Taxonomy of the Crested Wheatgrasses (Agropyron)

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ABSTRACT: The purposes of this paper are to review the position of the genus Agropyron in the tribe Triticeae and to examine alternative taxonomic treatments within Agropyron. When Agropyron is defined as those species with the P genome, it becomes a small genus with less than 10 species consisting of only the crested wheatgrasses. This narrow definition of Agropyron is now accepted in Europe and Asia; North Americans should accept that same definition. As treated in 1976 by N. N. Tzvelev in Poaceae URSS, Agropyron consists of 10 species and 9 subspecies, but most of those taxa are endemics of little interest to North American users of crested wheatgrass. North Americans need to consider only three species: 1) A. cristatum (L.) Gaertn. sensu lato, 2) A. desertorum (Fisch. ex Link) Schult., and 3) A. fragile (Roth) Candargy [=A. sibiricum (Willd.) Beauv.].

INTRODUCTION

To understand the taxonomy of the crested wheatgrasses, Agropyron cristatum (L.) Gaertn. and related species, it is necessary to view them in the context of the taxonomy of the entire tribe Triticeae (= Hordeeae). Revisions have recently been made in the taxonomy of the Triticeae (Tzvelev 1976, Melderis et al. 1980) and others are being proposed (Dewey 1984, Löve 1984). The significant taxonomic changes involve redefinition of most genera, deletion of a few genera, and establishment of several new genera. The primary catalyst for the current taxonomic activity and controversy in the Triticeae is a movement to bring classification into line with biological relationships.

Traditionally, genera of the Triticeae have been separated on the basis of morphological features of the spikes, such as number of spikelets per node, glume size and shape, and rachis characteristics (Hitchcock 1951). Although these traits lend themselves readily to construction of taxonomic keys, their use often results in placement of closely related species in different genera or distantly related species in the same genus. For example, Agropyron scribneri and Sitanion hystrix are closely related species (Dewey 1967), yet they have been placed in different genera on the basis of one vs. two spikelets per node. On the other hand, Elymus canadensis and Elymus cinereus are distantly related species (Dewey 1966), yet they have been placed in the same genus because they have two or more spikelets per node. To those who subscribe to the philosophy that taxonomy should reflect biological relationships, inconsistencies of this nature are unacceptable.

Over the past 30 to 40 years, cytogeneticists have accumulated a vast amount of information that measures biological relationships in terms of 1) the ability of species to hybridize, 2) the level of chromosome pairing in the interspecific hybrids, and 3) the fertility of the F_1 hybrids. In the Triticeae, a system of classification based on cytogenetic information differs substantially from one based on morphology. Both systems have advantages and disadvantages. The traditional system of classification based on morphology is stable and convenient to use, yet it is somewhat artificial. The system of classification based on cytogenetics will be unstable until all genetic relationships have been determined, and taxonomic keys will always be more difficult to construct and less convenient to use. Nevertheless, I am confident that science will be best served in the long run by a taxonomic system that groups species according to their biological relationships.

Through the process of genome analysis (analysis of chromosome pairing in interspecific hybrids) it has been possible to identify most of the basic chromosome sets (genomes) in the perennial Triticeae. The genomic system of classification as outlined by Löve (1982) is based on the concept that each genome or combination of genomes should be recognized as a different genus. Under this system, Löve recognized 37 genera in the Triticeae, which is almost double the number recognized by more traditional taxonomists (Table 1). I agree in principle with Löve's generic concepts; however, some adjustments in generic boundaries must be made as additional cytogenetic data are obtained.

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Löve's (1984) treatment encompasses the entire tribe (annuals and perennials), whereas I have concerned myself largely with the perennials (Dewey 1984). Table 2 presents a summary of the genera, as I view them, that contain perennial grasses. *Critesion* (= *Hordeum* pro parte) and *Elymus* will require further partitioning as genomic relationships become more clearly established. Fortunately, there is little likelihood that the newly defined generic boundaries of *Agropyron* will be changed.

REDEFINITION OF *AGROPYRON*

Agropyron (wheatgrass) in its traditional and broad sense (sensu lato) has been the largest genus in the Triticeae, encompassing more than 100 species distributed widely in temperate and subarctic regions of both the northern and southern hemispheres. *Agropyron* sensu lato contained almost all of the perennial species in the Triticeae that had single spiklets per node. North Americans have generally accepted this broad definition, which was advocated by A. S. Hitchcock (1935, 1951) in the United States and W. M. Bowden (1965) in Canada. Until recently, most British and other European agrostologists (Bor 1970, Hubbard 1968, Kerguelen 1975) treated *Agropyron* in its broad sense.

The Russian agrostologist Nevski (1933) treated *Agropyron* in a very narrow sense (sensu stricto) by restricting it to 13 species, the crested wheatgrasses. Nevski apparently reconsidered his 1933 decision to be too drastic because in the following year he redefined *Agropyron* as consisting of two subgenera: *Elytrigia* and *Eu-Agropyron* (Nevski 1934). Subgenus *Elytrigia* consisted of the rhizomatous species of *Agropyron*, e.g., *A. repens*, as well as some of the caespitose species, e.g., *A.*

Table 1.--Genera included in the tribe Triticeae by various authors.[1]

Nevski (1933)	Hitchcock (1951)	Tzvelev (1976)	Melderis et al. (1980)	Löve (1984)
Aegilops	*Aegilops*	*Aegilops*	*Aegilops*	*Aegilemma*
Agropyron	*Agropyron*	*Agropyron*	*Agropyron*	*Aegilonearum*
Aneurolepidium	*Elymus*	*Amblyopyrum*	*Crithopsis*	*Aegilopodes*
Anthosachne	*Hordeum*	*Dasypyrum*	*Dasypyrum*	*Aegilops*
Asperella	*Hystrix*	*Elymus*	*Elymus*	*Agropyron*
Brachypodium	*Lolium*	*Elytrigia*	*Eremopyrum*	*Amblyopyrum*
Clinelymus	*Monerma*	*Eremopyrum*	*Festucopsis*	*Australopyrum*
Critesion	*Parapholis*	*Henrardia*	*Hordelymus*	*Chennapyrum*
Crithopsis	*Scribneria*	*Heteranthelium*	*Hordeum*	*Comopyrum*
Cuviera	*Secale*	*Hordelymus*	*Leymus*	*Critesion*
Elymus	*Sitanion*	*Hordeum*	*Psathyrostachys*	*Crithodium*
Elytrigia	*Triticum*	*Hystrix*	*Secale*	*Crithopsis*
Eremopyrum		*Leymus*	*Taeniatherum*	*Cylindropyrum*
Haynaldia		*Psathyrostachys*	*Triticum*	*Dasypyrum*
Heteranthelium		*Secale*		*Elymus*
Hordeum		*Taeniatherum*		*Elytrigia*
Malacurus		*Triticum*		*Eremopyrum*
Psathyrostachys				*Festucopsis*
Roegneria				*Gigachilon*
Secale				*Gastropyrum*
Sitanion				*Henrardia*
Taeniatherum				*Heteranthelium*
Terrella				*Hordelymus*
Trachynia				*Hordeum*
Triticum				*Kiharapyrum*
				Leymus
				Lophopyrum
				Orrhopygium
				Pascopyrum
				Patropyrum
				Psathyrostachys
				Pseudoroegneria
				Secale
				Sitopsis
				Taeniatherum
				Thinopyrum
				Triticum

[1] The treatments are not necessarily comparable because all do not cover the tribe worldwide and most authors have worked from different geographical and historical perspectives.

