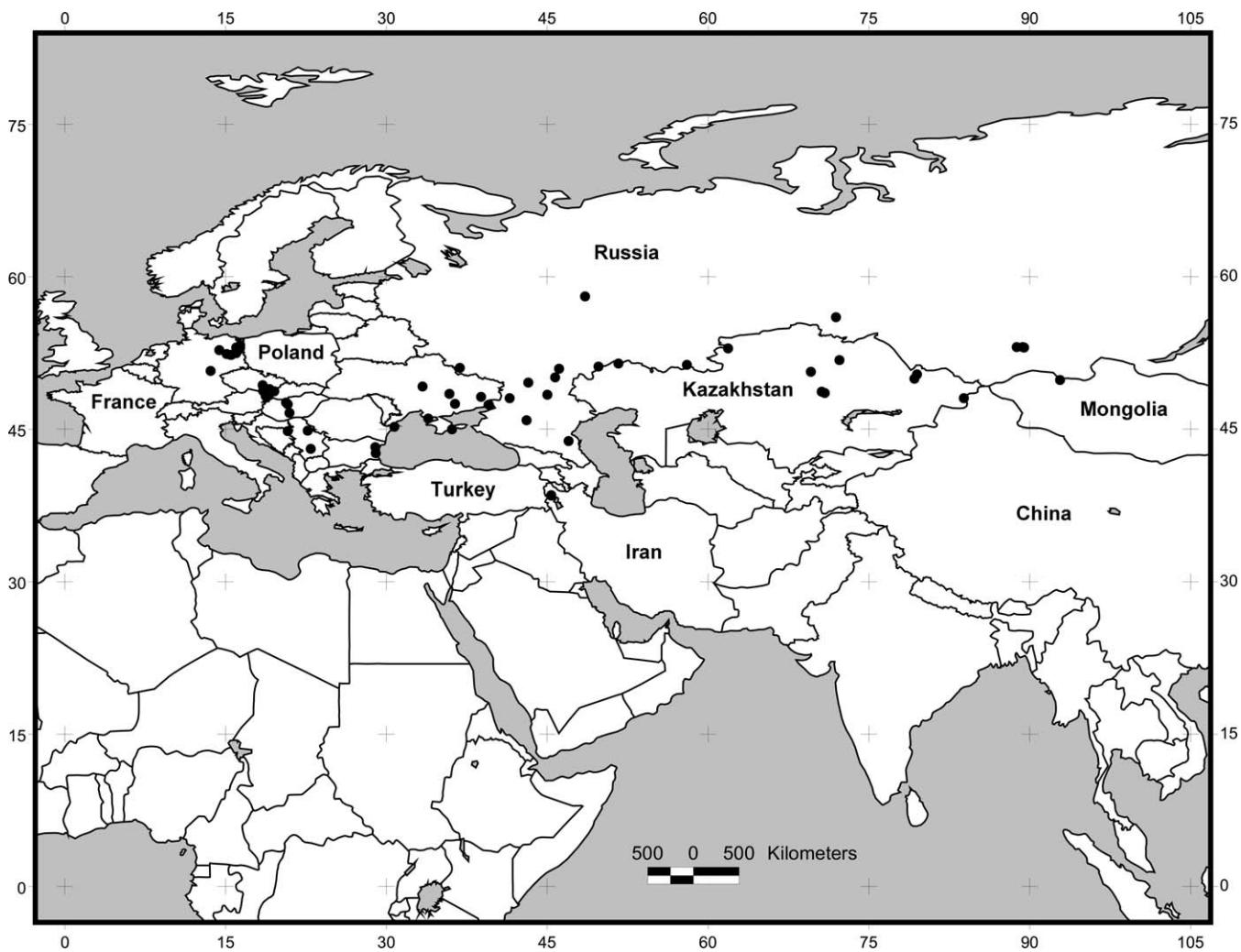


FIG. 11. Distribution map of *S. pennata* subsp. *sabulosa* (●).

MONGOLIA—Uvs: The eastern edge of Ubsunur Hollow., S Altan-els, 70 km to NE of Barun-Turun (Ybsunur Region), 49°50' N 95°5' E, 5 Jul 1988, Kamelin et al. 876 (LE).

POLAND—Zachodniopomorskie: North Polond, Nawodna near Chojna/Szczecin Province, 53°0' N 14°24' E, 30 Jun 1973, Ceynowa-Gieldon 297 (H); North Polond. Rudnica Stara. Szczecin Prov., on slope of river Odra valley, Rudnica Stara and the railway station Siekierki, 52°49' N 14°15' E, 10 Jun 1969, Ceynowa-Gieldon 296 (H).

ROMANIA—Transilvania, Jun, Schur s.n. (W). Tulcea. 18 km NNW of Sulina at Sfistofca, 45°12' N 29°35' E, 10 Jun 1987, Lundqvist 16738 (S).

RUSIA—Dagestan: Kizlyar District. Ravine Ary-su, prope Ariu-Su, 43°50' N 46°42' E, 23 Jun 1926, Prokofieva 122 (NY). Khakasiya: Minusinsk District, Yenisei River, the vicinity of Oznachennoe village, 53°5' N 91°23' E, 25 Jun 6 Jul 1926, Reverdator s.n. (S); Minusinsk Basin, Khakassia Autonomous Region, Beisk District, between B. Utu and Ust'-Kendryky, 53°4' N 90°47' E, 3 Jul 1959, Golubeva et al. s.n. (LE). Kurskaya: Flora Kurskaya, 51°0' N 36°0' E, 1906, Kashmenskiy s.n. (W). Omsk: Sibiria, prope oppid. Omsk, 56°0' N 73°0' E, Jun 1877, Weckman s.n. (H). Oremburg: Guberlinskie Mountains, 5 km above the mouth of Guberli river, 51°20' N 58°21' E, 18 Jun 1964, Vinogradova 61 (LE). Rostovskaya: Gow, Charkow, Pokrovskoye, 47°24' N 38°53' E, 29 May 1854, Reinhard s.n. (W); Voroshilovograd Region, Krasnodon District, 8 km S of Krasnodon on the highway to Sverdlovsk, 48°1' N 40°54' E, 14 May 1971, Ikonnikov & Litvinova 5099 (LE). Saratov: Ural Region, Chizhi district, from Chizhi II to Ozinki, on the top of Obschiy Syrt, 51°10' N 49°40' E, 2 Jun 1924, Larin & Musatova 218 (NY). Volgograd: Sarpa distr. inter Zaza et Plodovitoje, 48°22' N 44°37' E, 14 May 1970, Skvortsov s.n. (C); Left bank of river Don, Frolov District, between Serafimovich and Ar-cheda, 49°34' N 42°44' E, 17 Jun 1971, Ikonnikov et al. 6100 (LE).

SERBIA—Central Serbia: Banat, ad Deliblato, 44°49' N 21°2' E, May 1935, Soška s.n. (S); Banat, Deliblatska peščara inter Devojački bunari et Korn, 43°2' N 21°19' E, 29 Apr 1968, Mayer s.n. (H).

SLOVAKIA—Trenčiansky kraj: Nové Mesto nad Váhom, pagus Visnové, sub ruina Cachticky, 48°43' N 17°45' E, 12 May 2002, Šída 4387 (M).

UKRAINE—Chersons'ka Prov: Cherson, ins. Dscharylgacz, Srednij, 46°2' N 32°55' E, 23 May 1948, Pobedimova 5102 (C, H, JE, LE, M, W). Dnipropetrovs'ka Oblast: Marinpol district, pag. Czerdakly, supra fl. Kalczik, 48°27' N 34°59' E, 17 May 1926, Kleopou s.n. (S, W). Donetsk: Urochische Sosna, Mayatzkoe lesnichastvo (dendrological park), 48°10' N 38°7' E, 21 Jul 1973, Ivashin 1516 (LE). Krym: Sudak district, mountain Syry-Kay (Karadag Range) near village Planerskoe, 44°57' N 35°14' E, 25 Aug 1961, Tzvelev 353 (H). Zaporiz'ka Oblast: Distr. Ossypenkiensis, prope opp. Ossypenko, 47°30' N 35°30' E, 19 May 1930, Kleopou s.n. (S).

**Notes**—The name *S. pennata* was rejected by several authors, who considered it a “*nomen ambiguum*” (Scholz 1968; Fuchs-Eckert 1980; Kerguelen 1983). Mansfeld (1939) tried to clarify the taxonomic position of *S. pennata*, and cited a Clusius plate that belongs to what has been frequently recognized as *S. joannis*. Nevertheless, he did not make a formal lectotypification based on that plate. Martinovský and Skalický (1969) followed Steven's (1857) interpretation and retained *S. pennata* as *S. eriocaulis*, designating a Jussieu's plant as the lectotype, even though it did not represent original material studied by Linneaus. Freitag (1985) selected original material from the van Royen herbarium (L) as the lectotype; this material fit Mansfield's concept of *S. pennata*, restoring the use of this name, which is an earlier name than *S. joannis*. Most subsequent authors (Moraldo and Ricceri 2003; Vázquez and Devesa 1996) have followed Freitag's designation, which is the one followed in the present paper.

*Stipa pennata* is the most widespread and polymorphic of the three taxa belonging to subsection *Stipa*. The most distinctive character of *S. pennata* is the marginal rows of hairs ending 2–5 mm below the top of the lemma. Endtmann (1962) described *Stipa joannis* subsp. *germanica* and var. *marchica* from plants collected in Geesower and Gartz (Germany), both of which are characterized by a marginal row of hairs reaching the lemma apex. Despite that, specimens with the marginal row reaching the lemma apex and ending 2–5 mm before the lemma apex are found within single specimens,

indicating that this trait is not sufficient for species delimitation. We thus consider *S. joannis* subsp. *germanica* and var. *marchica* as synonyms of *S. pennata* subsp. *sabulosa*. This taxon is highly variable especially in the leaf ornamentation. Numerous varietal and subspecific names have been applied to plants of this species. The abaxial surface of the basal leaves ranges from glabrous to minutely scabrous, whereas the adaxial surface can be scabrous, pubescent or sparsely pilose. We could not find any relationship between geographical distribution and leaf ornamentation and therefore no infraspecific taxa were recognized.

*Stipa pennata* can be easily distinguished by the presence of an apical tassel of delicate hairs on the young leaves. However, these hairs are deciduous or may not develop in some populations. Specimens lacking those hairs have been treated as *S. lejophylla*. However, such variation is frequently found over the whole area of distribution, being considered a variable character, and of little taxonomic value (Freitag 1985).

The plants that have been recognized as *S. anomala* (= subsp. *pennata*) and *S. danubialis* (=subsp. *sabulosa*), exhibit a hairy column. However, individuals with hairy columns occur within populations of individuals with glabrous columns. For this reason they have been considered mutational forms that are distributed throughout its distribution area (Scholz 1985).

### 3. STIPA TURKESTANICA Hack., Acta Horti Petrop. 26: 59. 1906.—

TYPE: TAJIKISTAN. Shugnan, Dshidak, in valle fl. Badam-dara, 27 Jul 1904, Fedtschenko s.n. (holotype: W!).

