Cytological and morphological studies in the genus Agropyron (Gaertn)
by Peter Jurasits

A THESIS Submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of Master of Science in Agronomy
Montana State University

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Thirty-three Agropyron species were studied morphologically and cytologically. In the morphological studies emphasis was put on blade, collar, ligule, auricle, and vernation. In the cytological studies, special attention was given to the numbers, sizes, and shapes of the chromosomes, and the position of the secondary constrictions. With the available information, it was possible to group these 33 wheatgrass species into 4 sections. Cytological and morphological evidence is given for several polyploid relationships among these species.

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at

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ABSTRACT

Thirty-three *Agropyron* species were studied morphologically and cytologically. In the morphological studies emphasis was put on blade, collar, ligule, auricle, and vernation. In the cytological studies, special attention was given to the numbers, sizes, and shapes of the chromosomes, and the position of the secondary constrictions. With the available information, it was possible to group these 33 wheatgrass species into 4 sections. Cytological and morphological evidence is given for several polyploid relationships among these species.

INTRODUCTION

Grasses play an important role in our everyday life; they furnish the principal breadstuffs of most peoples and a large part of the food of domestic animals. They are used in industry, as ornamentals, and they stabilize soils and maintain soil fertility. Among the more than 6,000 different grasses of the world the genus Agropyron, usually bearing the English epithet "wheatgrasses", plays an outstanding role. Many members of this genus are used as forage crops and for possible breeding material for wheat improvement, while others are among our most troublesome weeds.

In the United States wheatgrasses have great value in the Northern Great Plains, the Intermountain Region, and the higher altitudes of the Rocky Mountain states. They are generally cold-hardy, drought-resistant, and versatile. They produce abundant forage that is acceptable to all classes of livestock. Thirty of about 150 existing species of wheatgrasses are native to North America. A few introduced species have gained agronomic importance. It seems logical that among those which have not yet been tested there will be some which may be of importance. There is hardly a region in the world that has yet recognized and developed the best combinations of genes in its agricultural grassland plants. The present investigation was initiated to study available gene resources of the genus Agropyron to determine their agronomic potential, and to investigate possibilities of incorporating valuable genes into otherwise already favorable plant material. A study of karyotypes of

Agropyron species is a necessary prerequisite to such a program. It facilitates predictions concerning the degree of evolutionary relationships among species and the possibilities of using some of these species in an interspecific breeding program.

According to Swallen (1943) a number of *Agropyron* species have been introduced into the United States. The taxonomic descriptions of these species are confusing, and some introductions have been incorrectly described while others remain unidentified. Therefore particular care must be taken to adequately and accurately describe the morphology of material used in karyological studies.

REVIEW OF LITERATURE

Morphological studies in the grass family have been done by several workers. The work of Nevski (1934) in Russia is of great importance. His study of systematics of the genus Agropyron was used as a basic reference. He designated the genus Agropyron as subtribe Agropyrinae and included Roegneria, Anthosachne, Eremopyrum, Eu-Agropyron, and Elytrigia as genera and subgenera.

In this country the work of Hitchcock and Chase (1950) is of great value.

Other workers who have contributed to a better understanding of the wheatgrasses are Beetle (1952, 1955) and Stebbins and co-workers (1941, 1950, 1952, 1953, 1956).

Stebbins (1950) grouped the grasses in the tribe Hordeae into three main groups on the basis of their habit of growth.

1. Sod-forming or rhizomatous perennials. Almost exclusively self-incompatible and cross-fertilized.
2. Caespitose or bunch type perennials, self- or cross-fertilized.
3. Annuals: Uncommon in cool temperate regions. Predominant in warm, dry regions with seasonal rainfall. Self-pollinated.

(General Statements)

The studies of Sears (1948), Matsumura and Sakamoto (1955), and

Kihara and Yamashita (1956) established that Agropyron did not contribute the B genome of wheat.

Agropyron was used by several workers as parent material for wheat improvement. According to Smith (1960) the following Agropyron characteristics would be of value in the cultivated wheats:

1. Resistance to heat and drought
2. Extreme winterhardiness
3. Resistance to frost
4. Tolerance to alkaline and acid soils
5. Resistance to rusts and smuts
6. Resistance to wheat streak mosaic, yellow dwarf, and soil borne mosaic viruses
7. Tolerance to excessive moisture
8. Resistance to lodging
9. Perennial growth habit
10. Wide geographic adaptation
11. Increased protein content
12. Resistance to insects, and
13. Resistance to Septoria disease and powdery mildew

Earlier workers (Peto 1936, 1938; Hartung 1946) reported that there was homology between Agropyron and Triticum chromosomes (or genomes), but a more recent study disproved this (Sears 1948).

Morphologically there are only slight differences between A. cristatum and A. desertorum. In order to clarify identification, the only factor which settles the problem is the chromosome number. Identification on morphological bases alone is very difficult because of great intraspecific variations. According to Vavilov (1951) the following variations occur in A. cristatum:

1. Awned and awnless forms
2. Hairy and smooth-glumed forms
3. Yelow, red (with anthocyanin), and black-headed forms
4. Forms with recumbent, erect, and intermediate habits
5. Forms with thin straw and others with thick straw; (solid straw, too)
6. Narrow-leaved and wide-leaved forms
7. Compact-headed and loose-headed forms
8. Forms with and without a waxy coating
9. Forms with yellow and others with violet anthers
10. Low-growing and tall-growing forms
11. Forms with hairy and others with smooth leaves
12. Late and early forms
13. Hydrophilic and xerophilic types

Cauderon (1958) studied eight French Agropyron species. She examined them cytologically and made several crosses between these species and wheat.

MATERIALS AND METHODS

Agropyron seed was obtained from 12 different sources which originated from 29 different places all over the world. The seed was germinated in plastic dishes in a germinator at 20° C. When the seedlings were strong enough, they were transplanted into individual pots which were filled with soil and kept in the greenhouse. As soon as the plants were established and there were enough young and vigorous roots, they were transplanted into vermiculite according to a method described by Schertz and Randolph (1958).