Table 2.-- The perennial genera of the Triticeae tribe based on genome content.

Genus	Type species	Basic genome[1]	Approx. no. species	Chromosome no. (2n)
Agropyron	A. cristatum	P	10	14,28,42
Pseudoroegneria	P. strigosa	S	15	14,28
Psathyrostachys	P. lanuginosa	N	10	14
Critesion	C. jubatum	H	30	14,28,42
Thinopyrum	T. junceum	J-E	20	14, 28, 42, 56, 70
Elytrigia	E. repens	SX	5	42,56
Elymus	E. sibiricus	SHY	150	28,42,56
Leymus	L. arenarius	JN	30	28, 42, 56, 70, 84
Pascopyrum	P. smithii	SHJN	1	56

[1]Genome designations are those proposed by Löve (1982).

elongatum. Subgenus Eu-Agropyron consisted of the same crested wheatgrasses that Nevski included in his 1933 definition of Agropyron. Under both the 1933 and 1934 treatments, Nevski treated the large number of self-fertilizing species previously in Agropyron (e.g. A. trachycaulum) as Roegneria. Nevski's treatments did not receive widespread acceptance outside of the U.S.S.R., except in China where a modified version of his 1933 treatment is still in use (Keng 1965).

Tzvelev (1973), another Russian agrostologist, reinstated Nevski's 1933 definition of Agropyron by restricting the genus to 10 species. This treatment was included in Tzvelev's (1976) comprehensive publication, Poaceae URSS, which is now the generally accepted treatment of the grass family in the U.S.S.R. In the recently published Volume 5 of Flora Europaea, British agrostologists (Melderis et al. 1980) have adopted the narrow Nevski (1933) and the Tzvelev (1976) definitions of Agropyron. The treatment in Flora Europaea will almost certainly become accepted throughout Europe and in most of the British Commonwealth.

The narrow definition of Agropyron—now accepted in Europe, China, and the U.S.S.R.—is in complete harmony with the genomic system of classification. In view of the almost worldwide acceptance of the narrow definition of Agropyron by both traditional taxonomists and cytotaxonomists, North Americans should also accept that definition. Considering the facts that all crested wheatgrasses are native to Eurasia (none is native to North America) and that all of the type specimens occur in European or Asian herbaria, it is both illogical and presumptous for North Americans to define Agropyron in terms drastically different from those accepted in Eurasia.

CYTOGENETICS AND GENOME CONSTITUTION OF AGROPYRON

The crested wheatgrasses occur at three ploidy levels--diploid (2n=14), tetraploid (2n=28), and hexaploid (2n=42) (Jones 1960b). The tetraploids are by far the most common, and they span the entire natural distribution range of crested wheatgrass from Central Europe and the Middle East across Central Asia to Siberia, China, and Mongolia (Tzvelev 1976, Keng 1965). Diploids also occur from Europe to Mongolia; but their distribution is very sporadic, much like scattered islands in an otherwise tetraploid crested wheatgrass sea (Dewey and Asay 1982). Hexaploids are very rare; they apparently occur only in northeastern Turkey and northwestern Iran (Dewey and Asay 1975). Tetraploid strains are the most commonly seeded types in North America, being represented by the so-called "Standard" crested wheatgrass with four varieties— 'Nordan', 'Summit', 'Ephraim', and 'P-27' (Asay & Knowles 1985). Diploid strains are also seeded in North America and include the broadly defined "Fairway" with two varieties, 'Parkway' and 'Ruff', selected from the 'Fairway' germplasm. No hexaploid varieties have been bred.

The genome of diploid crested wheatgrass is represented by the letter "P", as suggested by Löve (1982). I have previously designated this genome as "C" (Dewey 1983), but that letter has also been applied to certain species of Aegilops. To avoid duplication of genome symbols, I suggest following Löve's (1982) system, which accounts for all species of Triticeae worldwide. Chromosome pairing is almost complete in hybrids among various broad-spiked (A. cristatum s. lat.) diploid taxa (Dewey and Asay 1982), showing that they contain the same basic set of chromosomes. Nevertheless, some structural chromosome rearrangements--translocations, inversions, etc.--occur in the genomes of some of the diploid taxa. Structurally or otherwise modified genomes may be represented with subscripts applied to the basic P genome, i.e. P_1, P_2, etc. Recently, a narrow-spiked diploid (A. fragile ssp. mongolicum) has been obtained from China (Dewey 1981) and hybridized with broad-spiked diploid Fairway. Chromosome pairing in these hybrids is very similar to pairing in the broad-spiked hybrids (Dewey and Hsiao 1984). It is now evident that all crested wheatgrass diploids, regardless of spike type, contain the same basic genome.

Tetraploid crested wheatgrasses behave cytologically as strict autoploids or near autoploids (Dewey and Pendse 1968, Dewey 1969), meaning that they contain one basic genome repeated four times. Hybrids between diploid and tetraploid crested wheatgrasses form up to seven trivalent associations per cell at metaphase I (Dewey and Pendse 1967), which shows that the genome in the tetraploids is more or less homologous with the genome in the diploids. The genome constitution of the tetraploids may be represented as PPPP (strict autoploid) or $P_1P_1P_2P_2$ (near autoploid). Doubling of a diploid gives rise to a strict autoploid, PPPP; whereas hybridization between two diploids, $P_1P_1 \times P_2P_2$, followed by chromosome doubling gives rise to a near autoploid, $P_1P_1P_2P_2$, or in other words a segmental allopoloid (Schulz-Schaeffer et al. 1963).

Hexaploid crested wheatgrasses behave cytologically as strict autoploids or near autoploids by forming frequent hexavalent associations at metaphase I (Dewey and Asay 1975). Chromosome pairing in hybrids of diploids X hexaploids and tetraploids X hexaploids is consistent with the hypothesis that hexaploid crested wheatgrass contains the basic P genome with some structural variations (Dewey 1969, 1973, Asay and Dewey 1979).

CRESTED WHEATGRASS TAXONOMY

The taxonomic history of crested wheatgrass reflects widespread confusion and uncertainty. Any expectation of a simple and neat solution to crested wheatgrass taxonomy is unrealistic because the problem is inherently complex, and subjective judgments must be made. Multiple chromosome races and the ability of crested wheatgrass taxa to hybridize are at the root of the taxonomic problems. All crested wheatgrass taxa can be hybridized with each other, and many taxa hybridize with ease and produce fertile or partially fertile offspring (Knowles 1955). Consequently, a great deal of introgression occurs and a continuum of morphological types covering the full range between the parent taxa results (Fig. 1).