Herbs 15–65 cm high, perennial, caespitose; branching intravaginal. Culms 2–3 noded, nodes glabrous (rarely pubescent), violet; culm internodes scabrous, pubescent (rarely glabrous). Basal leaves 11–51 cm long, green and occasionally pruinose; leaf-sheaths glabrous, papillose, scabrous or minutely pubescent, margins glabrous or ciliate, cilia 0.1–1 mm long; leaf-blades 8–41 cm long, (0.2)0.3–0.5(0.7) mm in diameter, convolute, abaxial surface distinctly scabrous or with sparsely stiff hairs, adaxial surface scabrous, minutely pubescent or pubescent, hairs (0.02)0.04–0.22(0.28) mm long, leaf-blades apex acute, usually glabrous; ligules (0.5)0.9–6.7(10.2) cm long, truncate, rounded, acute or lanceolate, glabrous, scabrous or pilose, ciliate (rarely glabrous), cilia (0.05)0.09–0.38(0.5) mm long. Floriferous culm leaves 14–40 cm long; leaf-sheaths 12–36 cm long, somewhat scabrous with stiff hairs near the leaf-blades and the margins, glabrous, papillose, margins glabrous; leaf-blades 1–10 cm long, (0.14)0.18–0.4(0.5) mm in diameter, abaxial surface scabrous or with sparsely stiff hairs, adaxial face pubescent or minutely pubescent (rarely scabrous), hairs (0.03)0.04–0.22(0.36) mm long; ligules (0.8)1.1–5(20) mm long, obtuse, rounded, acute or lanceolate, scabrous or glabrous, margins glabrous, tip glabrous or ciliate, cilia (0.02)0.05–0.3(0.4) mm long. Panicles 6–27 cm long, contracted, exserted or partially enclosed by the upper leaf-sheaths, 3–5(7) noded; basal internode (1.4)4.7–16(28) cm long, scabrous (rarely pilose with hairs 0.07–0.41 mm long); branches (0.7)1.1–3.2(4.3) cm long, erect or almost erect, usually setulose, setae (0.02)0.05–0.55(0.79) mm long; basal nodes with (1)2 branches with 1–2 spikelets each. Glumes subequal, lanceolate, acuminate, glabrous or ciliate on the central nerves, cilia (0.09)0.15–0.7(1.1) mm long, green with purple stains, margins and tip hyaline, the lower (2.4)3.4–5.5(6.5) cm long and 3–5 nerved, the upper (2.3)3.2–5.1(6) cm long and 5–7 nerved. Antheicum

(8.3)10.4–14.4(14.8) mm long, (0.6)0.7–1.3(1.5) mm wide, fusiform, coriaceous, green, pale or brown; lemma (6.7)8.5–11.7(12.2) mm long, near the apex glabrous or aculeate, the ventral row ending (0.8)1.2–3.9(4.5) mm below the top, the dorsal row measuring  $\pm 1/2$ – $1/3$  the length of the lemma, the remainder rows shorter or equaling the dorsal row, rows with appressed to almost erect hairs (0.3)0.5–0.9(1.2) mm long; callus (1.6)1.8–3(3.2) mm long, acute, curved, villous, hairs (1.1)1.2–2(2.3) mm long on the ventral face and 0.7(0.8)–1.4(1.7) mm long on the dorsal face, scar elliptic, peripheral ring (0.6)0.7–1(1.1) mm long, (0.2)0.23–0.32(0.34) mm wide (ratio width/length = (0.25)0.27–0.37(0.43)); palea (6.8)8.4–11.3(12.1) mm long, lanceolate, margins and tip hyaline, dorsally 2-nerved, between the two nerves papillose or glabrous (rarely with a dorsal row of hairs up to 1/4 the length of the palea), margins glabrous and tip glabrous (rarely ciliate), pale, brown or green; lodicules 3, equal or subequal, with the dorsal ones slightly longer or shorter than the ventral one, acute, lanceolate or linear lanceolate, membranous, glabrous, dorsal lodicules (1.5)1.7–2.9(3.7) mm long, ventral lodicule (1.3)1.9–3.3(3.9) mm long. Awn (9.6)10.6–24.5(28.7) cm long, bigeniculate; column (2.3)2.8–5.3(5.4) cm long, base (0.31)0.35–0.57(0.62) mm in diameter, twisted, pale, brown, brown and green, and frequently with purple stains, glabrous or scabrous (rarely pilose); geniculation (0.8)1–1.7(1.9) cm long, glabrous, scabrous or with scattered hairs; seta (6.2)7.8–20.6(23.3) cm long, (ratio column length/seta length = (0.17)0.19–0.44(0.55)), flexuous, plumose, hairs in lower part (3.6)4.5–6(6.2) mm long. Anthers (3.6)4.5–6.8(8.3) mm long, glabrous. Ovary glabrous, styles 2. Caryopsis (4)6.1–9.6(9.9) mm long, fusiform; embryo 1–3.18(3.05) mm long.

**a. subsp. TURKESTANICA**

*Stipa tzveleviana* Kotuch, Bot. Zhurn. (Moscow & Leningrad) 79: 102. 1994.—TYPE: KAZAKHSTAN. Saur-Tarbagatai, brachia australi-occidentalia jugi Manrak, 11 Jul 1992, Kotuchov s.n. (holotype: LE!).

*Stipa kazachstanica* Kotuch, Bot. Zhurn. (Moscow & Leningrad) 79: 104. 1994.—TYPE: KAZAKHSTAN. Saur-Tarbagatai, praemontia australi-occidentalia jugi Manrak, locus Sarybulak, 12 Jul 1992, Kotuchov s.n. (holotype: LE!).

Herbs 15–53 cm long. Basal leaves 12–43 cm long; leaf-blades abaxial surface distinctly scabrous, adaxial surface, minutely pubescent, papillose or with scattered hairs, apex glabrous (rarely with a tassel of hairs); ligules 1.6–5.8(6.7) mm long, glabrous or scabrous, margins usually glabrous, tip glabrous or ciliate. Culms leaf-sheaths papillose or glabrous. Glumes (2.3)3–4.4(4.6) cm long. Antheicum (8.3)9.6–11.9(12.2) mm long; lemma (6.7)7.8–10(10.8) mm long, with seven distinct rows of hairs. Callus (1.6)1.8–2.6(2.8) mm long, villous, scar elliptic, curved. Awn (9.6)9.7–17(18.4) cm long; column glabrous, tuberculate or minutely scabrous. Figure 12 a–j.

**Chromosome Number**— $2n = 44$  (Sheidai et al. 2006);  $2n = 40$  (Freitag 1985).

**Habitat and Distribution**—This species grows on gravelly hills, stony, sandy or aleurite slopes, and open mountain communities, 1700–4600 m. It is found on high mountain ranges of Alburz and Kopet Dagh in northern Iran, Afghanistan, North Pakistan, and Kashmir (India); in Central Asia, it is distributed from Pamir and the southern range of the Alai mountains, rarely reaching East Kazakhstan at Saur-Tarbagatai range (Fig. 13).

**Phenology**—Flowering specimens have been collected in May, June, July and August.

**Representative Specimens Examined**—AFGHANISTAN—Badakhshan: Wakhan, östlicher Oberlauf des Darya-e Istmoch (Toli Bay Tal), 72°57' N 37°8' E, 6 Aug 1971, Anders s.n. (M). Ghazni: Berge südöstlich der Dashti-Nawar (Serpelo Buli), 33°32' N 67°47' E, 17 Jul 1967, Freitag 1514 (M); 12.5 miles N of Ghazni, road to Dasht-i-Nawar, 33°41' N 68°29' E, 30 Apr 1971, Grey-Wilson & Hewer 662 (K, W); Malestan Distr. Inter Maridina et jugum Ghouch Kol, N Sang-i Masha, 33°30' N 67°5' E, 2 Jul 1962, Rechinger 17627 (W). Kabul: Gipfel im Korogh-Massiv, 33°59' N 70°42' E, 13 Jul 1951, Gilli s.n. (W); Eingang zur Tang-i-Gharu, 25 km O von Kabul, 34°33' N 69°40' E, 18 May 1977, Podlech 30256 (G, M). Kapisa: Nedjerau-Tal bei Bagrami, 34°58' N 69°15' E, 27 Jun 1951, Neubauer s.n. (M, W); Bagrami, Nedjerau-Tal, im Talschluss, 34°58' N 69°15' E, 27 Jun 1951, Neubauer 294 (W, K). Nangarhār: Montes Safed Kuh, in montibus E jugi Altimir, 33°44' N 69°11' E, 7 Jul 1965, Rechinger 32005 (B, G, M, W). Paktiā: Umgebung von Urgun, 32°54' N 69°9' E, 30 May 1971, Volk 71/211 (M); Saroti Ghar, Pabbhōhe Wee Parei am dem Weg von Waza nach Sayd Karam, 33°41' N 69°21' E, 20 Jun 1971, Volk 71/369 (M); Prov. Maidan, umgebung von Qol-e Mazar, 34°26' N 68°3' E, 11 Jun 1973, Anders 10251 (G).

INDIA—Jammu and Kashmir: Tibet Occ. (Kashmir), Thomson s.n. (NY); Chupursan valley. upwards E end Reshith, 34°14' N 74°39' E, 2 Aug 2000, Eberhardt 8798 (GOET); Near Kargil, Ladakh, 34°34' N 76°6' E, 3 Jul 1976, Billiet & Leonard 6781 (BR).

KYRGYSTAN—Jalal Abad: Ala-Bukinskij District, Chatkal'skiy Range, Upper reaches of Mazar-su River, 41°23' N 71°30' E, 17 Aug 1962, Pavlov 181 (LE, H). Osh: Alai, the 12th km from Irkeshtam on the way to Sarp-Tash, mountains on the left bank of river Kyzyl-Su, 39°41' N 73°55' E, 25 Jul 1955, Stanyukovich et al. 2176 (LE).

PAKISTAN—Azad Jammu and Kashmir: Sheminjerav valley's end, 74°48' N 36°41' E, 4 Jul 2000, Eberhardt 7323 (GOET); Middle Khorperien valley, 74°48' N 36°39' E, 8 Jul 2000, Eberhardt 7885 (GOET). Balochistān: Hazarganj Nala, Gasht, 29°24' N 63°23' E, 2 May 1997, Rubina Rafiq and Sikander Hayat HG-97–102 (W); Kangri Nala-Nam Tal-Kumbi Top Gasht, 29°51' N 67°13' E, 18 Jun 1997, Rubina Rafiq, Sikander Hayat HG-97–368 (MSB, W); Quetta, haut vel de l'Hanne, 30°11' N 67°0' E, 1 May 1953, Schmid 128 (G). Khyber Pakhtunkhwa: Tangola, Purig (Kashmir), 35°36' N 71°52' E, 25–27 Jul 1933, Koelz 6046 (S); Chitral, Rosh Gol, NE of Tirich Mir, 36°15' N 71°50' E, 5 Jul 1958, Stainton 2806 (E, W).

TAJIKISTAN—Gorno-Badakhshan: Valley of River Duzah-Dara, Dzhaushatza valley at 3 km from the river mouth, 37°21' N 72°18' E, 11 Aug 1959, Ikonnikov 10562 (LE); Area of Sarez Lake, southern bank of Sarez Lake, 1.5 km east of Nisordaht river, 38°12' N 72°45' E, 16 Aug 1958, Gusev 5755 (LE); Western Pamir. Ravine of the river Gunt, near Chartymskiy Waterfall, 37°29' N 71°29' E, 10 Jul 1948, bad handwriting 863 (LE); Wakhan-Ishkashimskiy District, S slopes to the Pyandzh river near Nishgar, 37°1' N 72°28' E, 14 Aug 1935, Ovchinnikov & Afanasiev 1964 (LE); Shugnanskiy district, slopes to the river Pyandzh between Povodol and Gordzhak, 37°24' N 71°29' E, 4 Jun 1935, Ovchinnikov & Afanasiev 187 (LE); Upper reaches of river Shah-dara, W Pamir, Khorog, vicinity of the Botanical Garden, 37°29' N 71°33' E, 1 Jun 1943, Nepli s.n. (LE); Andarob, the valley of river Garm-Chashma (left bank), 5 km above Dasht village, 37°15' N 71°29' E, 9 Jul 1971, Sultanov 238 (LE); Wakhan, from Lake Zhui to Zung village, 37°2' N 72°37' E, 17 Jun 1914, Tuturin & Bessedin 291 (LE); river Toguz-Bulak, Mordzh village, 37°42' N 72°26' E, 19 Jul 1962, Ikonnikov 14026 (LE).

**b. subsp. TRICHOIDES** (P.A. Smirn.) Tzvelev, Novosti Sist. Vyssh. Rast. 11: 17. 1974; *Stipa trichoides* P.A. Smirn., Repert. Spec. Nov. Regni Veg. 21: 233. 1925.—TYPE: TURKMENISTAN. Turcmenia, Ludsha near Ashkhabad, Litvinov 2222 (holotype: LE!).

Herbs 22–65 cm long. Basal leaves 14–37 cm long; leaf-blades abaxial surface distinctly scabrous, adaxial surface minutely pubescent, papillose or with scattered hairs, apex glabrous (rarely with a tassel of hairs); ligules 0.5–1.4(1.5) mm long, pilose, scabrous or glabrous, margins and tip usually ciliate. Culms leaf-sheaths papillose or glabrous. Glumes 3.5–4.5(5.3) cm long. Antheicum (11)11.5–14.4 mm long; lemma 9.1–12.7(13.4) mm long, with seven distinct rows of hairs. Callus (2)2.1–2.9(3.2) mm long, villous, scar elliptic, curved. Awn (13.4)13.6–20.1(21.1) cm long; column glabrous. Figure 12 k–p.