Vermiculite, or expanded mica, is an inorganic material; therefore, it does not harbor diseases. It has good water retaining properties and good aeration. It does not furnish any essential elements, but with proper watering and fertilization an abundant supply of root-tip material is provided.

Root-tips were excised at 5:00 P.M. and placed into vials which were filled with cold water. The vials were put into a beaker filled with ice water and placed in a refrigerator for 24 hours, which was maintained at a temperature of 1° C. The examination was based upon a slightly modified method of Tjio and Levan (1950) and Markarian and Schulz-Schaeffer (1957). The root-tips were next placed into 19 parts of 5% Aceto-orcein and 1 part 10% HCl in a watchglass. The material was gently heated three times (never allowed to boil), allowing it to cool between heatings. The root tips were then transferred onto a slide, on which three drops of 1% Aceto-orcein were placed. The root-tips were squashed with a glass rod. The excess tissue was removed and a coverslip was placed on the material. The excess stain was squeezed out between two blotter papers by gently tapping with the eraser end of a pencil. The slides were then sealed and examined under a Zeiss standard microscope. The chromosome number was determined. When good cells were available, the chromosomes were measured with an eyepiece micrometer. At least 10 cells were measured for each species. By analyzing these data, idiograms were constructed using a chromosome arrangement suggested by Schulz-Schaeffer (1956). These idiograms are the diagrammatic representations of the karyotypes including the chromosome arm lengths given in Tables III, IV, and V. First the satellite chromosomes are shown starting with the shortest satellite. The non-satellited chromosomes are arranged from the shortest short arm to the longest short arm. Particular attention was paid to the satellite chromosomes and to secondary and tertiary constrictions.* Several microphotographs were also made (Figures 4 and 5).

The pollen-mother-cell (PMC) examination was done according to the method described by Geitler (1949).

The morphological study consisted of the general description of the species as established by morphologists and systematists. Such features as the height of the plant, number of stems, etc., were omitted

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* The term "tertiary constrictions" is used arbitrarily in designating constrictions which are not centromeres or nucleolar organizer regions. Consequently, the term "secondary constriction" is reserved for nucleolar organizer regions.

in this study due to the fact that the material was grown in the greenhouse under favorable conditions, and it is well known that the environment has a great effect upon the above mentioned features.

The morphological studies were made at that stage of plant growth when all the parts (stem, leaves, heads) were fully developed. In order to have the perennial species vernalized, the pots were kept outside during the months of January and February.

Vernation studies were done according to the method described by Fults (1959). When the morphological and cytological results were available, they were compared with published information, and it was learned that some of the source material had been misidentified; therefore, several specimens had to be discarded. A list of the species and the sources of the materials which were finally used in this study is given on the following page.

Table I. List of Agropyron plant material used in this study.

Scientific name	Accession number	Source (Hoover 1960, Plant Inventory 1907-1958)
A. acutum R. & S.	P.I. 202,727	From Belgium. Seeds presented by the Botanic Garden, Brussels. Received Sept. 10, 1952.
A. agropyroides	P.I. 202,147	From Argentina. Seeds collected by Alan A. Beetle, Agricultural Explorer, Bureau of Plant Industry, Soils, and Agricultural Engineering, Beltsville, Md. Received July 28, 1952. Facultad Agronomia, Buenos Aires. Feb. 19. Selection No. 16. Parodi Grass Garden, from A. scabriglume (Hack.) Parodi.
A. arizonicus Scribn.& Sm.	F-257	Goettingen, Germany
A. brachyphyllum Boiss. & Haussk.	P.I. 229,912	Iran. November 9, 1955. H. S. Gentry, east base of Kuhe Zard, Charmahal, Iran; ordered to Western and North Central Regional Stations, January 5, 1956.
A. caespitosum Koch.	P.I. 228,276	Iran. October 3, 1955. H. S. Gentry, 25 miles NW of Shar Kord, Charmal, Iran; ordered to Western and North Central Regional Stations, January 5, 1956.
A. caninum (L.) Beauv.	P.I. 172,364	From Turkey. Seeds collected by Jack R. Harlan, Agricultural Explorer, Bureau of Plant Industry, Soils, and Agricultural Engineering, Beltsville, Md. Received Jan. 4, 1949. Seeds collected in 1948. Karanlikmese, Tutunli, Coruh., Aug. 12.
A. ciliatiforme Roshev.	P.I. 207,452	From Afghanistan. Seeds collected by H. S. Gentry,

		Agricultural Explorer, Bureau of Plant Industry, Soils, and Agricultural Engineering, Beltsville, Md. Received Oct. 29, 1953. Collected in Kabul Province in September and October 1953. From Paghman.
A. cristatum (L.) Gaertn.		Bot. Gard. Taschkent, Russia.
A. dasystachyum (Hook.) Scribn.	P.I. 232,116	Montana, 1955 domestic collection, Hermann and Leese, 9 miles N. Augusta, Montana, Rt. 33, Teton Co., Montana.
A. desertorum (Fisch.) Schult.		Bot. Akad. Alma-Ata, Russia.
A. elongatiforme Drob.	P.I. 222,960	Iran. January 4, 1955, from E. E. Smith, 16 miles east of Tabriz, road to Sarab, Azerbijan, Iran; ordered to North Central Regional Station, Ames, Iowa, Feb. 14, 1955.
A. elongatum (2n = 14) (Host.) Beauv.		Pullman, Washington.
A. elongatum (2n = 42) (Host.) Beauv.		Bot. Gard. Taschkent, Russia.
A. inerme (Scribn. & Sm.) Rydb.	P.I. 236,668	Canada. 1956 domestic collection, Hermann and Leese. Two miles N. of Kimberly, B.C.
A. intermedium (Host.) Beauv.		Bot. Akad. Alma-Ata, Russia.
A. junceiforme		Bot. Gard. Coimbra, Portugal.
A. kosanini Nab.	P.I. 237,636	Turkey. January 6, 1953. R. K. Godfrey, near Zara, Sivas, Turkey. Distributed to North Central Region, July 16, 1953.
A. latiglume (Scribn. & Sm.) Rydb.	P.I. 236,673	Canada. 1956 domestic collection, Hermann and Leese. Sentinel Peak, Coleman, Kananaskes Road, Canada.