North Americans are at a particular disadvantage in addressing crested wheatgrass taxonomy because: 1) the type specimens are not readily accessible (most are located at the Komarov Botanical Institute in Leningrad), 2) the opportunities to see the taxa in their natural habitats, especially in the U.S.S.R. and China, are limited, and 3) taxa introduced into North America soon lose their taxonomic identity and genetic integrity because of extensive intercrossing that occurs in nursery situations where many accessions are grown in close proximity to each other. Therefore, taxonomic decisions made on introduced materials are often unreliable.

Before undertaking a serious study of crested wheatgrass taxonomy, one must have a clear understanding of the type specimen of A. cristatum, which is the type species of Agropyron (Jones 1960a). Some confusion has existed concerning the type specimen of A. cristatum because the original Linnaean description involves a herbarium sheet of Bromus cristatus (= Agropyron cristatum) with two specimens, one with glabrous spikelets and one with villous spikelets. After studying the type sheet and Linnaeus' description of A. cristatum, Jones (1960a) designated the specimen with villous spikelets as the type. This is in agreement with Nevski's (1934) view of A. cristatum as plants with very dense oblong-ovoid spikes and villous spikelets. Many North Americans have incorrectly assumed that typical A. cristatum consists of plants that look like the variety Fairway, which has glabrous spikelets.

Early Soviet Treatments

Prior to the 1930's, most Soviet agrostologists (Konstantinov 1923) recognized two basic groups of crested wheatgrass: 1) those with broad spikes (A. cristatum) and 2) those with narrow spikes (A. desertorum). Both groups had many morphological variations, but all were included in the two species (Table 3).

S. A. Nevski's Treatment

Nevski (1934), who has a reputation as a taxonomic splitter, recognized 13 species to accommodate the major morphological variations (Table 3). Nevski emphasized growth habit (rhizomatous vs. caespitose), spike shape (linear, imbricate, and pectinate) and the amount and location of pubescence in separating species. Three taxa--A. dasyanthum, A. tanaiticum, and A. cimmericum--have long rhizomes, and A. michnoi has short rhizomes. I suspect that the three taxa with long rhizomes are rare hybrid derivatives, possibly crested wheatgrass X quackgrass (Elytrigia repens) rather than bona fide species. I have never seen plants of this nature in crested wheatgrass introductions, so North Americans need not concern themselves with them. The one taxon with short rhizomes, A. michnoi, does not appear to have a hybrid history; it resembles typical A. cristatum very closely. Both taxa are plants of East Asia. The presence of very short rhizomes distinguished A. michnoi from A. cristatum, and I do not consider differences of this type sufficient to warrant recognition as separate species.

The remainder of Nevski's (1934) taxa fall into three groups based on spike type: 1) linear spikes (A. fragile and A. sibiricum), 2) subcylindrical spikes (A. desertorum, A. badamense, and A. ponticum), and 3) pectinate spikes (A. cristatum, A. pectiniforme, A. imbricatum, and A. pinifolium). The two linear-spiked taxa can be distinguished on basis of pubescent (A. fragile) vs. glabrous (A. sibiricum) leaf sheaths. Separating species on the basis of pubescence on any plant part is a doubtful practice. Genetic studies on hybrids between A. desertorum X A. fragile indicate that leaf-sheath pubescence is controlled by two genes, with pubescence being dominant (D. R. Dewey unpublished). In the group with subcylindrical spikes, swollen culm bases distinguish A. badamense and A. ponticum from A. desertorum, whose culm bases are non-swollen. Leaf-sheath pubescence is used to separate

Figure 1.--Variations in spike types of crested wheatgrass (Agropyron).

A. badamense (glabrous) from A. ponticum (pubescent). The taxa with pectinate spikes differ from one another with respect to traits such as culm height (A. pinifolium has culms less than 30 cm tall), spike pubescence (A. pectiniforme is glabrous), and spike density (A. cristatum spikes are so dense that no gaps occur between spikelets).

Other morphological characters as well as habitat and distribution differences entered into Nevski's decision to recognize the various crested wheatgrass taxa as species. Nevertheless, several of the key traits, especially pubescence, appear to have little taxonomic value, casting some doubt on Nevski's classification. The Nevski treatment was not widely accepted even in the U.S.S.R. where the tendency was to combine taxa into four species: A. cristatum, A. pectiniforme, A. desertorum, and A. sibiricum. (Kosarev 1949).

K. Jones' Treatment

No new and significant developments occurred in crested wheatgrass taxonomy until Keith Jones, a British cytotaxonomist, published the results of an extensive herbarium study (Jones 1960b). In his classification, Jones placed greatest emphasis on spike shape in combination with spike density, level of spike pubescence, and geographic distribution. Jones was able to recognize only three species (Table 3): 1) a western broad-spiked species (A. pectiniforme), 2) an eastern broad-spiked species (A. cristatum), and 3) a narrow-spiked species (A. sibiricum). Chromosome races were recognized, but Jones did not place much taxonomic significance on chromosome races.

Agropyron pectiniforme sensu Jones is a species located primarily in European Russia (west of the Ural Mountains) and eastern Europe including the Balkan countries, Turkey, and Iran. The spikes of A. pectiniforme are pectinate, generally broad, and spikelets are usually glabrous. This species includes chromosome races of 2n=14, 28, and 42. The Fairway variety of North America is included in Jones' A. pectiniforme. He placed the following taxa in synonymy: A. pectinatum, A. imbricatum, A. dagnae, and A. cristatiforme.

Agropyron cristatum sensu Jones occurs primarily in East Asia. It has broad, compact, imbricated spikes with densely pubescent glumes and lemmas. Plant of this nature agree with Linnaeus' original description of A. cristatum and also with Nevski's (1934) concept. Jones (1960b) placed no other Agropyron species in synonymy with A. cristatum, although he speculated that A. michnoi might be part of the A. cristatum complex.

All crested wheatgrasses with narrow or cylindrical spikes were placed in A. sibiricum, with A. desertorum being considered as part of the complex. Jones pointed out the widespread confusion concerning A. sibiricum (awnless plants) and A. desertorum (short-awned plants) and thought it best simply to combine the two taxa. Numerous head shapes and sizes occur within A. sibiricum as defined by Jones. This species is distributed primarily in Central Asia from the Caspian Sea to Lake Balkhash.

N. N. Tzvelev's Treatment

In 1973, N. N. Tzvelev (Curator of Vascular Plants, Komarov Botanical Institute, Leningrad) published a revision of Agropyron and expanded that revision in his major work, Poaceae URSS (Tzvelev 1976). As might be expected, Tzvelev used Nevski's 1934 treatment as the basis of his own treatment; yet he introduced a number of significant changes (Table 3). Tzvelev promoted the concept of polymorphic species consisting of several subspecies, whereas Nevski did not consider subspecies. Tzvelev relegated several of Nevski's species to the status of subspecies and placed others in synonymy.