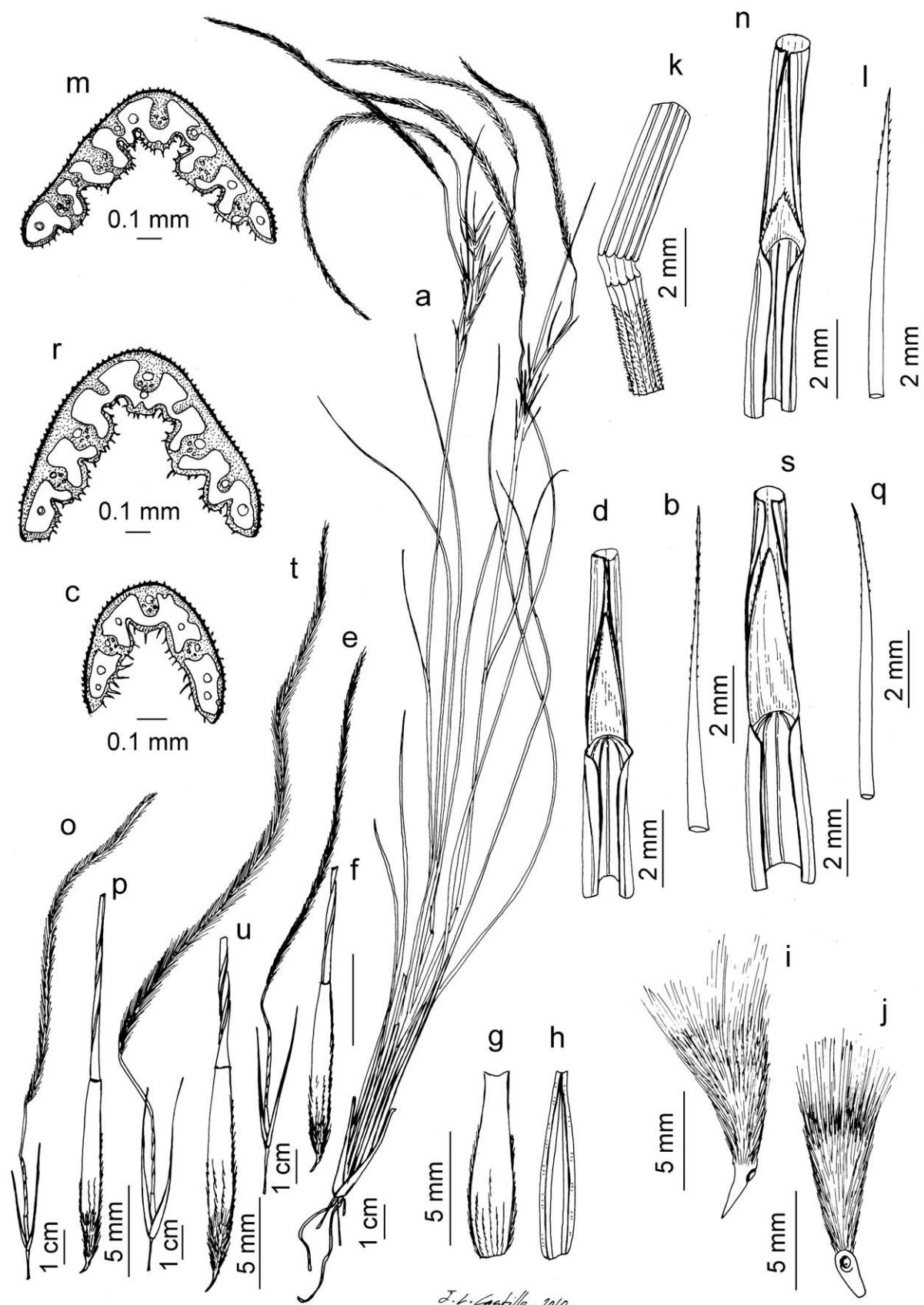


FIG. 12. *Stipa turkestanica* subsp. *turkestanica*. a. Habit. b. Basal leaf apex. c. Transversal section of the leaf-blades. d. Basal leaf ligule. e. Spikelet. f. Anthecium. g. Lemma. h. Palea. i. Callus, lateral view. j. Callus, ventral view. *Stipa turkestanica* subsp. *trichoides*. k. Culm node. l. Basal leaf apex. m. Transversal section of the leaf-blades. n. Basal leaf ligule. o. Spikelet. p. Anthecium. *Stipa turkestanica* subsp. *macroglossa*. q. Basal leaf ligule. r. Transversal section of the leaf-blades. [based on: a–j. Rechinger 32005 (S); k–p. Volk 71/242 (M 0139358); q–v. Smirnow, 14 Jun 1931 (H 1086827)].

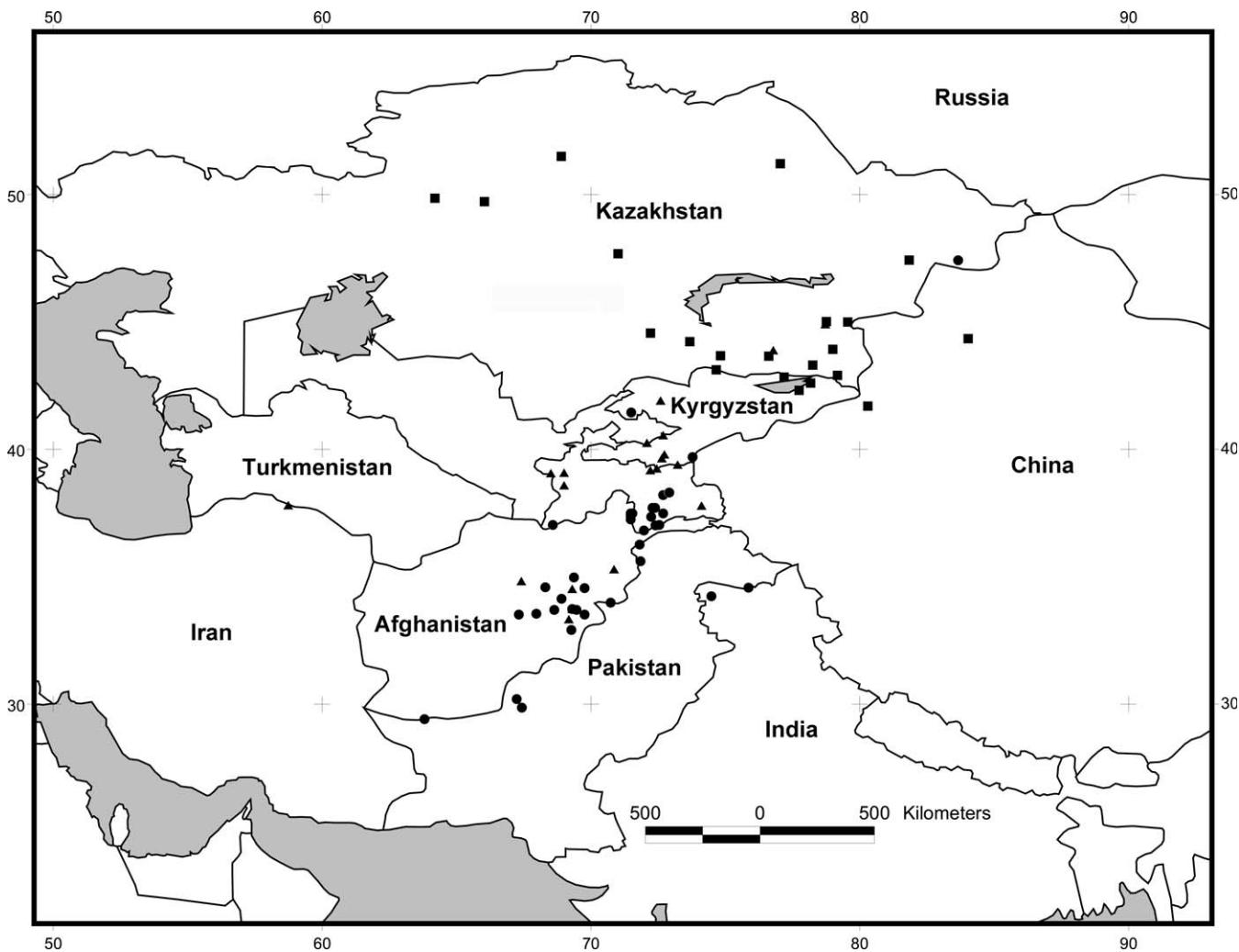


FIG. 13. Distribution map of *S. turkestanica* subsp. *turkestanica* (●), *S. turkestanica* subsp. *trichoides* (▲), *S. turkestanica* subsp. *macroglossa* (■).

**Chromosome Number**— $2n = 40$  (Chopanov and Yurtsev 1976).

**Habitat and Distribution**—Inhabits detrital-sandy, grained-gravelly slopes, and open communities from low mountains belt up to the peak, 700–4,000 m. Ranges from the mountains of North Afghanistan, to the Pamir region, Alai Mountains and the western Turkestan range, also occurring in isolated mountains of Turkmenistan (Kopet Dagh) and south eastern Kazakhstan (Fig. 13).

**Phenology**—Flowering specimens have been collected in May, June, July and August.

**Representative Specimens Examined**—AFGHANISTAN—Bāmyān: Band-i-Amir, Hänge des edacel-Tales zwischen Zulfikar-See und des Strasse, 34°48' N 67°11' E, 25 Jul 1971, Dieterle 1350 (M); (loc. 215.) ca. 15 Km E of Band-i-Amir, 34°48' N 67°11' E, 18 Jul 1972, Kukkonen 7263 (H). Kabul: Umgebung von Kabul, 34°31' N 69°11' E, 6 Jun 1971, Volk 71/242 (M); Band e Amir, 34°25' N 69°23' E, 28 Jun 1952, Volk 2773 (W). Nūrīstān: Zwischen Waigelek und Bardadesch, am Spuk pass, 35°18' N 70°50' E, 13 Jul 1935, Kerstan 1197 (W). Paktiā: Prov. Gardez, Montes Safed Kuh, in montibus E jugi Altimir, 33°44' N 69°11' E, 7 Jul 1965, Rechinger 32005 (S).

KAZAKHSTAN—Almaty: Between the towns of Kapchagay and Taldy-Kurgan, 43°53' N 77°5' E, 26 May 1976, Bochantsev & Bochantseva 950 (LE). Qaraghandy: Saur-tarbagatay, NE spurs of Manruk Range, mountains Zhambantu, 44°55' N 79°8' E, 20 Jul 1993, Kotukhov s.n. (LE).

KYRGYZTAN—Osh: Fergana Region, Margelan district, Alai Valley, opposite the tract Kizyl, 39°24' N 73°19' E, 26 Jun 1913, Dessoiaff 2199 (LE); Alai, 5 km to the east of Saryk-Mogol, near the road, 39°48' N 72°49' E, 15 Aug 1961, Ikonnikov, S. 12499 (LE); Fergana

Region, between Osh and pass Kizyl art, Alai valley, 40°33' N 72°46' E, 1901, Tulinov s.n. (LE); Close to the river Tuz-dara, 39°39' N 72°43' E, 2 Jul 1985, Korshinsky 5648 (LE).

Tajikistan—Gorno-Badakhshan: Basin of river Kaindy, right bank of Kaindy river, 10 km above the mouth of the river, Khorog, 39°11' N 72°16' E, 18 Aug 1958, Tzvelev 1499 (LE); Pamir-Alai, Alai Valley, 20 km W of Sary-tash village, 37°47' N 74°16' E, 19 Aug 1954, Polyakov 324 (LE). Khatlon: E slopes of Nishgar river close to the valley of river Pyandzh, 37°6' N 68°19' E, 14 Aug 1935, Ovchinnikov & Afanasiev 218 (LE); Hissar Range, vicinity of the pass Anzob, 1.5 km to the east of the meteorological station, 39°5' N 68°52' E, 7 Sep 1954, Kameshkina 163 (LE); Trans-Alai Range, first right tributary of Sauk-dara, 39°15' N 72°30' E, 27 Jul 1968, Grubov 422 (LE); Hissar Range, headwater of Somang River to the south of Iskander-kul lake, 39°4' N 68°21' E, 2 Sep 1933, Gordienko & Chilikina 473 (JE); Petri Magni (karategin orientalis) locus Fupeck, 38°34' N 68°49' E, 10 Aug 1935, Grigorjev 119 (S).

TURKMENISTAN—Ahal Turkmenistan: The top Chapan-dag, 37°48' N 58°2' E, 19 Jul 1928, Yarmolenko & Gontscharow 1120 (LE).

#### c. subsp. *macroglossa* (P. A. Smirn.) R. Gonzalo. *comb. nov.*

Basion. *Stipa macroglossa* P. A. Smirn., Bot. Mater. Gerb. Glavn.

Bot. Sada RSFSR 5: 47. 1924.—TYPE: KAZAKHSTAN.

Turgaisky district and post, Kizyl-Jingilskaya Volost, Sarysu River in its lower reaches, environs of Muyunkum, 1 Jun 1914, Kransheninnikov 5203 (holotype: LE!; isotype: W!).

*Stipa kungeica* Golosk., Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 16: 39. 1954.—TYPE: KAZAKHSTAN. Kungei

Alatau, Tauchilik, 1 Km bellow the fall of Kainda, 9 Jun 1953, *Goloskokov s.n.* (holotype: LE!; isotype: LE!)

Herbs 21–47 cm long. Basal leaves 11–51 cm long; leaf-blades abaxial surface distinctly scabrous, adaxial surface minutely pubescent, pubescent or papillose with scattered hairs, apex glabrous or setulose; ligules (2.3)2.8–9.8(10.2) mm long, pilose, somewhat scabrous or glabrous, margins usually glabrous and tip ciliate. Culms leaf-sheaths usually papillose or scabrous. Glumes (4.2)4.3–5.8(6.5) cm long. Antheicum (11.9)12–14.6(14.8) mm long; lemma 9.9–12.9(13.8) mm long, with seven distinct rows of hairs. Callus (2)2.4–3.1(3.2) mm long, villous, scar elliptic, curved. Awn (18)20–27(29) cm long; column glabrous or scabrous. Figure 12 q–v.