A. <u>lolioides</u> (Kar. & Kir.) Roshev.	P.I. 223,325	Iran. January 18, 1955. E. E. Smith, 21 miles NW of Tabriz, road to Marand, Azerbaijan, Iran; ordered to North Central Regional Station, Ames, Iowa, February 14, 1955.
A. <u>orientale</u> (L.) R. & S.	P.I. 193,264	From Afghanistan. Seeds presented by C. F. Deyoe, Food and Agriculture Organization, United Nations. Received Dec. 21, 1950. Two miles south of Soviet Union border, Anhuei.
A. <u>panormitanum</u> Parl.	P.I. 197,569	From Italy. Seeds presented by the Giardino Botanico e Coloniale, Palermo. Received July 24, 1951.
A. <u>popovi</u> Drob.	A-1115	SCS, SW Region, U.S.A.
A. <u>pseudorepens</u> Scribn. & Sm.	P.I. 236,676	Canada. 1956 domestic collection, Hermann and Leese, along Bow River, one mile west of Banff, Banff National Park.
A. <u>riparium</u> Scribn. & Sm.	P-2415 (Sodar)	SCS, Pullman, Washington.
A. <u>semicostatum</u> (Steud.) Nees.	P.I. 203,242	From Japan. Seeds presented by K. Ehara, Department of Agriculture, Kyushu University, Fukuoka. Received Oct. 22, 1952.
A. <u>spicatum</u> (Pursh.) Scribn. & Sm.	P.I. 232,123	Washington. 1955 domestic collection, Hermann and Leese, Steptoe Butte, Whitman Co., Washington.
A. <u>squarrosum</u> (Roth.) Link.	P.I. 223,323	Iran. January 18, 1955. E. E. Smith; road from Meshkinshahr to Ahar, Azerbaijan, Iran; ordered to North Central Regional Station, Ames, Iowa, February 14, 1955.

A. strigosum (M.B.) Boiss.		Bot. Gar. Heidelberg, Germany.
A. subsecundum (Link.) Hitchc.	P.I. 232,148	Wyoming. 1955 domestic collection, Hermann and Leese. Half Moon Lake (Wind River Mts.) Sublette Co., Wyoming.
A. subulatum Soland.	P.I. 204,379	From Turkey. Seeds collected by R. K. Godfrey, Agricultural Explorer, Bureau of Plant Industry, Soils, and Agricultural Engineering, Beltsville, Md. Received Jan. 6, 1953. Between Kayseri and Pinarbasi, Kayseri. Sept. 1, 1952.
A. trachycaulum (Link.) Malte.	P.I. 236,699	Canada. Two miles W of Wardner, B. C., on Rt. #3, alt. 2400 feet, Hermann and Leese, 1956.
A. trichophorum (Link.) Richt.	P.I. 229,916	Iran. November 9, 1955. H. S. Gentry and Ousqui, S. slope of Demavand Mt. El Borj. Range, Iran; ordered to Western and North Central Regional Stations, January 5, 1956.
A. triticeum Gaertn.		Gardiner, Montana. Collected by W. E. Booth about 3 miles south of Gardiner, Park Co., Montana, along west side of river on heavily used winter game range on June 20, 1954.

RESULTS

Nevski's description of the Agropyron species was used as a framework for the morphological studies. Four of his 5 genera and subgenera of subtribe Agropyrinae were used as sections of the genus Agropyron. Using this framework and other already available information combined with and supplemented by cytological results, the examined 33 wheatgrasses are described as follows:

A. Section Roegneria C. Koch.

Nevski: Spikes erect or pendant. Spikelets with (2) 5-7 (9) florets, laterally compressed to a slight extent, almost sessile, more or less awned; awns reflexed or straight, less commonly absent. Almost all florets fertile; as caryopses ripen, the florets drop off one by one, the glumes, however, remain on the rachis. Glumes lanceolate or linear-lanceolate, usually with widely spaced nerves, scabrous, less commonly scaberulous, without the cross-furrow at the base, fused with the rudimentary pedicel of the spikelet. Florets with a more or less hirsute, setaceous callus at the base. Lemma scabrous or hirsute, less commonly glabrous. Lodicules small, almost glabrous or ciliate on the margin. Anthers short, 1.5 - 3.6 mm, shorter than one-half or one-third of the palea. Caryopsis oblong-linear, hirsute in the upper part, on the inside slightly concave, almost flat. Plants perennial, caespitose, as a rule not stolon-forming. Blades flat, rarely convolute, thin, scabrous on both surfaces, glabrous or hirsute.

The following seven species were examined in this group:

1. Agropyron caninum
2. Agropyron latiglume

3. _Agropyron panormitanum_

4. _Agropyron pseudorepens_

5. _Agropyron semicostatum_

6. _Agropyron subsecundum_

7. _Agropyron trachycaulum_

Agropyron latiglume, _A. pseudorepens_, _A. semicostatum_, and _A. subsecundum_ were tentatively put into this section by the author based on the morphological and cytological evidence gathered during this study.

1. _Agropyron caninum_ (L.) Beauv.

Bearded wheatgrass, awned wheatgrass, dog's tooth grass.

Nevski: This species has eight subspecies; it originated in Eurasia. Perennial. Plant loosely caespitose, sciophilic; culms smooth; blades thin, flat, broadly linear, green or glaucescent, scabrous, glabrous or with scattered hairs on the upper surface. Spikes fairly dense, drooping or nodding, green or, less commonly, greenish-violet; spikelets 2-5 flowered; glumes lanceolate, abruptly narrowed and usually aristulate, with 3-5 widely separated nerves, scabrous, white membranaceous on the margin, unequal; lemma smooth. It is a self-pollinated species. Blades pubescent.

Author: Ligule short, no auricle (Figure 6).

Meiosis was found to be regular.

The chromosome number was 2n = 28, with one pair of satellite chromosomes (Tables III and V, Figure 1).