Tzvelev treated A. cristatum as a polymorphic species with nine subspecies (Table 3). All are broad-spiked taxa, but they differ with respect to spike details (density, pubescence, etc.), leaf type (flat, convolute, etc.), plant size, geographic distribution, and habitat. Sure recognition of all nine subspecies is very difficult if not impossible. When morphology is coupled with geographic distribution and habitat, Tzvelev may be able to recognize each subspecies; however, anyone with less expertise and lacking the information and herbarium facilities available to Tzvelev would probably be able to distinguish only two or three distinct subspecies. The subspecies cristatum is an East Asian taxon equivalent to Nevski's (1934) and Jones' (1960b) species A. cristatum. The subspecies pectinatum, which consists of 2n=14, 28, and 42 chromosome races, is the same entity as Jones' A. pectiniforme, i.e. the western element of broad-spiked crested wheatgrass (Fig. 2). Most of the other taxa treated by Tzvelev as subspecies are localized endemics that may or may not warrant subspecific status.

Tzvelev treated A. desertorum in the same manner as Nevski (1934). However, he placed A. sibiricum in synonymy with A. fragile, whereas Nevski recognized both taxa as distinct species. Jones took a different course of action and placed A. desertorum in synonymy with A. sibiricum.

The three rather strongly rhizomatous endemic taxa--A. cimmericum, A. tanaiticum, and A. dasyanthum--were recognized as species by Tzvelev, but he suggested that they may have a hybrid history. The last two species under Tzvelev in Table 3, A. pumilum and A. krylovianum, scarcely look like crested wheatgrasses and should not be accepted as such until more convincing evidence is given. Both taxa have very narrow spikes and were at one time included in Elytrigia (Appendix I). Tzvelev suggested that A. krylovianum is a hybrid of Agropyron X Elytrigia.

A. Löve's Treatment

Löve's (1984) treatment of Agropyron differs from all others in that he separated species exclusively on the basis of ploidy level. Inasmuch as the crested wheatgrasses occur at three ploidy levels--2n=14, 28, and 42--Löve recognized only three species--A. pectiniforme (2n=14), A. cristatum (2n=28), and A. deweyi (2n=42). However, he identified four subspecies within diploid A. pectiniforme and 21 subspecies within tetraploid A.

Table 3.--Taxonomic treatments of Agropyron s. str. by authors with broad but different perspectives of the genus.

Konstantinov (1923)	Nevski (1934)	Jones (1960b)	Tzvelev (1976)	Löve (1984)
A. cristatum	A. cristatum	A. cristatum	A. cristatum	A. cristatum
			ssp. cristatum	ssp. cristatum
A. desertorum	A. imbricatum	A. sibiricum	ssp. pectinatum	ssp. imbricatum
			ssp. puberulum	ssp. michnoi
	A. pectiniforme	A. pectiniforme	ssp. tarbagataicum	ssp. nathaliae
			ssp. kazachstanicum	ssp. puberulum
	A. pinifolium		ssp. baicalense	ssp. ponticum
			ssp. sabulosum	ssp. tarbagataicum
	A. michnoi		ssp. ponticum	ssp. kazachstanicum
			ssp. schlerophyllum	ssp. sclerophyllum
	A. ponticum			ssp. stepposum
			A. michnoi	ssp. birjutczense
	A. badamense		ssp. michnoi	ssp. bulbosum
			ssp. nathaliae	ssp. eriksonii
	A. desertorum			ssp. badamense
			A. badamense	ssp. desertorum
	A. sibiricum			ssp. sibiricum
			A. desertorum	ssp. fragile
	A. fragile			ssp. mongolicum
			A. fragile	ssp. pumilum
	A. cimmericum			ssp. pachyrrhizum
			A. cimmericum	ssp. dasyanthum
	A. tanaiticum			
			A. tanaiticum	
	A. dasyanthum			A. pectiniforme
			A. dasyanthum	ssp. pectiniforme
				ssp. baicalense
			A. pumilum	ssp. brandzae
				ssp. sabulosum
			A. krylovianum	
				A. deweyi

cristatum (Table 3). The tetraploid subspecies include narrow-spiked types (ssp. sibiricum), broad-spiked types (ssp. cristatum) and all intermediates.

Löve, who defines species in terms of genetic isolation, defends his position on the basis of putative sterility barriers between crested wheatgrass taxa at different ploidy levels and the general absence of those barriers between taxa within ploidy levels (personal communication with A. Löve, 21 September 1983). Unfortunately, crossing and sterility barriers between and within ploidy levels are not as consistent and distinct as Löve might think. It is true that diploid X tetraploid and diploid X hexaploid crosses are often difficult to make (Knowles 1955, Dewey 1973); however, tetraploids hybridize readily with hexaploids (Dewey 1969).

Sterility is sometimes as high or higher in intraploidy hybrids as in interploidy hybrids. Hybrids among three diploid taxa produced only 5 to 45% stainable pollen (Dewey and Asay 1982), whereas tetraploid X hexaploid hybrids produced 70 to 90% (Dewey 1969), and diploid X hexaploid hybrids produced 35 to 75% stainable pollen (Dewey 1973). In light of this information, I cannot accept Löve's premise that each ploidy level warrants species status.

Taxonomic History of Crested Wheatgrass in North America

The first five accessions of crested wheatgrass (PI's 835, 837, 838, 1010, and 1012)[1] entering the USDA Plant Introduction System came from the U.S.S.R. in 1898 under the name of A. cristatum. Four accessions identified as A. desertorum (PI's 19537-19541) and another accession of A. cristatum (PI 19536) were introduced from the U.S.S.R. in 1906. In that same year, the first accession of A. sibiricum (PI 20223) was introduced from Manchuria. Since those early days, many other accessions of A. cristatum, A. desertorum, and A. sibiricum and a few accessions of other crested wheatgrass taxa have been introduced. Inasmuch as virtually all crested wheatgrass grown in North America (except for that grown in experimental plots) is included in A. cristatum, A. desertorum, or A. sibiricum, the following discussion focuses on these three taxa.

The 1906 introductions of A. cristatum and A. desertorum played an especially important role in

[1] This and other information relative to PI (Plant Inventory) numbers come from USDA Plant Inventories, which contain a record of plant materials entering the National Plant Germplasm System.

crested wheatgrasses history and terminology in North America. The variety Fairway, released in Canada in the early 1930's, was almost certainly selected from PI 19536 (Dillman 1946). The name Fairway has since taken on a broader connotation than just the name of a variety; it now refers to one of the two major groups of crested wheatgrass seeded widely in North America, i.e. "Fairway" and "Standard". Fairway is one of the few diploid (2n=14) crested wheatgrasses and it is more or less morphologically and ecologically distinct. To most users of crested wheatgrass, Fairway includes all plants with broad pectinate spikes that resemble the variety Fairway. Many consider Fairway to be synonymous with A. cristatum, but the point needs to be made that A. cristatum encompasses more than just the variety Fairway or Fairway-like plants.