**Chromosome Number**—Unknown.

**Habitat and Distribution**—Dry steppes, stony and aleurite slopes and occasionally on sands and clays, from lowlands to middle mountain belts, 400–2,600 m. Distributed from central to east Tian-Shan range, and from central to east Kazakhstan (Fig. 13).

**Phenology**—Flowering specimens have been collected in May, June, July and August.

**Representative Specimens Examined**—CHINA— Xinjiang: Tien Shan, the basin of Kuitun River, right Bank of Bain-gol valley, S of Tushantszy village, 44°20' N 84°44' E, 29 Jun 1957, *Junatov, Li Shi-in, Yuan' I-fan* 505a (LE); E Tien Shan, the valley of Muzart River, the lowest right tributary of the river Lyangar before leaving Muzart to the Bahia basin, 41°42' N 80°48' E, 12 Sep 1958, *Junatov & Yuan' I-fan* 1019 (LE).

KAZAKHSTAN— Akmola: Atbasar uezd. Lower reaches of Sary-su river, vicinity of heights Orta-kasaun, 51°30' N 68°45' E, 9 Jun 1914, *Krascheninnikov s.n.* (LE); Chu-Ili Mountains. Tract Dzhevyan-kezen, 43°40' N 75°1' E, 7 Jun 1914, Titov 614 (LE); Atbasar District, basin of Beleudy river, headwater of River Dyusenbai (river Dzhideli), 49°43' N 65°45' E, 19 Jun 1914, *Krascheninnikov* 5354 (FI, W). Almaty: Semirechensk Region, Dzharkent uezd, mountains Karatau, rivers Kuru-kul'dek-Sumbe, 45°1' N 79°10' E, 9 Jul 1910, *Mikhelson* 1978 (LE); Sarydzhas village, 42°54' N 79°36' E, 17 Jul 1934, *Shischkin s.n.* (LE); Spurs of Dzhungarskiy Ala-Tau. Mountains Chulak. Ravine Chulak-Dzhigde, 45°0' N 80°0' E, 6 May 1956, *Goloskokov s.n.* (LE); Kungei Ala-Tau, Tau-Chilik 1 km below the confluence of Kaindy river, 42°50' N 77°30' E, 9 Jun 1953, *Goloskokov s.n.* (LE); Turgai region. Kizil-dzhigil'skaya Parish, Sary-su river, vicinity of Muyunkumy, 43°39' N 76°54' E, 1 May 1924, *Krascheninnikov* 5203 (WU). East Kazakhstan: Manra Range, tract Sary-Bulak, 47°25' N 82°25' E, 12 Jun 1992, *Kotukhov* 10 (LE). Karagandy: Taldy-Kurganskiy uezd, near Aina-bulak stream, 47°40' N 71°0' E, 10 Jun 1928, *Pavlov* 79 (LE). Zhambyl: Flora Iliensis. Kenduktas, 44°13' N 73°48' E, 1886, *Krassnow s.n.* (LE); Semirechensk Region, Chu-Ili Mountains, Chok-par valley, 43°7' N 74°51' E, 18 Jun 1914, Titov 1144 (LE); Pishpek uezd near the tract Kokuyrak, 44°33' N 72°16' E, 26 Jun 1913, *Shischkin & Genina s.n.* (LE).

KYRGYZSTAN— Issyk-Kul: Issyk-Kul Region, village Pokrovka, at 12 km S of the village, on the right bank of Chon-Kyzyl-Su river, 42°19' N 78°5' E, 1 Aug 1960, *Kurganskaya & Udintseva* 536 (W); Tian Shan centralis, Lacum issyk-kul prope pag Tschoktal, 51°13' N 77°21' E, 14 Jun 1931, *Smirnow* 32 (B, E, G, H, FI, JE, L, S, W); Loess hills on the southern bank of Issyk-kul' near the river B. Dzhirgalchak, 42°36' N 78°33' E, 24 Jun 1908, *Rozhevitz* 644 (LE).

**Notes**—*Stipa turkestanica* is widely distributed in Central Asia, covering a broad altitudinal range, which is translated into a rather variable size. *Stipa turkestanica* resembles a very delicate *S. pennata* (Freitag 1985), with smaller reproductive parts. Furthermore, some specimens of *S. turkestanica* show an apical tassel of hairs on the apex of the basal leaves, just like *S. pennata*. Besides the smaller size, *S. turkestanica* may be distinguished by the distinct rows of the lemma, distinctly scabrous abaxial surface of the basal leaves, and the pilose or scabrous culm internodes, whereas *Stipa pennata* has the dorsal and subdorsal rows slightly fused at the base, with the abaxial surface of the basal leaves glabrous or scabrous, and the culm internode usually glabrous.

4. *Stipa kirghisorum* P. A. Smirn., Repert. Spec. Nov. Regni Veg. 21: 231. 1925; *S. pennata* subsp. *kirghisorum* (P.A. Smirn.) Freitag, Notes Roy. Bot. Gard. Edinburgh 42: 438. 1985.—TYPE: KAZAKHSTAN. Prov. Semipalatinsk, m. Bokaj, Kossinsky s.n. (holotype: MW)

*Stipa violacea* E. Nikit. Tr. Biol. Inst. Kirg. Fil. AN SSSR 2: 68. 1947, nom. illeg.; *S. kirghisorum* var. *violacea* E. Nikit. ex Tzvelev, Novosti Sist. Vyssh. Rast.: 16. 1974.—TYPE: KYRGYZSTAN. Central Tian Shan, declivitas borealis jugi Kavaktau, 28 Jul 1937, Michajlova & Popova 66 (holotype: LE!)

*Stipa ikonnikovii* Tzvelev, Spisok Rast. Gerb. Fl. S.S.S.R. Bot. Inst. Vsesoyuzn. Akad. Nauk 21: 49. 1977.—TYPE: TAJIKISTAN. Badachsjan, ad ripam dextram fl. Gunt, Czarty, 5 Aug 1957, Ikonnikov 5654 (holotype: LE!; isotype: C!, H!, JE!, M!, NY!)

Herbs 22–72 cm high, perennial, caespitose; branching intravaginal. Culms 2–3(4) noded, nodes glabrous, violet; culm internodes scabrous or pubescent. Basal leaves 23–58 cm long, green and occasionally pruinose; leaf-sheaths minutely pubescent, papillose or scabrous, usually glabrous; leaf-blades 19–36 cm long, (0.3)0.35–0.56(0.63) mm in diameter, convolute, abaxial surface distinctly scabrous by prickles, adaxial surface papillose, scabrous, pubescent or minutely pubescent, hairs (0.04–0.4(0.45) mm long, leaf-blades apex acute, glabrous; ligules (0.25)0.42–1.7(2.5) cm long, rounded, obtuse or acute, usually scabrous, ciliate or ciliolate, cilia (0.03)0.04–0.28(0.47) mm long. Floriferous culm leaves 24–37 cm long; leaf-sheaths 21–31 cm long, scabrous, minutely scabrous or glabrous, margins glabrous; leaf-blades 1.5–8.3 cm long, (0.17)0.19–04(0.7) mm in diameter, abaxial surface scabrous, adaxial surface papillose, scabrous, pubescent or minutely pubescent, hairs (0.03)0.07–0.31(0.47) mm long; ligules (0.43)1–3.8(4.9) mm long, acute, obtuse or rounded, usually scabrous, ciliate or ciliolate (rarely glabrous), cilia (0.03)0.07–0.31(0.47) mm long. Panicles 11–48 cm long, contracted, exerted or partially enclosed by the upper leaf-sheaths, 3–5 noded; basal internode (4.9)6–28(38) cm long, pubescent (rarely scabrous); branches (1)1.6–3.3(4.2) cm long, erect or almost erect, setulose, setae (0.13)0.17–0.94(1.16) mm long; basal nodes with (1)2 branches with 1(2) spikelets each. Glumes subequal, lanceolate, long acuminate, glabrous or ciliate on the central nerves, cilia (0.1)0.13–0.17(1.2) mm long, green with purple stains, margins and tip hyaline, the lower (3.7)4–5.6(6) cm long and 3–5 nerved, the upper (3.5)3.7–5.3(5.6) cm long and 5–7(9) nerved. Antheicum (13.7)14.3–17.5(18.5) mm long, (0.8)0.9–1.3(1.4) mm wide, fusiform, coriaceous, green or brown; lemma (11.2)11.3–13.9(14.8) mm long, near the apex glabrous, with 7 distinct rows of hairs (rarely fused at the base), the ventral row ending (0.35)0.75–3.14(3.67) mm below the top (rarely reaching the top), the dorsal row measuring 2/4–3/4 the length of the lemma, the remainder rows slightly shorter or ± equalling the dorsal row, rows with appressed to almost erect hairs (0.67)0.7–0.98(1.02) mm long; callus (2.42)2.64–3.75(3.9) mm long, acute, curved, villous, hairs (1.45)1.8–2.46(2.75) mm long on the ventral face and (1)1.1–1.6(1.9) mm long on the dorsal face, scar elliptic to broadly circular, peripheral ring (0.74)0.76–1.06(1.17) mm long, (0.21)0.24–0.35 mm wide (ratio width/length = (0.25)0.27–0.37(0.38)); palea (10.4)11–13.6(14.8) mm long, lanceolate, margins and

tip hyaline, dorsally 2-nerved, between the two nerves papillose or glabrous, margins glabrous and tip glabrous or ciliate, rarely with a dorsal row of hairs, brown or green; lodicules 3, equal or subequal, with the dorsal ones slightly longer or shorter than the ventral one, acute, lanceolate or linear lanceolate, membranous, glabrous, dorsal lodicules (1.6)2.1–3.2(3.5) mm long, ventral lodicule (1.8)2.2–3.5(4.2) mm long. Awn (19.6)20.7–26.5(27) cm long, bigeniculate; column (4.4)4.8–7(7.5) cm long, base (0.37)0.4–0.6(0.7) mm in diameter, twisted, brown, brown and green and frequently with purple stains, glabrous or tuberculate; geniculation (1.1)1.4–2.2(2.5) cm long, glabrous, tuberculate or scabrous; seta (14.4)15.2–19(20) cm long, (ratio column length/seta length = (0.26)0.28–0.42(0.43)), flexuous, plumose, hairs in lower part (3.2)4–5.7(5.89) mm long. Anthers (3.8)4.6–8.2(9.1) mm long, glabrous (rarely with scattered hairs), yellow or purple. Ovary glabrous, styles 2. Caryopsis (7.4)8.1–9.9(10.01) mm long, 2; embryo (1.2)1.5–2.1(2.3) mm long. Figure 14.

**Chromosome Number**— $2n = 32$  (Freitag 1985; Tzvelev 1976).

**Habitat and Distribution**—Steppes, debris and rocky slopes, from lowlands up to middle mountain belts, 1,200–4,300 m. North-east Afghanistan, North-west Turkey, Kashmir (India), Pamir and Alai mountains, Tian Shan range, Central and East Kazakhstan, Xinjiang, West Mongolia and western and central Siberia (Fig. 15).

**Phenology**—Flowering specimens have been collected in June, July and August.

**Representative Specimens Examined**—AFGHANISTAN—Badakhshan: Darrah-i-Parshui (Centr Afgh. Hindukusch) orogr. Rechter ast., 36°53' N 73°15' E, 12 Aug 1965, Frey 414 (W); Wakhan, oberes Baroghil Tal und Baroghil PaB, 36°53' N 73°22' E, 30 Jul 1971, Anders 7883 (M). Nuristan: Ost-Nuristan, West-Seite des Semeneck-Passes, 34°57' N 70°24' E, 1 Aug 1960, Kerstan 1509 (W); Nuristan, Vaigel, 34°57' N 70°24' E, 1949, Edelberg 2034 (C). Parwan: Parwan, Summer valley, 35°0' N 68°55' E, 18 Jul 1965, Gilbert 32 (K).

CHINA.—Xinjiang: Eastern Tien Shan, basin Kuitun, Right Bank of Bain-gol valley, S of Tushantszy, 44°20' N 84°51' E, 29 Jun 1957, Junatov, Li Shi-in, Yuan' I-fan 530 (LE); Eastern Tien Shan, Ili Valley, Ketmen-tau Range, 3–4 km above the Sarbushin village on the road from Kul'dzhi to Kyzyl-kure, 44°14' N 84°48' E, 23 Aug 1957, Junatov, Li Shi-in, Yuan' I-fan 1438 (LE).

INDIA.—Jammu and Kashmir: SE oberh. Matayan/Ladakh, 34°22' N 75°36' E, 17 Jul 1976, Hartmann 2384 (G); Ebene van San modangra (pr. Parkutze u. Julidak) Ladakh, 34°6' N 75°56' E, 30 Aug 1976, Hartmann 2383 (G). Himachal Pradesh: Punjab, Kulu. Lahaul, 32°30' N 77°50' E, 1 Jun 1888, Drummond 23332 (E); Chandratal, Lahul, Kangra, Punjab, 32°10' N 76°15' E, 1 Sep 1933, Koelz 6924 (GH, S).