2. _Agropyron latiglume_ (Scribn. & Sm.) Rydb.

Hitchcock and Chase: Perennial. Culms loosely tufted, curved or geniculate below; blades flat, short, 3-5 mm wide, short-hirsute on both surfaces, rarely glabrous or nearly so beneath; spikelets usually closely imbricate; glumes broad, flat, thin-margined, awn-tipped; lemmas commonly appressed pubescent, awnless or awn-tipped. Leaf blade, sheath pubescent.

Author: Ligule and auricle present (Figure 7).

The chromosome number (2n) is 28. One pair of satellite chromosomes was observed (Tables III and V, Figure 1).

3. Agropyron panormitanum Parl.

Nevski: Rhizomes short, culms straight, smooth; blades thin, green, almost glabrous on both surfaces, only on the upper surface with scattered white hairs, sharply scabrous. Spikes bilateral, slender, rachis stiffly ciliate on main angles; spikelets green, appressed, 3-5-flowered, glumes linear-lanceolate or lanceolate, longer than the lower floret, sharply scabrous; lemma lanceolate, almost smooth; palea lanceolate.

Author: Ligule short, no auricle (Figure 7).

Meiosis was found to be regular in this species.

The somatic chromosome number is 28. Two pairs of satellite chromosomes were found (Tables III and V, Figure 1).

4. Agropyron pseudorepens Scribn. & Sm.

False quackgrass, western couchgrass.

Hitchcock and Chase: Specimens without rhizomes resemble A. trachycaulum. This species also resembles A. repens, but it is often stouter, and the rhizomes are not yellow.

Perennial with creeping rhizomes. Spike 10-20 cm long, the spikelets contracted and appressed, the flat or scarcely keeled glumes 2 - 2.5 mm wide, nearly equaling the spikelets; lemmas scaberulous to minutely hispidulous, rachilla villous.

Author: Auricle and collar distinct (Figure 8).

The chromosome number is 2n = 28 in this species. Two pairs of satellite chromosomes were found, this being the main cytological difference between this species and its close relative A. trachycaulum, in which only one pair of satellite chromosomes was found (Tables III and V, Figure 1). The one pair of satellite chromosomes of A. trachycaulum is of the same type as one pair in A. pseudorepens.

5. Agropyron semicostatum (Steud.) Nees.

Drooping wheatgrass.

Perennial species, which originated from Asia.

Hitchcock and Chase: Blades flat, spike nodding, not compact; spikelets several-flowered, imbricate; glumes several-nerved, much shorter than the spikelets, acute but scarcely awned; the awns of lemma are toothed, flexuous or finally divergent.

Author: Ligule straight and long, collar and auricle distinct (Figure 8).

Chromosome numbers of 28 and 42 were reported earlier (Nielsen and Humphrey 1937, Nakajima 1936). The material of the present study had 42 chromosomes including 2 pairs of satellite chromosomes, which are of the same type. This may indicate an autoploid origin of this species (Tables III and V, Figure 2).

6. Agropyron subsecundum (Link.) Hitchc.

Bearded wheatgrass.

Hitchcock and Chase: This is a self-pollinated species which American botanists generally call A. caninum.

Green or glaucous, without creeping rhizomes, culms erect, tufted; sheaths glabrous or rarely pubescent; blades flat; spike erect or slightly nodding, sometimes unilateral; the rachis scabrous; spikelets rather closely overlapping, few-flowered, the rachilla villous; glumes broad, 4-7-nerved, nearly as long as the spikelet, tapering into an awn; lemmas obscurely 5-nerved, the awn straight.

Author: Ligule lacerate, auricle short (Figure 8).

One satellite chromosome pair was found among the 28 chromosomes (Tables III and V, Figure 1).

7. Agropyron trachycaulum (Link.) Malte.

Slender wheatgrass, western rye-grass, McIvor's rye-grass.

Beetle: A native of North America, resembling A. subsecundum. It was called A. tenerum, A. pauciflorum, A. violaceum, etc.

It is a self-pollinated perennial bunchgrass. According to Nevski (1934) this is the only species in this genus used as a forage plant in several countries. Because of its origin, he calls it "American wheat-grass".

Tufted plant, culms erect; leaf blades broad, flat, or somewhat involute; spike slender, the spikelets distant, 3-7-flowered; glumes 3-7-nerved, about equaling the spikelet, acute to awn-tipped; lemmas long, obscurely nerved, acute or short-awned.

Author: Ligule, auricle, and collar distinct (Figure 8).

This species is an allotetraploid (Stebbins and Love, 1952). Only one pair of satellite chromosomes was found among the 28 chromosomes (Tables III and V, Figure 1).

B. Section Eremopyrum Jaub. & Spach.

Nevski: Spikes elliptic-oval or oblong-oval with a shortened brittle awn and rachis. Spikelets uniform, solitary, sessile, almost perpendicular to the rachis, 3-6-flowered, laterally compressed, aristulate or awnless. Glumes navicular, keeled, with one prominent keel, coriaceous, with more or less thickened, later corneous margins, sometimes fused at the base. Lemma navicular, acuminate or aristulate. Lodicules ciliate on the margins. Annual plants.

Two species were examined in this section:

1. Agropyron orientale
2. Agropyron triticeum

1. Agropyron orientale (L.) R. & S.

Oriental wheatgrass.

An annual species, originating in Asia.

Nevski: Culms geniculate, hirsute below the spikes; blades flat, spikes elliptic-oval, villous, dense and brittle. Glumes hirsute, awned (almost as long as the glumes), keeled; lemmas hirsute and awned.

Author: Ligule straight; collar, auricle present (Figure 7).

The 2n chromosome number is 28, and there are two pairs of satellite chromosomes, in both of which the satellites are extremely small (Tables III and V, Figures 1 and 5).

2. Agropyron triticeum Gaertn.

Annual wheatgrass.

An annual species which originated in Eurasia.

Beetle: Vigorously branching at the base; culms up to 40 cm tall; the sheaths and blades are short and scabrous; spikes numerous; spikelets crowded, rigidly spreading, 3-6-flowered. Glumes acuminate, lemmas awn-tipped.