The name Standard crested wheatgrass has an even broader meaning than Fairway. The term Standard was first applied to an accession of A. desertorum, PI 19537, by the Montana Seed Growers Association, who chose that Plant Introduction as the standard for comparing the performance of various crested wheatgrasses. The meaning of Standard soon expanded to encompass all crested wheatgrasses that were not included in Fairway. Many users now consider Standard crested wheatgrass as being synonymous with A. desertorum. Equating Standard with A. desertorum is not appropriate because some of the variations found in Standard crested wheatgrass do not fall within the description of A. desertorum, which consists of tetraploid (2n=28) plants with cylindrical spikes and imbricated spikelets.

"Siberian" crested wheatgrass is the other common name that needs clarification. This name is usually applied to accessions identified as A. sibiricum. Between 1906 and 1940, about 50 A. sibiricum accessions entered the U.S., which is considerably more than the number of A. desertorum accessions during the same period. Despite this, references to A. sibiricum in crested wheatgrass literature are relatively infrequent. Apparently many of the A. sibiricum accessions fell into the broad category of Standard crested wheatgrass and were treated as A. desertorum. A variety of Siberian crested wheatgrass, 'P-27', was released by the Soil Conservation Service in 1953 from selections made in PI 108434, a 1934 A. sibiricum introduction from the U.S.S.R. (Hanson 1972). Today the names Siberian and A. sibiricum are applied to any crested wheatgrass with very narrow spikes and awnless lemmas.

Taxonomic confusion has surrounded the crested wheatgrasses from the time of their introduction until the present (Table 4). Although the five introductions in 1906 came under two names, A. cristatum and A. desertorum, they were combined under A. cristatum. Dillman (1946) gave the following account of the decision to combine the species: "When they were grown to maturity at the Belle Fouche Station in 1909, it was apparent that the two types were quite distinct. However, editorial changes in the manuscript of the published report referred to both types as A. cristatum. This has caused confusion ever since." This editorial decision set a precedent that continued for many years. Although only one species was recognized, the separation was maintained between Fairway and Standard. Hitchcock (1935) helped perpetuate the one-species concept for crested wheatgrass by including only A. cristatum in the first edition of the Manual of the Grasses of the United States. Swallen and Rogler (1950) reinstated the idea that crested wheatgrass consisted of at least two species, A. cristatum and A. desertorum. The second edition of the Hitchcock Manual recognized three species--A. cristatum, A. desertorum and A. sibiricum (1951). Because of the wide usage of the Hitchcock Manual, this three-species concept of crested wheatgrass is still the most common in North America.

Weintraub (1953) listed the three species recognized by Hitchcock and added a rather obscure taxon, A. michnoi (Table 4). For practical purposes, we can ignore A. michnoi because it probably does not occur in North America outside of experimental plots, and the identity of the A. michnoi spoken of by Weintraub is questionable.

Knowles (1955), a grass breeder at Saskatoon, Canada, accumulated a large collection of crested wheatgrass introductions. He grouped these accessions into six morphological forms, which were equated to six of the species recognized by Nevski (1934) (Table 4). Knowles was aware that Nevski considered Fairway to be A. pectiniforme, yet he put Fairway in A. cristatum to conform to the usage in North America at the time. Knowles demonstrated that most tetraploid crested wheatgrasses hybridize rather easily and produce fully or partially fertile hybrids. Definitive taxonomic conclusions could not be drawn from Knowles' material because most of it had been increased under cultivation and very likely had become genetically mixed by intercrossing between taxa.

Sarkar (1956) recognized six species of crested wheatgrass (Table 4). Sarkar's treatment has not received much acceptance, yet he made an important point that typical A. cristatum is a plant with densely hirsute glumes and lemmas, a fact not widely recognized in North America. He pointed out that Fairway differs from typical A. cristatum in having glabrous spikes; he described a new species, A. cristatiforme, to accommodate Fairway. Sarkar placed tetraploid (2n=28) plants that resembled Fairway into A. pectiniforme. I question the separation of taxa at the species level if they can only be distinguished by a chromosome count.

Bowden (1965) recognized three species of crested wheatgrass (Table 4), but none corresponded fully with those listed by Hitchcock (1951). Bowden viewed A. cristatum in the same fashion as Sarkar, i.e. plants with ovoid spikes, closely imbricated spikelets, and densely villous glumes and lemmas. Plants of this type occur only in experimental plots in North America. Bowden's A. pectiniforme is equivalent to Hitchcock's A. cristatum and includes diploid Fairway as well as broad-spiked tetraploids and hexaploids. Bowden followed Jones' (1960b) recommendation to consolidate A. sibiricum and A. desertorum.

In recent years, the trend has been to place all crested wheatgrasses into one species, A. cristatum (Table 4), thus returning to the course followed between 1910 and 1950. The varied treatments in Table 4 do not foster confidence, so it is tempting for the nonspecialist to accept the broadest definition of A. cristatum at least until some consensus is reached.

Table 4.--Species of crested wheatgrass (Agropyron) recognized by North American authors.

Author(s)	cristatum	desertorum	sibiricum	pectiniforme	cristatiforme	michnoi	imbricatum	fragile
Hitchcock (1935)	X							
Swallen & Rogler (1950)	X	X						
Hitchcock (1951)	X	X	X					
Weintraub (1953)	X	X	X			X		
Knowles (1955)	X	X	X			X	X	X
Sarkar (1956)	X	X	X	X	X	X		
Bowden (1965)	X		X	X				
Holmgren & Holmgren (1977)	X							
Arnow et al. (1980)	X							

SYNTHESIS AND RECOMMENDATIONS

The proposed redefinition of the perennial Triticeae genera on the basis of genome constitution (Table 2) will not gain total or immediate acceptance because it is a drastic departure from taxonomic tradition, especially in North America. However, Agropyron in its narrow sense is one of the least controversial genera with respect to its limits. The narrow definition of Agropyron as a small genus encompassing only the crested wheatgrasses has already been accepted by agrostologists throughout Europe and Asia.

Those working with crested wheatgrasses are confronted with a difficult choice of treatments. I recommend Tzvelev's (1976) treatment, but with certain modifications. I place confidence in Tzvelev's classification because: 1) it is relatively recent, 2) he considers a combination of morphological, geographical, ecological, and cytological data, and 3) he is curator of the world's most extensive collection of Triticeae grasses and has access to many type specimens. Because Tzvelev's treatment in Poaceae URSS is not readily accessible to most North Americans his key to Agropyron is reproduced in Appendix II. Reference to this key will give the user an appreciation of the nature and range of variation found in Agropyron in Eurasia.