KAZAKHSTAN.—Aktobe: Mugodzhary, E Dzhaman-tau, 48°38' N 58°32' E, 26 May 1927, Rusanov 167 (LE). Almaty: SW spurs of Dzungarskiy Ala-Tau, Chulak mountains, Gorge of Kzyl-Aus river, 43°57' N 77°56' E, 4 Jun 1955, Goloskokov s.n. (GH). East Kazakhstan: Semipalatinsk Province, Krasnooptyabyr'skaya parish. About 8.5 km from Taubinka, 49°48' N 80°0' E, 1928, Enden 159 (NY); Altai, Ustj-Kamenogorsk mons Prigonnaya, 50°43' N 81°46' E, 29 May 1931, Schischkin et al. s.n. (NY); Manrak range. At 15 km from Priozerne village, 47°45' N 84°11' E, 2 Jun 1976, Kotukhov s.n. (B); Altai, Ustj-Kamenogorsk mons Prigonnaya, 50°43' N 81°46' E, 29 May 1931, Schischkin et al. s.n. (NY). Karagandy: Central Kazakhstan hills (Karaganda Region). 20 km W of Akgatau village to Agadyr village, 48°15' N 72°50' E, 10 Jun 1964, Vasilevich et al. 70 (LE).

KYRGYZSTAN.—Chui: Talas Range. The southern macro-slope, Susamyr riverhead, 42°12' N 73°58' E, 26 Jul 1971, Ikonnikov S. et al. 7538 (LE); Alai Range. Route Osh-Khorog, the pass "40 years of Komsomol Kigizstan", 21 Aug 1971, Ikonnikov, S. et al. 8756 (LE). Issyk-kul: Tian Shan central. jugum Kungei-Alatau, fauces Utasch prope pag. Tschoktal, 42°34' N 76°41' E, 27 Jun 1931, Smirnow 29 (H, JE, S, W). Naryn: Tian Shan Region, the vicinity of lake Son-kul, near the road to the lake from the side of Tyulek river valley, 41°50' N 75°8' E, 6 Aug 1960, Kurganskaya & Udintseva 565 (W); Naryn, 41°27' N 75°59' E, 26 Aug 1926, Abolin 1094 (LE). Osh: Fergana Region, Osh uezd, Plain of Alai, near the mouth of Taldyn, 40°59' N 73°33' E, 30-VI-1913,

Knorring 684 (LE, NY). Talas: Semirechenskaya Province, Aksu gorge, Aleksandrovskii Range, 42°37' N 71°35' E, 16 Jun 1903, Lipsky 2355 (LE).

MONGOLIA.—Uvs: Mongolia borealis. Altai. Circa lacus Ubsa, Kirghiz-nor et Kosogol. Ad Ienisei superiorem et jugum Tannu-ola, 50°20' N 92°45' E, 1–20 May 1879, Potanin 87 (LE); Altai. Ubsunur Region, Hyargas district, 38 km to the north of Mogoi-bulak. The bottom of the dry bed of temporary watercourse, 49°0' N 93°0' E, 18 Jul 1973, Banzrych et al. 4761 (LE).

PAKISTAN.—Gilgit-Baltistan: Baltestán Chatpani Nukarh west of Drún, 36°13' N 74°6' E, 28 Aug 93, Duthie 13857 (W); Shingo valley, Deosai region, 34°46' N 75°16' E, 7 Aug 1946, Stewart & Stewart 22201 (NY). Khyber Pakhtunkhwa: Prov. Chitral, haute vallée de Yarkhun, 36°44' N 72°52' E, 22–27 Aug 1954, Schmid 2335 (G). Punjab: Punjab, 31°0' N 76°0' E, 17 Jun 1888, Drummond 23344 (G).

TAJIKISTAN—Gorno-Badakhshan: Wakhan-Ishkashimsky District, NE slopes of the river Matz, 36°43' N 71°36' E, 24 Aug 1935, Ovchinnikov & Afanasev 2047 (LE); The south-western spurs of Dzhungarskiy Ala-Tau. Mountains Chulak. Gorge of river Kzyl-Aus, 38°0' N 71°46' E, 1 Aug 1964, Ikonnikov, S. 16537 (GH); Eastern Pamir, the northern spurs of the Wakhan Range, basin of river Karadzhilgasai (above the lake Chakankul), 37°23' N 73°49' E, 9 Jul 1985, Medvedev 63 (LE); Alai valley, the right bank of Kyzyl-su River, near Lenin Peak, 39°20' N 72°52' E, 24 Jul 1967, Ladygina et al. 18219 (LE); Basin of upper reaches of river Shah-dara, middle reaches of river Kok-bai, 37°20' N 72°34' E, 4 Sep 1943, Nepeli s.n. (LE); Western Pamir, Khorog, vicinity of the Botanical Garden, 37°29' N 71°33' E, 28 May 1943, Nepeli s.n. (LE); Andarab, the valley of Garm-Chashma river, 38°26' N 71°51' E, 14 Jul 1971, Sultanov 528 (MA, W).

TURKEY—Rize: Aufstieg auf eine Alm knapp SE fundort: des Kackar Hauptkammes, beginnend 10 km oberhalb Sargöl, 40°50' N 41°9' E, 20 Jul 1982, Sorger & Buchner 82–84–52 (W).

**Notes**—Tzvelev described *Stipa ikonnikovii* Tzvelev, endemic to Shugnan (Tajikistan) and distinguished this species from *S. kirghisorum* by the adaxial surface of the basal leaves minutely pubescent and the ventral row reaching the top. Even though *S. kirghisorum* shows rather uniform morphological variation, the ornamentation of the adaxial surface is highly variable. Specimens with scabrous, minutely pubescent or pubescent surface are found throughout its geographic distribution. Likewise, some specimens from Afghanistan present the ventral rows that reaches (or almost reaches) the top, overlapping with the range of variation of this character in *S. kirghisorum*.

#### EXCLUDED NAMES AND UNIDENTIFIED SPECIMENS

*Stipa ammophilla* Czern. ex Bordz, Flora URSR 2: 123. 1940, nom. inval., pro syn.

*Stipa fallacina* Klokov & Osychnyuk Novosti Sist. Vyssh. Nizsh. Rast. 1975: 62. 1976. TYPE: UKRAINE. Donetskia. Steppa reservata Chumotoviensis, 10 Jun 1974, Osychnyuk s.n. (holotype: KW; isotype: LE!). This taxon is very similar to *S. lessingiana* Trin. & Rupr., from which it is distinguished by having seven distinct rows of hairs instead of a completely pubescent lemma. The isotype examined exhibits panicle scarcely developed, and the application of this name is in doubt until the holotype and more material can be examined.

*Stipa fontanesii* var. *planifolia* Roshev. ex B. Fedtschenko, Izv. Imp. Bot. Sada Petra Velikago. 14(Suppl. 2): 49. 1915. nom. nud.

*Stipa hippura* Czern, nom. nud. (in sched., LE!).

*Stipa kempirica* Kotukhov, Bot. Zhurn. (Moscow & Leningrad) 79: 101. 1994—TYPE: KAZAKHSTAN. Saur-Tarbagatai, brachia australi-occidentalia jugi Manrak, locus Kempirbulak, 11 Jul 1992, Kotukhov s.n. (holotype: LE!). This taxon is only distinguished from *S. kirghisorum* by

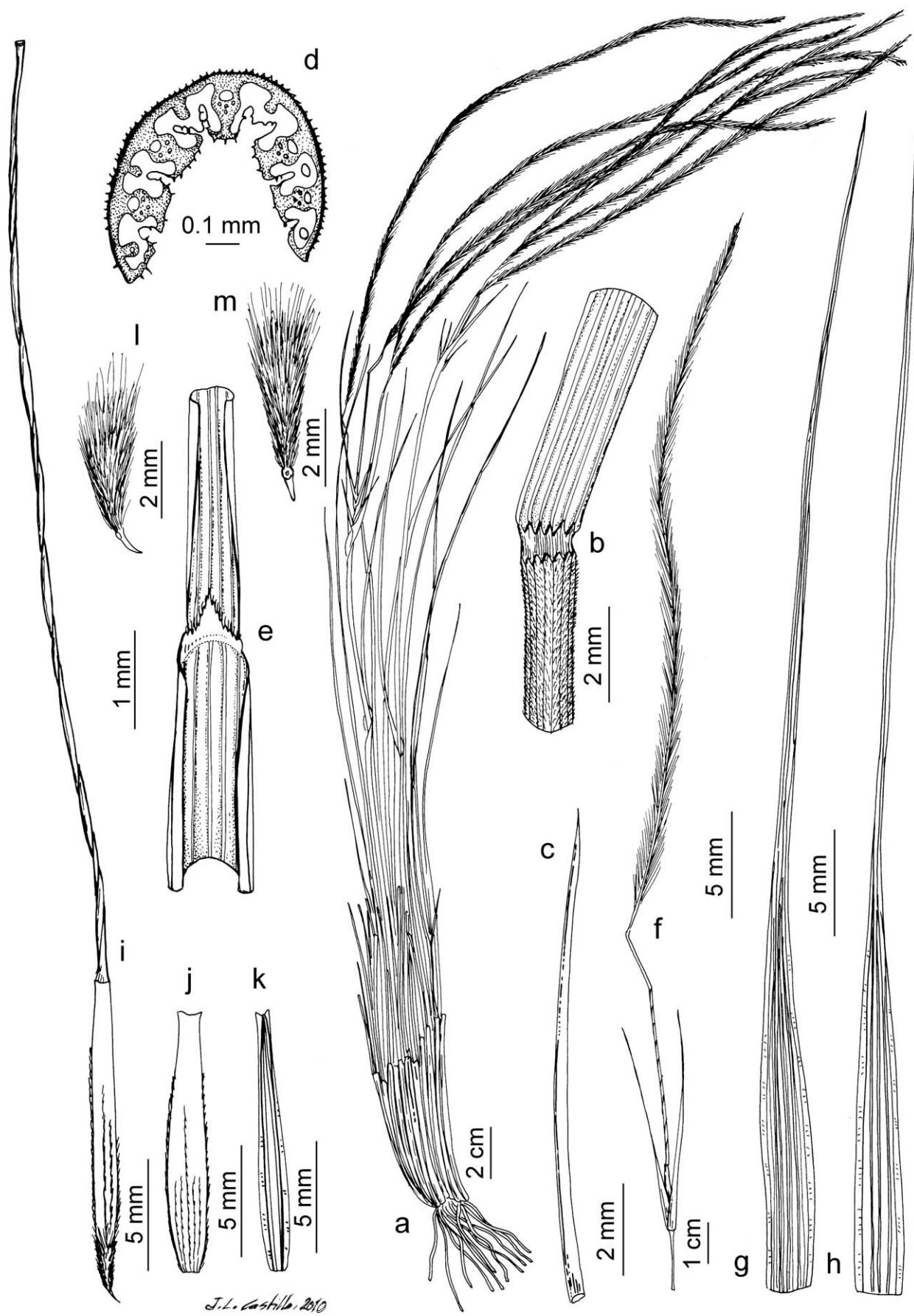


FIG. 14. *Stipa kirghisorum*. a. Habit. b. Culm node. c. Basal leaf apex. d. Transversal section of leaf-blades. e. Basal leaf ligule. f. Spikelet. g. Upper glume. h. Lower glume. i. Antheicum and column. j. Lemma. k. Palea. l. Callus, lateral view. m. Callus, ventral view. [based on: Smirnow 29 (JE)]