Author: Ligule large, auricle and collar small (Figure 8).

The chromosome number is 14. No satellite chromosomes were observed. The centromeres are subterminal (Table III, Figure 3).

C. Section Eu-Agropyron Nevski

Nevski: Spikes linear or oval on a strong, flexible rachis with short internodes. Spikelets solitary, squarrose, almost horizontal or at an acute angle to the rachis, sessile, 3-1-flowered, laterally compressed, navicular, keeled with a very strong midnerve (keel) and obscure lateral nerves, on the margin thinly white-membranaceous, smooth or ciliate on the keel. Lemma navicular, aristulate or awnless. Palea bidentate, ciliate on the keel. Anthers long, slightly shorter than the palea. Caryopsis oblong, hirsute in the upper part, grooved on the inside. Perennial plants, with creeping rhizomes or densely caespitose.

The following species were examined in this group:

1. <u>Agropyron agropyroides</u>
2. <u>Agropyron brachyphyllum</u>
3. <u>Agropyron ciliatiforme</u>
4. <u>Agropyron cristatum</u>
5. <u>Agropyron desertorum</u>
6. <u>Agropyron kosanini</u>
7. <u>Agropyron squarrosum</u>

<u>Agropyron agropyroides</u>, <u>A</u>. <u>brachyphyllum</u>, <u>A</u>. <u>ciliatiforme</u>, <u>A</u>. <u>kosanini</u> and <u>A</u>. <u>squarrosum</u> were tentatively put into this section by the author based on the morphological and cytological evidence gathered during this study.

1. <u>Agropyron agropyroides</u>

Author: Tall, light greenish grass, upper surfaces of leaves, glumes, lemmas and rachis scabrous. Spikelets overlapping, glumes 5-nerved, with membranaceous margins, glumes and lemmas awned.
Auricle purplish. Ligule long (Figure 6).

The somatic chromosome number is 42 including 2 pairs of satellite chromosomes (Tables III and V, Figure 2).

2. <u>Agropyron brachyphyllum</u> Boiss. & Haussk.

Author: Tall, bluish-green, scaberulous grass. Spikelets overlapping, 5-6-flowered. Glumes and lemmas membranaceous on the margins, several nerved, pubescent, short awned, auricle, ligule and collar distinct (Figure 6).

The somatic chromosome number is 42. One pair of satellite chromosomes was observed (Tables III and V, Figure 2).

3. *Agropyron ciliatiforme* Roshev.

Author: Tall, scabrous perennial plant. Leaves yellow-green on the lower, bluish-green on the upper surface. Spike extended. Spikelets overlapping, 4-5-flowered. Glumes awned, lemmas awn-tipped; ligule lacerate, auricle long, collar distinct (Figure 6).

The somatic chromosome number is 28 including one pair of satellite chromosomes (Tables III and V, Figure 1).

4. *Agropyron cristatum* (L.) Gaertn.

Crested wheatgrass, fairway crested wheatgrass.

Author: Perennial bunchgrass, originated in Eurasia. A cross-pollinated species.

A light bluish-green plant. Leaves rolled in the budshoot. Sheath not compressed, not keeled, glabrous or the lowest usually soft pubescent, slightly scabrous, dark green, split with margins overlapping. Auricles present, 1.0 - 1.5 mm long, clawlike, not clasping. Collar distinct, glabrous or ciliate, light green or yellow, V-shaped, divided. Ligule membranous, 0.5 - 1.5 mm long, truncate, lacerate. Blade 2 - 6 mm wide, 5 - 20 cm long, flat, tapering to a sharp point, pale bluish-green; upper surface scabrous, conspicuously ridged and usually soft pubescent; lower surface smooth; margins scabrous (Figure 6).

The chromosome number was found to be $2n = 14$. No satellite chromosomes were found in this study (Table III, Figures 3 and 4).

5. _Agropyron desertorum_ (Fisch.) Schult.

Standard crested wheatgrass, Nordan crested wheatgrass, desert wheatgrass, mountain crested wheatgrass.

Booth (1950): Similar to _A. cristatum_ but differing in having narrowly ascending or appressed spikelets, and thin, translucent margins around the glumes.

Author: It is a tetraploid species with 2n = 28 chromosomes. It is characterized by chromosomes with median or submedian centromeres and by the lack of any secondary constrictions or satellites.

This probably is an autotetraploid species which arose from _A. cristatum_ by a duplication of chromosome number, a theory which is substantiated by the similarities of the two idiograms (Table III, Figures 1 and 5).

6. _Agropyron kosanini_ Nab.

Author: Dark greenish, scabrous grass. Spikelets overlapping, 5-7-flowered. Glumes blunt, many-nerved but not distinct. margins membranaceous. Lemmas with faint nerves and membranaceous margins. Auricle long, collar and ligule small (Figure 7).

In meiotic anaphase I, fragments were found in several cells, and nucleoli were found in prophase. The latter supports the idiogram which shows one pair of satellite chromosomes.

The somatic chromosome number is 56 including one pair of satellite chromosomes (Tables III and V, Figure 3).

7. _Agropyron squarrosum_ (Roth.) Link.

Author: Shiny, green, scabrous, awned grass. Spikelets 3-5-flowered. Glumes 5-nerved, margins membranaceous, awns about 2 cm long.

Lemmas also awned. Collar and ligule short, auricle long (Figure 8).

In meiotic division, bridges and fragments were observed quite frequently in anaphase I, which gives evidence of inversions.

The somatic chromosome number is 42. No satellite chromosomes were observed (Table III, Figure 2).