Many North American users of crested wheatgrass may feel overwhelmed by the many taxa (10 species and 9 subspecies) described by Tzvelev. From a practical standpoint, most of us need to be concerned with just three species: 1) A. cristatum, 2) A. desertorum and 3) A. fragile. The remaining "species" are either hybrids or relatively uncommon endemics that have not been introduced into North America. The distinguishing characteristics of the three species are summarized in Table 5.

Classification of crested wheatgrass accessions or individual plants into one of the three species will often be difficult and unsatisfying. Variation is continuous between the morphological extremes of the narrow linear-spiked A. fragile to the broad pectinate-spiked A. cristatum (Fig. 1). Classification problems are accentuated in North American introductions because many are genetically mixed by hybridization, and single accessions often contain several morphological forms. Some may question the wisdom of attempting to partition a morphological continuum into discrete units. An alternative is to treat all crested wheatgrasses as a single species, A. cristatum, and recognize distinctive morphological or ecological types as subspecies. This approach would accomplish very little other than to move the problem to the subspecific level. As imperfect as it may be, I feel that recognition of three species--A. cristatum, A. desertorum, and A. fragile--is the most practical approach to crested wheatgrass taxonomy in North America.

North American crested wheatgrass workers must examine their use of the name A. cristatum to insure its correct application. Many users equate A. cristatum to the variety Fairway and Fairway-like plants. That perspective is much too narrow because A. cristatum is a polymorphic species that encompasses Fairway and a multitude of other broad-spiked taxa. When speaking of Fairway, it is appropriate to use the name A. cristatum ssp. pectinatum. However, the subspecies pectinatum includes tetraploid and hexaploid races in addition to the diploid Fairway (Fig. 2). If one wishes to become even more precise, the name A. cristatum ssp. pectinatum var. pectinatum can be applied to diploid Fairway because Tzvelev (1976) describes the variety pectinatum as being $2n=14$. Whenever a particular subspecies cannot be designated, it is best to use the terminology A. cristatum sensu lato, meaning that one is unwilling or unable to specify a subspecies.

The correct nomenclature for plants qualifying as A. desertorum is simple and straightforward because no subspecies or botanical varieties have been described in this species. The cultivated varieties (cultivars) Nordan and Summit are correctly identified as A. desertorum, whose spikes are illustrated in Figure 3.

The name A. fragile, which is applied to the narrow-spiked crested wheatgrasses, may be new to

Table 5.-- Distinguishing characteristics of the three crested wheatgrass (Agropyron) species grown in North America.

Species and Synonyms	Chromosome No.	Typical Characteristics
A. cristatum sensu lato (A. pectinatum) (A. pectiniforme) (A. cristatiforme) (A. imbricatum) (A. michnoi)	2n=14 (Fairway) 2n=28 (common) 2n=42 (rare)	Spikes broad, pectinate. Spikelets diverging from rachis at angles from 45° to 90°. Glumes not appressed to lemmas, giving the spike a bristly appearance. Lemmas with short, straight awns to 5 mm.
A. desertorum	2n=28 (always)	Spikes subcylindrical, oblong to linear. Spikelets diverging from rachis at angles from 30° to 45°. Glumes appressed to lemmas. Lemmas with short, straight awns to 3 mm.
A. fragile (A. sibiricum) (A. mongolicum)	2n=14 (rare) 2n=28 (common)	Spikes linear. Spikelets diverging from rachis at angles $<30^{\circ}$. Glumes appressed to lemmas. Lemmas mucronate or awnless.

some, because North Americans have traditionally used the name A. sibiricum for these grasses. If one accepts Tzvelev's decision to combine A. sibiricum and A. fragile, the epithet fragile must be chosen because it is the older of the two names. Tzvelev described two botanical varieties: 1) var. fragile (plants with pubescent leaf sheaths and 2) var. sibiricum (plants with glabrous leaf sheaths). Most narrow-spiked crested wheatgrasses in North America, including the cultivated variety, P-27, have glabrous leaf sheaths and fall under A. fragile var. sibiricum.

Narrow-spiked crested wheatgrass from China is identified by Chinese agrostologists as A. monogolicum (Keng 1965). Most, if not all, A. monogolicum is diploid and looks like a diminutive strain of tetraploid A. fragile (Fig. 3). The differences in ploidy levels and geographic distributions of tetraploid A. fragile and diploid A. mongolicum are what I perceive to be differences between subspecies, and I am making the following new combination to reflect those differences: A. fragile ssp. mongolicum (Keng) D. R. Dewey comb. nov., based on Agropyron mongolicum Keng, 1938. J. Wash. Acad. Sci. 28:305.

Common names for crested wheatgrass taxa have also been the source of some confusion and disagreement. Early workers spoke of the entire complex as crested wheatgrasses, and most current workers continue that usage. Swallen and Rogler (1950) commented that the common name "crested wheatgrass" was taken from the latin name "cristatus" (meaning crested or comb-like) and such a name is misleading if applied to the narrow-spiked taxa. However, they did not suggest another name. Weintraub (1953) applied the following common names to various crested wheatgrass taxa: A. cristatum = crested wheatgrass, A. desertorum = desert wheatgrass, A. michnoi = transbaikal wheatgrass, A. mongolicum = mongolian wheatgrass, and A. sibiricum = siberian wheatgrass.

Beetle (1961) endorsed Weintraub's common names, but those names have never become widely used except the names crested wheatgrass for A. cristatum and siberian wheatgrass for A. fragile (= A. sibiricum). Only rarely have I heard the name desert wheatgrass applied to A. desertorum. Agropyron michnoi and A. mongolicum are so uncommon that they do not need a common name. Hanson (1972) added some confusion by suggesting the common names "Fairway wheatgrass

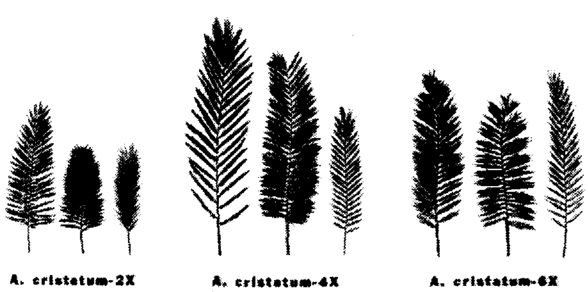

Figure 2.--Spikes of A. cristatum ssp. pectinatum, consisting of diploid (2n=2x=14), tetraploid (2n=4x=28), and hexaploid (2n=6x=42) chromosome races.

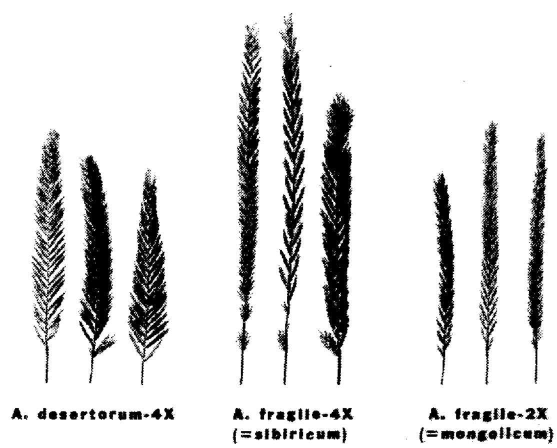

Figure 3.--Spikes of A. desertorum, tetraploid A. fragile, and diploid A. fragile ssp. monogolicum.