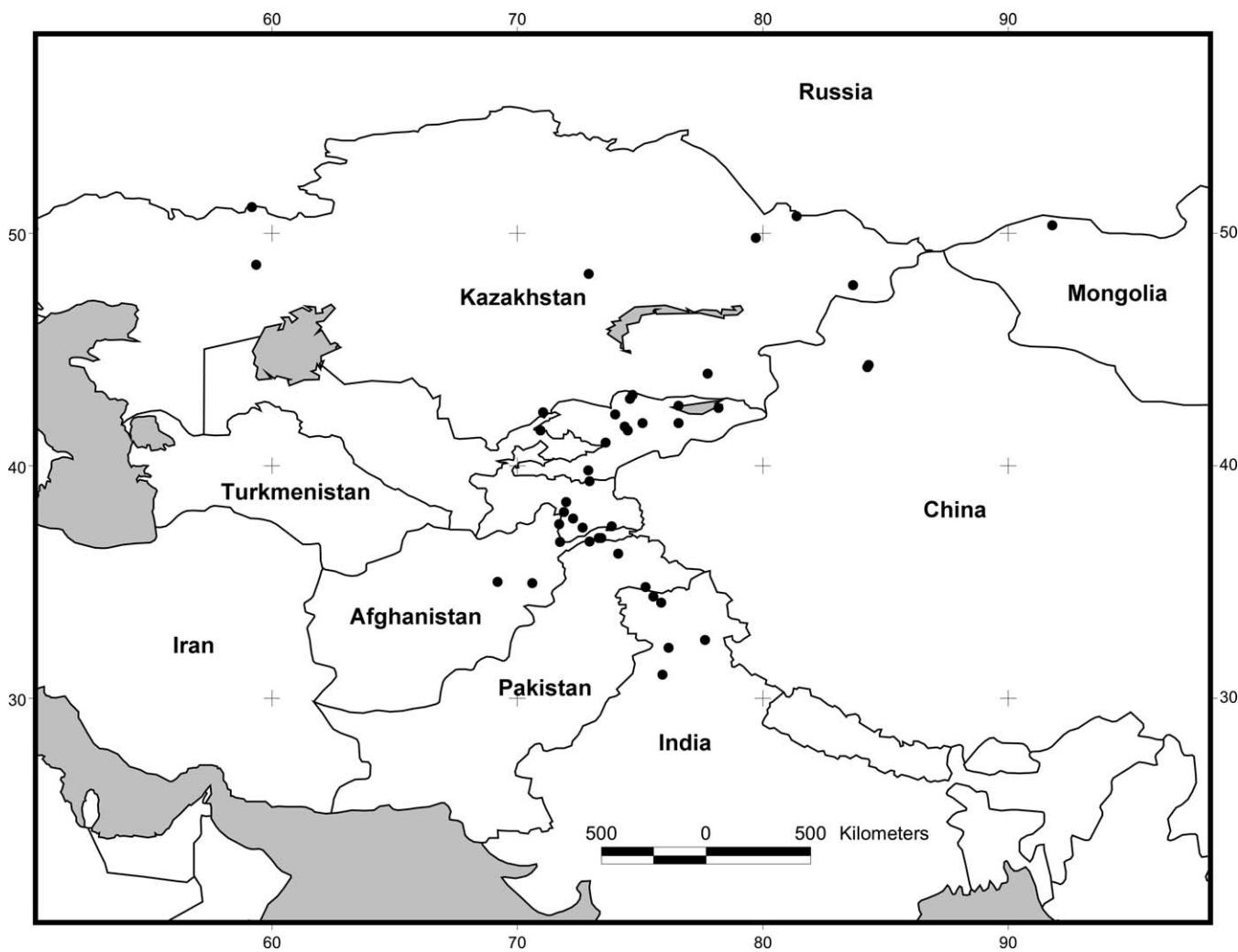


FIG. 15. Distribution map of *S. kirghisorum* (●).

its longest awn with shorter seta hairs (2–3 mm long). The application of this name is in doubt until more material can be examined.

*Stipa joannis* var. *microtricha* Borbás, Balat. Fl.: 316. 1900; *Stipa joannis* [unranked] *microtricha* (Borbás) Jáv. Magyar Fl. 1: 69. 1924.—TYPE: CZECH REPUBLIC. Gys hegyein s a budai Lipótmezőn. (type: no original material located).

*Stipa joannis* f. *okensis* P.A. Smirn., Tabl. Opred. Kovile: 4. 1927; *Stipa pennata* var. *okensis* (P.A. Smirn.) Tzvelev, Novosti Sist. Vyssh. Rast. 11: 19. 1974; *Stipa pennata* subsp. *okensis* F.M. Vázquez & M. Gutiérrez, Telopea 13: 169. 2011.—TYPE: (type: no original material located).

*Stipa joannis* var. *puberula* Podpera & Suza, Spisy Přír. Fak. Masarykovy Univ. 12: 7. 1922; *S. joannis* subsp. *puberula* (Podpera & Suza) Martinovský, Preslia 48: 172. 1976; *S. pennata* var. *puberula* (Podpera & Suza) Kubát, Severceskou Přir 33–34: 156. 2002; *Stipa pennata* subsp. *puberula* F.M. Vázquez & M. Gutiérrez, Telopea 13: 169. 2011.—TYPE: CZECH REPUBLIC. Mohelno, Jun 1921 Suza s.n. (type: no original material located).

*Stipa joannis* f. *subpuberula* Podpera & Suza, Spisy Přír. Fak. Masarykovy Univ. 12: 7. 1922.—TYPE: CZECH REPUBLIC. Monte Pavlovské: ad rupes calcarias ad declive

orientale loci Soutěska (vel Klause). (type: no original material located). *Stipa kleopovii* Klokov & Zoz, nom. nud. (in sched., LE!)

*Stipa lessingiana* var. *dubia* Hack. ex Fed., Izv. Imp. Bot. Sada Petra Velikago. 14(Suppl. 2): 48. 1915, nom. nud.

*Stipa longifolia* Borbás, Magyar Növényt. Lapok 10: 117. 1884.—TYPE: HUNGARY. Kolozsvári, Szénafüveken, Jul 1878 (holotype: no original material found).

*Stipa macroglossa* f. *pubescent* P. A. Smirn., Repert. Spec. Nov. Regni Veg. 5: 235. 1925.—TYPE: KAZAKHSTAN. Prov. Semireczje. Distr. Prshewalsk, ad fl. Kugart, Saposhnikow s.n. (holotype: original material not located)

*Stipa* sect. *Parastipa* Klokov, Novosti. Sist. Vyssh. Nizsh. Rast. 1975: 23. 1976. nom prov., nom inval.—TYPE: *Stipa syreitschikowii* P.A. Smirn.

*Stipa pennata* f. *asperior* Podp. Práce Morav. Přír. Společn. 2: 694. 1926; *Stipa joannis* f. *asperior* (Podp.) Soó, Acta Bot. Acad. Sci. Hung. 17: 123. 1972.—TYPE: CZECH REPUBLIC. Mohelno. May 1921, Suza s.n. (holotype: no original material located).

*Stipa pennata* [2] *appendiculata* Asch. & Graebn., Syn. Mitteleur. Fl. 2: 105. 1898; *Stipa joannis* f. *appendiculata* (Asch. &

- Graebn.) Soó in Acta Bot. Acad. Sci. Hung. 17: 123. 1972.—TYPE. GERMANY. Selten, bisher nur in der Prov. Brandenburg, Freinwaldea. O. s.n. (type: no original material located).
- Stipa pennata* [A] *eupennata* Asch. & Graebn., Syn. Mitteleur. Fl.: 104. 1899, nom. inval.; *S. pennata* subsp. *eupennata* (Asch. & Graebn.) Hayek, Prodr. Fl. Penins. Balcan. 3: 349. 1932. nom. inval.
- Stipa pennata* f. *glaucescens* Novak in Preslia 2: 80. 1922; *Stipa tirsia* f. *glaucescens* (Novak) Soó, Acta Bot. Acad. Sci. Hung. 17: 123. 1971.—Type: SLOVAKIA. Montis Blasenstein [prope Plavecký Sv. Mikulás] in Carpathis Minoribus, Novak s.n (holotype: no original material found).
- Stipa pennata* [b] *krauseana* Asch. & Graebn., Syn. Mitteleur. Fl. 2(1): 105. 1899; *Stipa joannis* f. *krauseana* (Asch. & Graebn.) Soó, Acta Bot. Acad. Sci. Hung. 17: 123. 1971.—TYPE: GERMANY. Waldform, bisher nur Prv. Sachsen: Burg: Grabauer Forst, Eggert s.n. (holotype: original material not located).
- Stipa pennata* f. *penicillifera* Pacz. Zlaki Khers. Gub: 21. 1913; *Stipa joannis* subsp. *penicilliferae* (Pacz.) Lavrenko Flora URSR 2: 123. 1940.—TYPE: not found.
- Stipa pennata* [II] *valida* Asch. & Graebn., Syn. Mitteleur. Fl. 2: 105. 1898; *Stipa joannis* f. *valida* (Asch. & Graebn.) Soó, Acta Bot. Acad. Sci. Hung. 17: 123. 1972.—TYPE: GERMANY. Im nördlichen Gebiet selten. Frankfurt a. O. Reitweiu s.n. (holotype: original material not located).
- Stipa pinneticola* Klokov & Zoz, nom nud (in sched LE!)
- Stipa stenophylla* Czern., Consp. Pl. Charcov.: 79 0.1859., nom. nud
- Stipa vulagris* Gueldenst., Reis. Russland 2: 39. 1791, nom. inval., pro syn.
- ACKNOWLEDGMENTS. The authors wish to thank the staff of the cited herbaria for their support on our visits and/or loans of herbarium specimens. We are also indebted to Dr. Félix Muñoz Garmendia for his authorized advices in nomenclature, to Dr. Elena Glazcova for the Russian translation, to Dr. Heimo Ryner for his collaboration with the loan of *S. styriaca*, to Dr. Sorin Stefanut for the digital images of *S. danubialis*, and to Joel Calvo for providing us digital images. This work was supported by the *Flora iberica* project CGL2008-02982-C03-01/CLI, Ministerio de Educación y Ciencia, Spain. Our visit to the W herbarium was funded by the FPVI European-funded Integrated Infrastructure Initiative grant SYNTHESYS.
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APPENDIX 1. Index to numbered collections cited. Numbers in parentheses refer to the corresponding taxon in the text.

- Aach 10 Jun 1947 (2a), 23 Apr 1951 (2a). Abolin 196 (4), 1094 (4). Abramov, Bezak & Kovaleva 352 (4). Adamovic 11 Jul 1896 (2a). Alanko 2 Jul 1961 (1). Alpers Jun 1910 (1). Anderberg 3 Jul 1936 (1), 1 Jul 1936 (2a). Anders 7883 (4), 10251 (3a), 6 Aug 1971 (3a). André Jul 1879 (2a), Jun 1894 (2a). Anhel Jun 1878 (2a). Antal 29 May 1924 (2a). Aschuz Jun 81 (2a). Asplund 13 May 1927 (2a). Ausl. 15 Jun 1922 (2a). Bach 174 (2a). Banzyrich, Karamysheva, Munhbayar & Tzegmid 4761 (4). Barth 29 Jun 1887 (1), 22 Jun 1906 (1). Basilev 22 Jul 1920 (4). Bauer 1840 (2a). Baumgartner 8090 (2a), Jun 1884 (2a). Beauvard 22 Aug 1932 (2a), 24 Jul 1934 (2a). Becker Jun 1848 (2a), 1882 (2a) 1883 (2a), 1886 (2a). Berger 2957 (2a), 16735 (2a), 17773 (2a), 19938 (2a), 25 May 1957 (2a). Bergfaldt 1881 & 1871 (1). Berghen 13 Jul 1975 (2a). Bergqvist, Eldenäs, Källersjö & Lundin 05 (2b). Billiet & Leonard 6781 (3a). Bischoff 1828 (2a). Bisse 23 Jun 1960 (1), 10 Jul 1962 (2a), 29 May 1963 (2a),