D. Section Elytrigia (Desv.) Nevski

Nevski: Spikes always straight, with solitary spikelets. Spikelets 3-11-flowered, entirely sessile, awnless or less commonly awned; awns short and straight, less commonly long and reflexed. Glumes lanceolate, linear-lanceolate or oblong, nerves (3) 6-11, closely spaced, smooth (only the midnerve sometimes scaberulous in the upper part), less commonly glumes softly hirsute; lemma lanceolate, with 5 nerves converging or almost converging in the upper part, glabrous, or less commonly hirsute at the base, with a shallow cross-furrow and shortened small glabrous callus. Lodicules ciliate on the margin or hirsute in the upper part. Florets often sterile. Ripe spikelets sometimes drop off entire with glumes. Anthers long (5.6) 4-7 (8) mm, longer than half of the palea. Caryopsis oblong, hirsute in the upper part, with a deep groove on the inside. Plants perennial, with long creeping rhizomes or densely caespitose, with or without short stolons. Blades convolute, less commonly flat, hirsute or scabrous on the upper surface, usually smooth, glaucescent or glaucous on the lower surface.

The following species were examined in this section:

1. Agropyron acutum
2. Agropyron arizonicus

3. _Agropyron_ _caespitosum_

4. _Agropyron_ _dasystachyum_

5. _Agropyron_ _elongatiforme_

6. _Agropyron_ _elongatum_ (2n = 14)

7. _Agropyron_ _elongatum_ (2n = 42)

8. _Agropyron_ _inerme_

9. _Agropyron_ _intermedium_

10. _Agropyron_ _lolioides_

11. _Agropyron_ _popovi_

12. _Agropyron_ _riparium_

13. _Agropyron_ _spicatum_

14. _Agropyron_ _strigosum_

15. _Agropyron_ _subulatum_

16. _Agropyron_ _trichophorum_

Agropyron _acutum_, _A_. _arizonicus_, _A_. _dasystachyum_, _A_. _inerme_, _A_. _popovi_, _A_. _riparium_, _A_. _spicatum_, and _A_. _subulatum_ were tentatively put into this section by the author based on the morphological and cytological evidence gathered during this study.

1. _Agropyron_ _acutum_ (_A_. _junceiforme_ x _A_. _pungens_) or
(_A_. _junceum_ x _A_. _repens_) R. & S.

Author: It is said to be a cross between two _Agropyron_ species, originated in Europe.

Plant green, scabrous all over, with wide leaves. Spikelets 4-5-flowered and overlapping. Glumes blunt, 5-nerved, margin membranaceous and hairy. Lemma also with membranaceous and hairy margins. Nerves visible only on the upper half. Ligule, auricle, and collar short (Figure 6).

The 2n chromosome number was reported to be 35 (Cauderon 1958). In the present study 30, 34, 35, and 36 chromosomes each were found in one cell, 37 in two cells and 42 chromosomes in 4 cells. This variation may result from the hybrid nature of this species. One pair of satellite chromosomes was found in this study (Tables IV and V, Figure 2).

2. Agropyron arizonicus Scribn. & Sm.

Arizona wheatgrass.

Hitchcock and Chase: Resembling A. spicatum, but usually taller and coarser; light-greenish plant; blades commonly 4-6 mm wide; spike flexuous, the rachis more slender; spikelets distant but overlapping, 3-5-flowered; glumes short-awned; awns of the lemmas stouter.

Author: Collar small, ligule and auricle very distinct (Figure 6).

The chromosome number was found to be 2n = 28 with 2 pairs of satellite chromosomes. If we compare the two idiograms of A. spicatum and A. arizonicus, it is evident that there is a cytological similarity as well as a morphological resemblance. The two identical satellite pairs of chromosomes of A. arizonicus are present in A. spicatum. This may indicate that in the evolution of both species, autoploidy took place. A. spicatum possesses an extra satellite type, which is marked by a minute satellite (Tables IV and V, Figures 1 and 5).

3. Agropyron caespitosum Koch.

Couch grass.

Author: Perennial. Culms thin, glabrous, and smooth over the entire length; margins or sheaths not ciliate; blades glaucous, very narrow, hirsute on the upper surface. Spikes thin, rare; rachis scabrous on two main angles; spikelets not appressed, slightly reclined, glaucescent, faintly tinted violet, small, 3-4-flowered; glumes lanceolate, acute, almost equal to or slightly shorter than the lower floret, 5-6-nerved, smooth; lemma narrow-lanceolate, obtuse or obtuse-acuminate, 5-nerved; palea equal to or very slightly longer than lemma, subobtuse, very shortly and barely noticeably ciliate on the keels in its upper two-thirds. Ligule, auricle, and collar very distinct (Figure 6).

The 2n chromosome number is 42. One pair of chromosomes has a very small satellite chromosome (Tables IV and V, Figure 2).

4. Agropyron dasystachyum (Hook.) Scribn.

Thickspike wheatgrass, benchland wheatgrass, northern wheatgrass, Yukon wheatgrass, downy wheatgrass.

Pechanec (1936): Cross-pollinated, sod-forming perennial with creeping rhizomes, native of North America.

Slender, glaucous; shoot round, leaf rolled in bud; leaf sheath round, white to pinkish below ground and immediately above, glabrous, smooth, veins distinct, usually open at least halfway; ligule very short, truncate, erose; collar narrow to medium, distinct, continuous often tinged with red in the spring, glabrous or pubescent; auricles long, acute, tinged with red in spring, glabrous or pubescent; leaf blade flat, drying involute, little constricted at the base, midvein not distinct on lower surface, slightly twisted, striately veined above, scabrous above, smooth below, sparsely strigose or glabrous above, yellowish-green to dark-green, erect, stiff (Figure 6).

Similar to A. smithii in growth habits and general appearance and strongly resembling A. riparium but separated by the fine puberulence on the lemmas (Figure 8).

Meiosis was found to be regular.

The 2n chromosome number is 28 including 2 pairs of satellite chromosomes. One of these satellite pairs is present in A. riparium which is morphologically similar to this species (Tables IV and V, Figure 1).

5. Agropyron elongatiforme Drob.

Nevski: Perennial. Plant glaucescent; blades on the upper surface scabrous, shortly setaceous, on the lower surface also more or less scabrous, flat; sheaths smooth; culms geniculate at the base. Spikes straight; spikelets divergent, often curved; glumes 5-7-nerved, white membranaceous on the margin, lanceolate, obtuse, smooth; lemma white-membranaceous on the margins in the upper part; palea shorter than lemma, minutely ciliate on the keels in the upper part.