(also crested wheatgrass)" for A. cristatum and "crested wheatgrass (also standard crested wheatgrass)" for A. desertorum.

I feel strongly that all taxa of Agropyron should be referred to as "crested wheatgrasses" regardless of their spike shape. This designation implies that they are a related group of species and separates them from other wheatgrasses such as tall wheatgrass, intermediate wheatgrass, and western wheatgrass. A descriptive or modifying word may be used in front of the name crested wheatgrass to specify a particular form or type. In North America the following names seem to be appropriate for the three main species groups: A. cristatum = fairway crested wheatgrass, A. desertorum = standard crested wheatgrass, and A. fragile (= sibiricum) = siberian crested wheatgrass. Lower case letters are used with the modifying words--fairway, standard, and siberian--to avoid confusing these names with cultivated variety names. Regardless of one's choice of modifying words, I plead with all to use the general name "crested wheatgrass" for all of the taxa now placed in Agropyron.

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APPENDIX I. Species, subspecies, and synonyms of Agropyron sensu Tzvelev (1976).

Species	Subspecies	Synonyms
A. cristatum (L.) Gaertn.[1]	ssp. cristatum	
	ssp. pectinatum (Bieb.) Tzvel.	A. pectinatum (Bieb.) Beauv. A. imbricatum Bieb. A. pectiniforme Roem. & Schult. A. dagnae Grossh. A. karataviense Pavl. A. litvinovii Prokud.
	ssp. puberulum Boiss. ex. Steud.	A. puberulum (Boiss. ex Steud.) Grossh.
	ssp. tarbagataicum (Plotn.) Tzvel.	A. tarbagataicum Plotn.
	ssp. kazachstanicum Tzvel.	A. badamense auct. non Drob.
	ssp. baicalense Egor. & Sipl.	
	ssp. sabulosum Lavr.	A. lavrenkoanum Prokud.
	ssp. ponticum (Nevski) Tzvel.	A. ponticum Nevski
	ssp. sclerophyllum Novopokr.	A. sclerophyllum Novopokr. A. pinifolium Nevski A. karadaghense Kotov A. ponticum auct. non Nevski
A. michnoi Roshev.	ssp. michnoi	
	ssp. nathaliae (Sipl.) Tzvel.	A. nathaliae Sipl.
A. badamense Drob.		A. desertorum auct. non Schult.
A. desertorum (Fisch. ex Link) Schult.		A. sibiricum var. desertorum (Fisch. ex Link) Boiss.
A. fragile (Roth) Candargy		A. sibiricum (Willd.) Beauv. A. variegatum (Fisch. ex Spreng.) Roem. & Schult. A. angustifolium (Link) Schult.
A. cimmericum Nevski		A. dasyanthum var. birjutczense Lavr. A. dasyanthum ssp. birjutczense (Lavr.) Lavr.
A. tanaiticum Nevski		
A. dasyanthum Lebed.		
A. pumilum Candargy		Elytrigia praetermissa Nevski
A. krylovianum Schischk.		Elytrigia kryloviana (Schischk.) Nevski

[1]Tzvelev cited Palisot de Beauvois as the authority for A. cristatum (L.) Beauvois, but all other authors have cited Gaertner as the authority, i.e. A. cristatum (L.) Gaertn.

APPENDIX II. Description of Agropyron and key to its species and subspecies from Tzvelev (1976). Translation courtesy of U.S. National Herbarium, Washington, D.C. with technical corrections by M. E. Barkworth, Utah State University, Logan, Utah.

Genus 17. Agropyron Gaertner 1770

Inflorescence--Linear, oblongate or ovate spikes (1)1.5-12(16) cm long, with a nondisarticulating rachis; spikelets solitary and arranged in longitudinal rows, sessile, 6-12(15) mm long, with (2)3-8(10) bisexual florets; rachilla scabrous or short-pilose, weakly disarticulating; glumes lanceolate-ovate, unequal, 2.5-5 mm long (excluding awns), glabrous or pilose, more or less asymmetrical, with the mid rib raised to form an obvious keel along the entire length of the glumes and 1-3 less prominent (sometimes not visible) additional ribs, apex acute or with a straight awn to 3 mm long; lemmas 4-8.5 mm long (excluding awns), lanceolate-oblongate, leathery, glabrous or more or less pilose, with 5 veins, the mid rib forming a weak keel, apex acute or with a straight awn to 5(7) mm long; callus very short (to 0.2 mm long), broadly rounded, glabrous or short-pilose; palea almost equal in size to the lemma, more or less scabrous or pilose along the keels, rarely glabrous and smooth; lodicules 2, usually entire, ciliated along the margins; stamens 3, with anthers 2.5-6 mm long. Caryopses 3-5.5 mm long, more or less adnate to the flowering glumes. Perennial plants 15-100(150) cm tall, with or without rhizomes or forming more or less dense tufts; culms erect, sheaths of cauline leaves open over more than 2/3 of their length, auricles (if present) lanceolate, sheaths of innovation leaves almost completely closed, usually with lanceolate auricles; ligules 0.1-1 mm long, leathery-membranous, minutely ciliate along the margins; leaf blades 1.2-8(12) mm wide, flat convolute. Chromosomes large; X=7.

Economic value: All species of the genus are very valuable; they are predominantly pasture-fodder plants, distinguished by their high level of drought tolerance. Of these, the "narrow-spiked wheatgrasses" (A. desertorum and A. fragile) and the "broad-spiked wheatgrasses" (A. cristatum s. lat.) are already under cultivation in the southern regions of the U.S.S.R. The highest hay yields can probably be obtained from such relatively mesophilic subspecies of the broad-spiked wheatgrasses as A. cristatum subsp. pectinatum and subsp. tarbagaticum; however, the narrow-spiked wheatgrasses are more drought tolerant. The sand-adapted species--A. dasyanthum, A. tanaiticum, A. cimmericum, A. michnoi, and A. fragile--can be used successfully for fixing drifting sands.