- 7 Jun 1963 (1). *Bochantsev & Bochantseva* 950 (3b). *Bodemk. exc.- Th. J. Visser* 141 (2b). *Boggiani* 29 Aug 1912 (2a). *Bolle* May 1847 (2a). *Bonnot* 23 Jun 1948 (1), 18 Jul 1961 (2a). *Boom* 8695 (2a). *Borbás* 1 Jul 1887 (1), 5 Jul 1877 (1), 31 May 1888 (2a), 22 Jun 1895 (1), 4 Jun 1897 (1), 7 Jun 1897 (1), 20 Jun 1897 (1), May 1900 (2a). *Bornmüller* 5192 (2a), 1898 (2a), 14 Jun 1916 (2a). *Boros* 28 Jun 1937 (1), 21 Jun 1939 (1), 21 Jun 1942 (1), 15 Jun 1947 (1), 9 Jun 1949 (1). *Botezoni* 11 Jun 1958 (1). *Branco* 6 Jun 1937 (2a), 22 May 1953 (2a). *Bronevsky* 661 (3b). *Brummer-de Vries* 12 Jun 1916 (2a). *Bruynseels* 20 Jul 1975 (2a). *Bunyashina* 6 Jul 1951 (1). *Burri & Krendl* 6 Jul 1982 (2a). *Buxbaum* 261 (2a). *Buysman* 524 (1). *Buzuk* 79 (4), 194-15 (3b). *Callier* 219 (1). *Cavalluy* Jul 1875 (2a). *Cedercreutz* 11 May 30 (2a). *Cefrube* 30 Jul 27 (1). *Celakovský* 20 Jul 1886 (1). *Ceynowa-Gieldon* 296 (2b), 297 (2b). *Charpin* 19 Jun 1960 (2a), 9 Jul 1967 (2a). *Chernova* 209 (1). *Cofrabay* Jun 1926 (1). *Colrube* 5 Jul 1911 (1), 30 Jun 28 (1). *Cowan & Darlington* 20 May 1929 (2b). *Cufodontis* 19 May 1929 (1). *Czerniaëw* 1853-1854 (1), 29 Jun 1853 (1), 31 May 1854 (2a). *Hylmö* 1980 (1). *Degen* 10 (2a), 252 (1), 352 (1), 488 (1), 488B (1), 16 Jun 1899 (1), 11 Jun 1900 (2a), 20 May 1916 (1), 21 May 1916 (1), 22 Jun 1916 (1). *Degen & Flatt* 82 (2a). *Delarze* 40284 (2a). *Dervtz* 16 Jun 1937 (2a), 26 Jun 1937 (2a). *Dessiatoff* 2169 (3b), 2199 (3b). *Dieterle* 1350 (3b). *Dimitrijin* May 94 (2a). *Dimonie* Jul 1908 (2a). *Döbbeler* 241 (2a). *Doerfler* 866 (1). *Doreff* 20 Jun 1894 (2a). *Drobov* 19 Apr 1906 (2b). *Drummond* 23332 (4), 23344 (4). *Dubovik* 12 Jun 1957 (1). *Dufft* May 1845 (2a), 26 May 1884 (2a). *Dulfer* Jun 1961 (2a). *Dunkel* 22 Jun 1991 (2b). *Duthie* 13857 (4). *Duty* 6 Jun 1955 (2a), 4 Jul 1972 (2a). *Duval-Jouve* 3 Jul 1861 (2a). *Duvigneaud* Jul 1955 (2a). *Dvořák* 29 May 1971 (2a), 24 May 1972 (2a). *Dzen-Litovskaja* 742a (4), 482 (4). *Dzevanovsky* 2 (1). *Eberhardt* 7323 (3a), 7885 (3a), 8798 (3a), 9362 (3a). *Ecklon* 1808 (2a). *Edelberg* 2034 (4). *Eggert* 3 Jun 1869 (2b). *Einsander* 25 May 1880 (2a). *Enden* 102 (2b), 159 (4). *Endtmann* 10 Jul 1960 (2b), 11 Jun 1960 (2a), 20 Jun 1962 (2b), 18 Jul 1962 (2b), 25 Jun 1963 (2b), 15 Jun 1964 (2b), 19 Jun 1964 (2b). *Esetreppig* 28 Jul 1881 (2a). *Fayush, Tamanyan, Oganesyan, Ter-Voskanyan & Vitke* 04-0516 (2a). *Fedtschenko* 49 (3a), 2 Aug 1897 (4), 27 Jul 1904 (3a). *Fedtschenko, Noskov, Bobrov & Monyushko* 201 (2a). *Fetsch* 24 May 1889 (2a). *Folkenson* 16 May 1958 (2a). *Frame* 7 Jun 1905 (1). *Freiberg* 105/6 (2a). *Freitag* 1514 (3a). *Frey* 414: (6) (4). *Gabrielian* 27 May 1960 (2a). *Gailing* 21 May 193 (2a). *Ganeshin* 374 (2a). *Geisenheyner* Jul 1877 (2a). *Gilbert* 32 (4). *Gilli* 13 Jul 1951 (3a), 2 Jun 1950 (3a). *Goloskokov* 20 May 1953 (3c), 9 Jun 1953 (3c), 12 Jun 1953 (3c), 4 Jun 1955 (4), 6 May 1956 (3c). *Golubeva, Denisova, Nadezhina, Krasil'nikov, Semidel & Sokolov* 20 Jun 1959 (2a), 23 Jun 1959 (2a), 3 Jul 1959 (2b). *Golubkova* 1221 (1). *Gordienko & Chilikina* 473 (3b). *Gordyagin* 1260 (2a). *Gorschikova* 119 (1). *Görz* 16 May 1909 (2a). *Grebner* 198 (2a). *Grey-Wilson & Hewer* 662 (3a). *Grigorjev* 119 (3b), 303 (1). *Grolle* May 1953 (2a). *Gross* 18 Jun 1882 (2a), 26 Jun 1895 (2a), 1923 (2a). *Grubov* 21 (2b), 422 (3b). *Grubov & Lybarskiy* 282 (4). *Grudzińska* 23 May 1961 (2b). *Güemes & Bacchetta* 2510 (1). *Gugnacka-Fiedor* 195 (2a). *Gusev* 5275 dublet (3c), 5755 (3a). *Hackel* 7383 (2a), May 1880 (2b). *Hadinec* 2 Jun 1990 (2b). *Hainfolz* 399 (2a). *Handel-Mazzetti* 23 May 1898 (2a), 30 May 1898 (2a), 1 Jun 1902 (2a), Jun 1935 (2a). *Hartmann* 2383 (4), 2384 (4). *Harver* 3 Jul 1923 (2a). *Hasslerot, T.E.* 8 Jun 1928 (2a). *Hasslerot, B.E.* 20 Jun 1950 (2a). *Haussknecht* May 1854 (1), 25 May 1874 (2a). *Jeník* 1879 (2a), 6 Jun 1887 (2a), 15 Jun 1899 (2a). *Heiland* Jun 1872 (2a). *Henil* 1965 (2a). *Hirth* 20 May 1897 (2a). *Höfer* 1 Jun 1860 (2a). *Holubey* Jun 1880 (2a). *Höpflinger* 29 May 1955 (2a). *Hora* 2099 (1), 10 Jun 89 (1), 20 Jun 1984 (1). *Hosek* 4-2002 (2a). *Houbey* 6 Jun 1900 (2a). *Ikonnikov* 5654 (4), 10562 (3a), 12499 (3b), 14026 (3a), 16537 (4). *Ikonnikov, Ladygina & Litvinova* 7424 (4), 7538 (4), 8756 (4). *Ikonnikov & Litvinova* 5099 (2b), 6517 (2b), 6616 (2b), 6747 (2b). *Ikonnikov, Litvinova & Gladkova* 6100 (2b). *Ilić* 10 Jun 1932 (2a). *Ilijn* 40 (2a), 101 (2a). *Ilijn & Grigorjev* 137 (2a). *IPSE* 18 Jun 1963 (1). *Ivanova & Tonshina* 704 (1), 836 (2a), 1193 (1). *Ivashin* 1516 (2b). *Jachan* 9 (2a). *Jakouschev* 26 May 1910 (1). *Janka* 1 Jun 1869 (2a), 5 Jun 1868 (1), 30 Jun 1868 (1), 19 Jun 1877 (1). *Jávorka* 29 May 1928 (2a). *John* 1827 (2a). *Jorges* 6 Jun 87 (2a). *Junatov, Li Shi-in & Yuan I-fan* 505a (3c), 530 (4), 1438 (4). *Junatov & Yuan I-fan* 1019 (3c), 1104 (2a). *Jurisic* 16 May 1931 (2a). *Kalheber* 78-464 (1). *Kamelin, Darymaa, Gambold, Budantzev & Gubanov* 876 (2b). *Kameshkina* 163 (3b). *Karamysheva, Sanchir & Sumerina* 527 (2a). *Karelin & Kirilloff* 1841 (2a). *Kárpati* 26 May 1936 (1). *Kasatkina* 255 (3c). *Kashmeniskiy* 1906 (2b). *Kästner* 15 Jun 1997 (1). *Kazakov* 94 (2a). *Kazakova* 16 Jun 1922 (1). *Kerstan* 1197 (3b), 1509 (4). *Khokhryakov & Mazurenko* 8 Aug 1949 (1). *Kiev* 10-30 Jun 1905 (2a). *Kivenheimo* 10 Jul 1978 (1), 23 Jul 1978 (1). *Kleopow* 17 May 1926 (2b), 19 May 1930 (2b). *Klopotov* 8 Jun 1912 (2a). *Knorrung* 178 (2a), 341 (1), 467 (4), 684 (4). *Koch* 8 May 1934 (2a), 11 Jun 1935 (2a). *Koelz* 6046 (3a), 6924 (4). *Koop* 27 May 1960 (2a). *Korb* 22 May 1913 (2a), 16 Jun 1922 (2b), 21 May 1923 (2a), 26 Jun 1923 (1), 23 May 1933 (2a), 17 Jun 1942 (2a), 6 Jun 1943 (1). *Korotkova* 443 (2a), 541 (3b). *Korshinsky* 5644 (4), 5648 (3b), 1878-1887 (2b), 23 May 1889 (2a). *Koskinen* 27 Jun 1945 (1). *Kotukhov* 25 Jun 1970 (2a), 2 Jun 1976 (4), 3 Jul 1991 (2a), 12 Jun 1992 (3c), 20 Jul 1993 (3b), 11 Jul 1998 (3a). *Kozlovskiy* 1347 (2a). *Kramer* 4962 (2a). *Kramer & Westra* 4117 (2a). *Krascheninnikov, H.* 5203 (3c), 5345 (2a), 5345 (3c), 5354 (3c), 5903 (3c), 9 Jun 1914 (3c). *Krascheninnikov, I.M.* 111 (1). *Krasnoborov & Pyatak* 28 Jun 1964 (2a). *Krassnow* 1886 (3c). *Krenberger* 3 Jul 1877 (2a). *Krendl* 11 Jun 1961 (2a), 21 Jul 1968 (2a), 7 Jun 1970 (2a), 12 May 1973 (2a), 5 Jul 1973 (2a), 5 May 1975 (2a), 11 May 1975 (2a), 30 May 1976 (2a), 23 Apr 1977 (2a), 5 Jul 1978 (2a), 10 Jul 1978 (2a), 31 May 1987 (2a). *Krist* 3 Jul 1938 (1). *Kronotov* 1912 (2a). *Krylov* 18 Jun 1892 (2a), 10 Jun 1912 (2a). *Krylova & Dervin* 4 Jun 1951 (1). *Kučerovská* 697 (1), 8 Jul 1912 (2a). *Kugelberg* Jul 1865 (1). *Kukkonen* 7263 (3b). *Kulshnova & Buturlina* 19 Jun 1957 (2a). *Kuminova & Luikova* 5818 (2a). *Künz* 5 May 2000 (2a). *Kurganskaya & Udtintseva* 536 (3c), 565 (4), 6 Aug 1960 (4). *Kurlyushkin* 12 Jun 1939 (1), 4 Jul 1939 (1). *Kuznetsov* 114 (2a), 430 (2a), 688 (2a), 3 Jun 1911 (2a). *Kuznetsova* 1 Jun 1954 (2a). *Kuznezov* 310 (1). *Lachashvili* 29 (1). *Ladygina* 1200 (3a). *Ladygina, Ikonnikov & Litvinova* 18219 (4). *Lagarski* 13 Jun 1886 (2a). *Lagerheim* 1843 (2a). *Lamont & Thermé* 44360 (2a). *Landauer* 691 (2a). *Lang* 3 May 1964 (2a), 14 May 1989 (2a), 1 Jul 1991 (1). *Langerak & Den Haag* 1545 (2a). *Larin & Musatowa* 218 (2b). *Laudberg* Jul 1898 (1). *Laus* Jun 1930 (2b), Jun 1931 (2a), Jun 1933 (1), Jun 1934 (1), Jun 1935 (1), Jun 1935 (2b), Jun 1936 (2a), Jun 1938 (2b) Jul 1938 (1). *Lavrenko & Rodin* 944 (3a). *Lemke* 586 (2a). *Lenz* 1865 (2a). *Leute* 50 May 1969 (2a). *Licht* 941 b (2a), 941 c (2a). *Likendrat* May 1867 (2a). *Lindberg* 11 Aug 1939 (2a). *Lindemann* Jun 1866 (2a), 10 Jun 1873 (2a). *Lippert* 20891 (1). *Lippert & Merxmüller* 17331 (2a). *Lippold* 16 Jun 1975 (2a). *Lispky* 2355 (4). *Litvinov* 4902b (1), 5 Jul 1914 (1). *Ljirft* 22 May 1897 (2a). *Loewenberg* 1011/178 (2a). *Longberg* 29 Jun 1845 (2a). *Lovelius* 29 May 1973 (2b). *Lundberg* Jun 1897 (2a). *Lundqvist* 16738 (2b). *Makonsky* 5 Jun 1858 (2a). *Maljtsev* 376 (2a), 670 (2a), 8 Jun 1907 (2a). *Marchesetti* Jun 1869 (2a). *Marret* 104 (2a). *Mathesius* Jun-Jul (1), Jun-Jul (2). *Mayer* 29 May 1921 (2a). *Medina & al.* 2591 (1). *Medvedev* 63 (4). *Melzer* 10 Jun / 15 Jul 1962 (1), 7 Jul 1962 (2a), 15 Jul 1962 (1), 24 Jun 1964 (2a), 9 Jun 1965 (2a), 18 Jun 1969 (2a). *Mertens* 18 Jul 42 (1). *Merxmüller & Angerer* 33 321 (2a). *Merxmüller & Wiedmann* 8 Jun 1950 (2a), 23 May 1953 (2a). *Metlesics* 29 May 1961 (2b). *Meyer & Lippold* 20 Jun 1965 (1). *Meyer, F.* 15 Jul 1977 (1), 25 May 1995 (2a). *Meyer, K.* 11 May 1950 (2a). *Meyer & Manitz* 5 Jun 1966 (1), 20 Jun 1976 (1), 20 Jun 1976 (2a). *Michajlova & Popova* 66 (4). *Michelson* 1978 (3c). *Missbach* Jun 1912 (1), Jun 1912 (2a). *Moraldo* 15 Jun 1984 (1), 20 Jun 1984 (1). *Morariu* Jun 1965 (2a). *Mrkvicka* 8437 (2a), 13645 (2a). *Müller* 1873 (2a), Jul 1879 (2a), 25 May 1879 (2a). *Murbeck* 19 Aug 1889 (2a). *Negrean* 1 Jun 1969 (2a). *Nepli* 28 May 1943 (4), 1 Jun 1943 (3a), 4 Sep 1943 (4). *Neubauer* 230a (3a), 233 (3a), 294 (3a). *Neuman* Jul 1901 (2a). *Neumayer* 11 May 1932 (2a), 8 Jun 1935 (2a), 28-29 May 1939 (2a). *Ničić* 8 Jun 1886 (2a). *Nilsson* 8 Jun 1928 (2a), 4 Jul 1948 (2a). *Novichkova* 9 Jun 1965 (2a), 29 Jun 1965 (2a). *Nyárády* 1430 (1). *Nydegger* 43755 (2a). *Obernderer* 17 May 1924 (2a). *Oborny* 12 Jun 1884 (2a). *Oenicke* 23 May 1933 (2a). *Oertel* Jul 1861 (2a). *Otruba* 165 (1). *Ovchiinnikov & Afanásiev* 187 (3c), 218 (3b), 405 (3a), 842 (3a), 851 (3a), 1196 (3a), 1964 (3a), 2047 (4), 2094 (4). *Pachoskii* 9 May 1909 (2a), 18 Jul 1911 (2b). *Pallon* 6813 (2a). *Pastor Fest* 1111 (1). *Pavlov* 79 (3c), 181 (3b), 535 (4). *Pazij* 19 (2b). *Peshkova & Tarasova* 2043 (2a). *Pichauer* Jun 1921 (1). *Pisopliczka* 25 May 1925 (2a). *Pobedimova* 127 (2b), 5102 (2b). *Podjakova* 25 Jun 1930 (2a). *Podlech* 8209 (2a), 28441 (2a), 30256 (3a). *Podpera* 28 May 1896 (2a), 1 May 1897 (2a), 9 May 1897 (2a), May 1898 (2a), Jun 1898 (2a), May 1899 (2a), Jun 1899 (2a), 12 May 1921 (1), 6 Jul 1926 (1). *Podpera & Jirásek* 164 (2a), 165 (1). *Pokorný & Strudl* 31 May 1982 (2b), 8 Jun 1982 (2a), 20 May 1985 (2b), 29 May 1985 (2a), 14 Jul 1986 (1). *Poltawa* 25 May 1891 (2a). *Polyakov* 324 (3b). *Potanin* 87 (4). *Pralrow* Jul 1898 (2b). *Preiss* May 1910 (2a). *Prilipko & Vichert* 27 Jul 1931 (1). *Printz* Jun 1914 (2b). *Prodán* 14 Jun 1910 (2a). *Prokofjeva* 122 (2b). *Prokofiev & Agafanov* 10 Jun 1973 (2b). *Puolanne* 1918 (1). *Quelle* 13 May 1894 (1). *Raus & Pina Gata* 24-1-4 (2b), 35-1-13 2 Jun 1999 (2b). *Rechinger* 17627 (3a), 32005 (3a), 13 May 1926 (2a). *Regel* 1838 (2a). *Regel* 15 Jul 1928 (1). *Rehmann* 216 (2a). *Reinhard* 29 May 1854 (2b). *Reschikov* 14 Jul 1967 (2a). *Reverdatto* 25 May-6 Jul 1926 (2a), 25 Jun-6 Jul 1926 (2b). *Richter* K. 18 May 1833 (2a), 14 May 1871 (2a). *Richter* L. 313 (1), 312 (1), 312 (2a). *Rickmers-Bremen* 1928 (4). *Roborowski* 4 Jun 1893 (4). *Roessler* 321 (2a), 2465 (2a), 6363 (2a). *Ronniger* 22 May 1913 (2a), 23 May 1926 (2a), 13 May 1928 (2a), 17 May 1928 (2a), 19 May 1929 (2b), 16 May 1932 (2a), 27 May 1936 (2a), 25 May 1941 (2a). *Roslyak* 17 Jun 1958 (1). *Rothmaler* 19947 (2a), 20142 (2a), 30 May 1928 (2a). *Rozhevitz* 644 (3c). *Rafiq & Hayat HG-97-102* (3a), *HG-97-368* (3a). *Rubtsov* 16 Jun 1929 (2b). *Ruppert* 30 May 1929 (2a). *Rusanov* 167 (4). *Sahlén* Jun 1872 (2a). *Sarycheva* 26 May 1956 (2a). *Savič & Sokolova* 73 (4). *Schahel* 2 Jul 1975 (2a). *Schellauf* 15 Jun 1936 (2a). *Scheppig* 28 Jul 1881 (2b), 18 Jun 1882 (2a), 26 Jun 1895 (2a). *Schiffers* 2138 (1), May 1885 (2a). *Schischkin* 30 Jul 1919 (1). *Schischkin, Steinberg & Sunnevicz* 29 May 1931 (4). *Schleiden* 1843 (2a). *Schlyters* 16 Jun 1879 (2a). *Schmarf* 28 Aug 1930 (1). *Schmid* 128 (3a), 2335 (4). *Schneeweiß & Schönswetter* 2211 (2a). *Schneider* 20 May 1923 (2a), 13 May 1938 (2a), 21 Jun 1960 (1), 29 Jun 1960 (2a), 14 Jun 1962 (2a), 26 May 1963