Author: Auricle, ligule, and collar are small (Figure 7).

Meiosis was found to be regular.

The somatic chromosome number was found to be 58, which is an aneuploid number; 2n = 28 was reported by Myers (1947). There are two pairs of satellite chromosomes. One pair of the satellite chromosomes is particularly interesting because the shorter arm of the chromosome is shorter than the satellite. This was reported in other genera, but this is the only case where a type of this kind was found in this genus (Tables IV and V, Figure 3).

6 and 7. Agropyron elongatum (Host.) Beauv.

Tall wheatgrass, couch grass.

Beetle: A cross-pollinated perennial bunchgrass. There have been 4 different somatic chromosome numbers reported in the literature (Table II) for A. elongatum. In the available material of this study, two different chromosome numbers were found of which one has not previously been reported. Morphological differences were not found between representatives of different chromosome numbers.

Blue-green or glaucous, erect, glabrous, producing an abundance of long basal and culm leaves; blades firm, flat or loosely rolled and prominently nerved, scabrous on the upper surface and smooth beneath; spike erect, elongate, interrupted, the spikelets not overlapping. Spikelets and the four to ten enclosed caryopses diverge from the stem in a sickle shape. Glumes glabrous, truncate, less than half the length of the spikelet; lowest lemmas rounded or subtruncate at the minutely lobed apex, often mucronate, occasionally long-awned; palea short, ciliate on the keels, about as long as the lemma.

Author: Auricle, ligule, and collar not very distinct (Figure 7).

In examining the PMC's of the 2n = 42 plants, several quadrivalents were found. In the material of the 2n = 14 plant, meiosis was found to be regular.

The two different somatic chromosome numbers were 2n = 14 and 2n = 42. The 2n = 14 and the 2n = 42 individuals have two pairs of satellite chromosomes. They represent 2 different satellite chromosome types. The type with the shorter satellite differs slightly within the 2 accessions. The satellite in the 2n = 14 plants appears slightly larger while the long arm is longer. The satellite chromosome type with the longer satellite is the same in the 2n = 14 and 2n = 42 plants (Tables IV and V, Figures 2 and 3).

8. Agropyron inerme (Scribn. & Sm.) Rydb.

Beardless wheatgrass, beardless bluebunch wheatgrass, awnless bluebunch wheatgrass.

A bunchgrass differing from A. spicatum in the awnless spikelets.

The 2n chromosome number was found to be 14, with 2 pairs of satellite chromosomes which are similar to the satellite chromosomes of A. spicatum, therefore supporting the morphological relationship between these two species (Tables IV and V, Figure 3).

9. Agropyron intermedium (Host.) Beauv.

Intermediate wheatgrass.

Nevski: Perennial, rhizomatous, sod-forming, cross-pollinated species which originated from Europe.

Culms glabrous, smooth; sheaths ciliate on the margins; blades flat, 3-7 mm wide, on the upper surface long-hirsute or glabrous; spikes straight; rachis scabrous on the two main angles; spikelets 3-5-flowered, 10-16 mm long; glumes oblong or lanceolate, obtuse, shorter than the lower floret, smooth; lemma broad-lanceolate, ca. 1 cm long, somewhat obtuse, glabrous; palea subequal.

Author: Auricle, ligule, and collar distinct (Figure 7).

In the PMC's occasionally quadrivalents and other multivalents were found. Laggards at anaphase I and bridges and fragments were also found.

The chromosome number (2n) is 42 including two pairs of satellite chromosomes (Tables IV and V, Figure 2).

10. Agropyron lolioides (Kar. & Kir.) Roshev.

Nevski: Perennial. Plant glaucescent; sheath glabrous and smooth; blades convolute, narrow, less commonly flat, involute, on the upper surface very shortly pubescent or with sparse, long, white hairs, on the lower surface glabrous, smooth. Spikes straight; rachis scaberulous on the two main angles; spikelets appressed or slightly reclined, glaucescent; glumes lanceolate, obtuse, on the margin white-membranaceous, shorter than the lower floret; lemma lanceolate, obtuse, white-membranaceous on the margin in the upper part, 5-nerved; midnerve extends into a very short, rather thick, slightly projecting point; palea almost equal to lemma, ciliate on the keels.

Author: Ligule lacerate, auricle and collar present (Figure 7).

The somatic chromosome number was found to be 58, and there was one pair of satellite chromosomes (Tables IV and V, Figure 3).

11. Agropyron popovi Drob.

Author: Bluish-green plant with small spikes, originating in

Russia. Spikelets spreading, overlapping, 3-4-flowered. Glumes and lemmas awn-tipped and white-membranaceous on the margins. Young leaves involute; the entire plant scaberulous; ligule large, auricle and collar medium size (Figure 7).

This species is related to A. trichophorum, A. intermedium, and A. elongatum. It has a somatic chromosome number of 42 just like A. trichophorum, A. intermedium, and A. elongatum, and it has one pair of satellite chromosomes which is very similar to one pair possessed by the above mentioned species (Tables IV and V, Figures 1 and 5).

12. Agropyron riparium Scribn. & Sm.

Beetle: A sod-forming perennial with rhizomes, native of North America.

Culms glabrous, erect; leaf blades strongly involute, scabrous; the spikelets more or less imbricate, 5-7-flowered; glumes 3-5-nerved, broad and green with scarious margins; lemmas glabrous, scabrous, or pubescent on the lower edges, nerves faint, acute or very short-awned.

Author: Ligule, auricle, and collar not distinct (Figure 8).

Hitchcock and Chase: It resembles A. dasystachyum, but with vigorous rhizomes; blades usually narrower; spikelets usually more imbricate; lemmas glabrous or somewhat pubescent along the edges of the lower part of the lemma.

The somatic chromosome number is 42 with one pair of satellite chromosomes which is the same as one of the satellite chromosome pairs of A. dasystachyum, thereby supplementing the morphological resemblance (Tables IV and V, Figure 2).