1. Plants with rhizomes, not forming tufts . 2

\+ Plants without rhizomes, forming fairly dense tufts. 9

2. Keels of palea glabrous and smooth or with a few (up to 10) spinules or cilia; lemmas awnless or with awns to 1.2 mm long; plants from the sands of southern European U.S.S.R. 3

Keels of palea with more than 15 spinules or cilia, rarely about 10 spinules, but in that case the awns of the lemma 2-4 mm long; in European U.S.S.R. restricted to southern coast of Crimea 5

3. Spikes linear, 4-7 mm wide, not pectinate, spikelets relatively distant and appressed to the rachis; lemmas glabrous or more or less pilose, awnless; paleas with 1-10 spinules per keel; plants of the Don Basin . . . . 6 A. tanaiticum

\+ Spikes broadly ovate, 7-18 mm wide, more or less pectinate, but not very densely arranged spiklets 4

4. Spikelets relatively distant on rachis, lower rachis internodes 3-10 mm long; lemmas usually densely pilose, awnless; keels of palea usually smooth, rarely with 1-3 spinules per keel; plants of the lower Dneiper and Molochnaya rivers . . . . 7 A. dasyanthum

\+ Spikelets closer togather on rachis, lower rachis internodes 2-5 mm long; lemmas more or less pilose, apex with a cusp or awn 0.5-1.2 mm long; keels of palea with 1-10 spinules per keel, rarely glabrous; plants of the coastal sands of the Azov Sea. . . . . .8 A. cimmericum

5. Spikes very dense (without spaces between spikelet bases), pectinate (spikelets strongly divergent from the rachis), oblongate or ovate in outline, 2.1-8 cm long and 1-2 cm wide; spikelets villous-pilose; plants of sandy sites in Eastern Siberia, not forming tufts . . . . 9 A. michnoi s. lat. 6

\+ Spikes less dense, not pectinate (spikelets ascending), linear in outline, up to 1 cm wide 7

6. Upper surface of leaf blades densely covered with short hairs; awns of lemma up to 2(3) mm long; plants of Selenga Basin . . . . 9a A. michnoi ssp. michnoi

\+ Upper surface of leaf blades covered with scattered thin spinules or very short hairs; awns of lemmas 2-3.5 mm long; plants of Chara Basin . . . . 9b A. michnoi ssp. nathaliae

7. Awns of lemma 1.5-4 mm long; plants often forming tufts with a few short rhizomes; plants of the Crimea, Transcaucasia, and Kopetdag . . . . Taxa of the hybrid genus X Agrotrigia

\+ Awns of lemma up to 1(1.5) mm long; plants usually not forming tufts; plants of Altai and Eastern Siberia 8

8. Plants of rocky and aleurite (melkozem) slopes of Altai and Sayan, 40-100 cm tall; leaf blades 1.2-6 mm wide; lemmas usually short-pilose, rarely glabrous, apex with a cusp or awn up to 1.5 mm long . . . . .1 A. krylovianum

+ Plants of Enisei sands, 12-40 cm tall; leaf blades 1-3 mm wide; lemmas usually glabrous, without cusp or awns; glumes more or less ciliate along the keel . . . . 2 A. pumilum

9. Spikes (1.5)2-12(15) cm long and 0.5-1 cm wide, not pectinate (spikelets appressed to the rachis or barely away from it); glumes usually glabrous, rarely sparsely pilose; leaf blades 1-4(5) mm wide, usually convolute. 10

+ Spikes (1.5)2-6(8) cm long and 0.8-2.3 cm wide, pectinate (spikelets diverging from rachis at angles of 30-60°); lemmas glabrous or more or less pilose . . . . 10. A. cristatum s. lat. . .12

10. Lemmas awnless or with a cusp up to 1 mm long; spikes linear, 3-15 cm long; plants of sandy sites, 30-100 cm tall. . . . . .5 A. fragile

+ Lemmas with awns 1-3(4) mm long; plants of the plains or hilly steppes with aleurite or rocky soils. 11

11. Spikes ovate or oblongate in outline, 1.5-3.5 cm long; keels of palea densely covered with spinules, more than 30 spinules . . . . .3 A. badamense

+ Spikes oblongate or linear in outline, 2-7 cm long; keels of palea with fewer spinules, less than 30 . . 4 A. desertorum

12. Lowest culm internode strongly thickened toward the base; leaf blades usually convolute; plants of southern European U.S.S.R. and surroundings of Novorossiisk 13

+ Lowest culm internode not thickened . 15

13. Spikes 2-6 cm long, with relatively distant spikelets; lemmas glabrous or mildly pilose; leaf blades glabrous and smooth on the lower side; plants of sandy sites, 25-70 cm tall, without long vegetative shoots . . . . . .10g A. cristatum ssp. sabulosum

+ Spikes 1.5-4 cm long, with densely arranged spikelets (rarely without space between their bases); lemmas more or less pilose or glabrous; leaf blades covered with sparse hard bristles or spinules on lower surface; plants of gravelly slopes and rocks, 10-40 cm tall, with long vegetative shoots carrying stiff leaf blades horizontally divergent from the culms 14

14. Upper surface of leaf blades densely covered with very short hairs on the ribs; plants primarily of limestone outcrops. . . . . . 10h A. cristatum ssp. ponticum

+ Upper surface of leaf blades sparsely covered with spinules on the ribs; plants primarily of slate (shale) outcrops . . . . . .10i A. cristatum ssp. sclerophyllum

15. Spikes very dense, with closely compressed spikelets (no spaces between their bases); spikelets usually densely pilose, rarely glabrous; plants of Eastern Siberia, also entering into South Ural, Altai, and mountains of East Asia 16

+ Spikes less dense, with less crowded spikelets (obvious spaces between their bases); spikelets glabrous or more or less pilose; plants of Eastern Siberia . . 17

16. Plants 50-100 cm tall; leaf blades 2-6 mm wide, usually flat; awns of lemmas 4-7 mm long. . . .10e A. cristatum ssp. baicalense

+ Plants 20-60 cm tall; leaf blades 1.2-4 mm wide, frequently rolled lengthwise; awns of lemmas 1.5-4 cm long . . . . .10f A. cristatum ssp. cristatum

17. Culms immediately below the spike and below all nodes short-pilose; leaf sheaths and leaf blades frequently short-pilose; leaf blades 1-2.5 mm wide, usually rolled lengthwise; spikelets more or less pilose, rarely glabrous; plants of Transcaucasia . . . .10d A. cristatum ssp. puberulum

+ Culms immediately below the spike glabrous or more or less pilose, below the nodes glabrous or with a few scattered hairs 18

18. Leaf blades 1-2.5 mm wide, rolled lengthwise and very stiff, usually more or less arcuately bent; tufts very dense, with a relatively large number of vegetative culms; culms with 1-2 nodes, upper node usually located below the middle of the culm; spikelets usually pilose, rarely glabrous; plants of Kazakh hillocky area, 20-40 cm tall . . . . 10c A. cristatum ssp. kazachstanicum

+ Leaf blades 1.5-8(12) mm wide, flat or rolled lengthwise, less stiff, straight; tufts less dense, usually with only a few vegetative culms; culms with 2-4 nodes, the upper node usually above the middle of the culm 19

19. Plants 50-150 cm tall, with 3-4 culm nodes; leaf blades 4-10(12) mm wide, flat; plants of Eastern Kazakhstan . . . . .10a A. cristatum ssp. tarbagataicum

+ Plants 25-80 cm tall, with 2-3 culm nodes; leaf blades 1.5-7 mm wide, flat or rolled lengthwise; widely distributed plants . . . . . . .10b. A. cristatum ssp. pectinatum