(2a), 30 May 1963 (1). *Schneller* May 1868 (2a). *Schneller* May 1868 (1), May 1868 (2a). *Schühe* 1957 (2a). *Schuhwerk* 81/163 (2a), 86/140 (2a). *Schwarz* 30 May 1928 (2a), 20 May 1947 (2a). *Šestka* 765 (2a). *Shischkin* 17 Jul 1934 (3c). *Shischkin & Genina* 26 Jun 1913 (3c). *Shulga* 1907 (2a). *Šída* 4387 (2b). *Simonkai* 3986 (2a), 3990 (1), 10 May 1878 (2a), 24 May 1894 (2a), 1 Jun 1904 (1). *Sishkin* 6 Jun 1914 (2a). *Sjoberg* 4 Aug 1890 (1). *Skwortsov* 17 Jun 1963 (1), 14 May 1970 (2b), 6-7 Jul 1979 (2a), 1 Jun 1985 (2a), 7 Jul 1993 (1). *Smidt* 387 (2a). *Smirnova* 525 (2a), Jul 1931 (1). *Smirnow* 4 (2a), 28 (2a), 29 (4), 32 (3c), 40 (1), 54 (2a), 101 (2a), 4902a (1). *Sobolevskaya & Stennikova* 9 Jun 1946 (2a). *Sorger & Buchner* 82-84-52 (2a). *Soška* May 1935 (2b). *Sosnowsky* 5 Jul 1925 (2a). *Spiridonow* 294 (2b). *Spitsnes* May 1899 (2a). *Stainton* 2806 (3a). *Stanjukovich, Sidorov, Krivonogova, Ladygina & Ikonnikov* 1161 (4), 1172 (4), 1317 (4), 1634 (4), 1703 (4), 2176 (3a), 4632 (4). *Staudinger* 98/4/8 (2a). *Stewart R. R. & Stewart I. D.* 22201 (4). *Sticfelhagen* 2412 (2a). *Strudl* 145 (2b), 18 Jun 1984 (2a), 20 May 1985 (2b). *Stud. Biol. Rheno-Trai. in itinera* 271 (2a), 17 Jul 1960 (2a), 27 May 1967 (2a). *Suhova* 18 (2a). *Sultanov* 238 (3a), 528 (4). *Suza* Jun 1911 (1). *Švestka* 765 (2a). *Theurillat* 4010 (2a). *Timmermans* Jul 1936 (2a). *Titov* 614 (3c), 1144 (3c). *Tod* 8753/4 (2a). *Tschech* Jun 1935 (2a). *Tulinova* 1901 (3b). *Tuturin & Bessedin* 291 (3a). *Tzvelev* 353 (2b), 1499 (3b), 1636 (3b), 17 Jun 1952 (4), 15 Jul 1952 (4). *Ullepitsch*. 6 Jul 1895 (2a), May 1909 (2a). *Vagina & Kovachevich* 28 Jun 1956 (2a). *Hoiaislouma* 1964 (1). *Valina & Kovacevilk* 15 Jul 1988 (2a). *Vallen* 10 Jun 02 (2a). *Vandakurova* 22 May 1949 (1). *Vandas* 27 Aug 1922 (1). *Vašák* 23 May 1974 (2a), 7 Jul 1975 (2a), 31 Jul 1975 (1), 29 Jul 1981 (2a). *Vasilevich et al.* 70 (4). *Vasiliev & Korovkin* 222 (2a). *Vautier* 21 May 1949 (2a). *Velenovsky* 1 Jun 1884 (2a), 30 Jul 1884 (1), 2 Aug 1884 (1), 1 Aug 1886 (1), 21 Jul 1887 (1). *Vestergren* 30 Jul 1922 (2a). *Vetter* 28 May 1905 (2b), 11 Jun 1911 (2a), 27 May 1912 (2b), 9 Jun 1922 (2b), 12 Jun 1912 (2a), 16 May 1913 (2a), 22 May 1913 (2a). *Vinogradova* 61 (2b). *Vogel* 6 Jun 1921 (2a). *Vogeler* 8 Jul 62 (2a). *Voike* 21 May 1985 (1). *Vollman* 15 May 1910 (2a). *Volk* 71/188 (3a), 71/211 (3a), 71/242 (3b), 71/369 (3a), 2251 (3b), 2773 (3b). *Wagner* 958 (1), 1942 (1), Jun 1921 (1). *Walger* 14 May 1939 (2a). *Wallengren* Jul 1875 (1). *Walter* 8175 (2b). *Weber* 384 (1), 30 Jun 1931 (1), 20 May 1932 (1), Jun 1933 (2a), Jun 1935 (1), Jun 1936 (1). *Wettstein* 1908 (2a), May 1909 (2a), 21 May 1914 (2a). *Weyner* 4 Jun 1867 (2a). *Winter* 1865 (2a), 1867 (2a). *Wirtgen* 596 (2a), Jun 1910 (2a). *Witasek* Apr 1904 (2a). *Wittmer* 10 May 1881 (2a). *Wolaszezak* 22

May 1913 (2a). *Wolf* May 1898 (2a). *Yanishevsky* 2 Jun 1904 (2b). *Yarmolenko & Gontscharow* 1120 (3b). *Zaikan* 30 May 1913 (2a). *Zepnhaar* 1818 (2b). *Zermetti* 27 Jun 1937 (1). *Zerny* 17 May 1920 (2a). *Zetterstedt* 6 Jul 1871 (2a). *Zigmundik* 22 May 1915 (2a). *Zotterman* 29 May 1953 (2a). *Zvereva & Chesnokova* 2 Jul 1967 (2a).

#### APPENDIX 2. Variables used in the morphometric analyses.

**Quantitative characters:** **GLL:** Glume length (cm); **LEML:** Lemma length (mm); **CAL:** Callus length (mm); **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); **AWN:** Awn diameter (mm); **COL:** Column length (cm); **SET:** Seta length (cm); **COL / SET:** Ratio column length and seta length; **LEMH:** Lemma hair length (mm); **BASD:** Basal leaf blade diameter (mm); **LL:** Basal ligule length (mm); **LUL:** Ligule uppermost leaf length (mm); **D\_S:** Dorsal and subdorsal rows joining length (mm); **D\_S / LEML:** Ratio between the dorsal and subdorsal rows joining length and lemma length; **ML:** Ventral row length (mm); **DL:** Dorsal row length (mm); **DL / LEML:** Ratio between the dorsal row length and lemma length; **PH:** Plant height (cm).

**Qualitative characters:** **ABIND:** Abaxial surface of basal leaf blade: glabrous (0); minutely scabrous (1); distinctly scabrous (2); sparsely stiff hairs (3); **ADIND:** Adaxial surface of basal leaf blade: scabrous (0); pubescent (1); papillose (2); minutely pubescent (3); **LBA:** Leaf-blades apex: glabrous or scabrous (0); finished in a tassel of hairs (1); long acuminate (2); **BLM:** Basal leaf ligule margin: glabrous (0); ciliate (1); ciliolate (2); **BLT:** ligule tip: glabrous (0); ciliate (1); ciliolate (2); **UPO:** Upper sheaths ornamentation: glabrous (0); papillose (1); scabrous (2); scabrous with stiff hairs (3); **CO:** Culm ornamentation: glabrous (0); scabrous (1); pubescent (2); **PA:** Panicles: exserted (0); partially enclosed (1); enclosed (2); **PBI:** Panicle basal internode surface: glabrous (0); scabrous (1); pubescent (2); **DSDF:** dorsal and subdorsal free: no (0); yes (1); **CS:** callus shape: slightly curved (0); straight (1); **ACS:** awns column surface: hairy (0); glabrous (1); tuberculate (2)