13. Agropyron spicatum (Pursh.) Scribn. & Sm.

Bluebunch wheatgrass, bearded bluebunch wheatgrass, spiked wheatgrass, bunch wheatgrass, spike wheatgrass.

Pechanec: A perennial cross-pollinated bunchgrass, native of North America.

Slender, rather wiry, densely tufted; leaf rolled in bud, sheath round, red to purple below ground, glabrous, slender, veins indistinct, open, margins hyaline, smooth; ligule very short, truncate, erose, glabrous; collar narrow, tinged with purple or red in spring and often later, glabrous, divided or continuous; auricles long, clasping, twisted, tinged with red or purple, glabrous; leaf blade flat or drying involute, little constricted at base, tapering to tip, little twisted, prominently striately nerved, midvein not prominent below, margins scabrous, scabrous above, smooth below, densely strigose pubescent above, glabrous below (Figure 8).

The somatic chromosome number is 28 with three pairs of satellite chromosomes. Stebbins and Singh (1950) report that this species and A. inerme have one genome in common which may be indicated by the two idiograms (Tables IV and V, Figure 1).

14. Agropyron strigosum (M. B.) Boiss.

Nevski: Perennial. Culms thin, straight, smooth; blades narrow-linear, convolute, less commonly subconvolute, glaucous, very shortly pubescent on the upper surface, smooth on the lower surface. Spikes straight, thin, rachis scaberulous on the angles; spikelets appressed, slightly longer than the joints of the rachis, 4-5-flowered, glaucescent; rachilla glabrous; glumes slightly unequal, linear-lanceolate, smooth acuminate, 5-7-nerved, somewhat shorter than the lower floret; lemma linear-lanceolate, smooth with 5 very distinct nerves in the upper half. Awn longer than lemma, scaberulous; palea equal to lemma, ciliate on the keels in the upper part.

Author: Ligule, auricle, and collar very distinct (Figure 8).

The somatic chromosome number is 28 with one pair of satellite chromosomes (Tables IV and V, Figures 1 and 4).

15. Agropyron subulatum Soland.

Author: Plant dull green, scabrous, with wide leaves. The upper part of the plant is more scabrous than the lower part. Spikelets overlapping, 3-5-flowered. Glumes with membranaceous margins and 3-5 cm long awns. Lemmas also equipped with 3-5 cm long awns; ligule, auricle, and collar small (Figure 8).

The chromosome number was found to be 2n = 56 with 2 pairs of satellite chromosomes (Tables IV and V, Figure 3).

16. Agropyron trichophorum (Link.) Richt.

Pubescent wheatgrass, stiffhair wheatgrass, Ree wheatgrass.

Nevski: Sod-forming, cross-pollinated perennial species with rhizomes. Originally from Eurasia.

Culms glabrous; blades flat, sheaths of the lower leaves hirsute; rachis more or less hirsute; spikelets densely hirsute, awnless, 4-7-flowered; glumes several-nerved, acutish, hirsute; lemma hirsute with long white hairs on the upper surface and margins; palea slightly shorter than the lemma, long-ciliate on the keels.

Author: Ligule, auricle, and collar distinct (Figure 8).

Relatively high frequencies of laggards were found at anaphase I. Bridges and fragments were also reported (Myers 1947).

The somatic chromosome number is 42 with two pairs of satellite chromosomes (Tables IV and V, Figure 2).

Agropyron junceiforme

Due to the fact that *Agropyron junceiforme* never headed, despite receiving the same cultural treatment as the rest of the species so far described, the complete morphological examination of this species was not accomplished. The cause of this phenomenon is not known to the author. However, cytological examinations were completed for this species, and the somatic chromosome number was found to be 28 with one pair of satellite chromosomes (Tables IV and V, Figure 1).

Table II. Chromosome numbers (2n) of Agropyron species.

Species	Author's obs.	Reported	Source
A. acutum	42	35	Simonet 1934
A. agropyroides	42		
A. arizonicus	28		
A. brachyphyllum	42		
A. caespitosum	42	14	Stebbins & Pun 1953
		70	Peto 1936
A. caninum	28	28	Peto 1930, Avdulov 1931, Simonet 1935a, Hartung 1946, Stebbins & Snyder 1956
A. ciliatiforme	28		
A. cristatum	14	14	Peto 1930, Hartung 1946
		42	Araratian 1938
A. dasystachyum	28	28	Peto 1930, Senn et al 1947
A. desertorum	28	28	Sarkar 1956
A. elongatiforme	58	28	Veruschkine 1936
A. elongatum	14	14	Simonet 1935
	42		
		56	Hanson & Carnahan 1956
		70	Hanson & Carnahan 1956
		72	Matsumura & Sakamoto 1955
A. inerme	14	14	Hartung 1946
		28	Hanson & Carnahan 1956
A. intermedium	42	28	Khiznyak 1936a
		42	Peto 1930, Simonet 1935a Khiznyak 1936a, Araratian 1938, Hartung 1946
		43	Hartung 1946
A. junceiforme	28	28	Östergren 1940
A. kosanini	56		
A. latiglume	28	28	Senn et al 1949
A. lolioides	58		
A. orientale	28	28	Avdulov 1931
A. panormitanum	28		
A. popovi	42		
A. pseudorepens	28		
A. riparium	42	28	Hartung 1946
		42	Tateoka 1956
A. semicostatum	42	28	Nielsen & Humphrey 1937
		42	Nakajima 1936
A. spicatum	28	14	Hartung 1946, Senn et al 1947, Stebbins & Singh 1950
		28	Hartung 1946, Senn et al 1947
A. squarrosum	42		
A. strigosum	28		
A. subsecundum	28	28	Peto 1930, White 1940

A. subulatum	56		
A. trachycaulum	28	28	Peto 1930, Avdulov 1931, Nielsen & Humphrey 1937, Stebbins *et al* 1941, Senn *et al* 1947
A. trichophorum	42	42	Araratian 1938, Hartung 1946, Heinrichs 1953
A. triticeum	14	14	Matsumura & Sakamoto 1955

Table III. Lengths of chromosome arms (excluding the satellite chromosomes) of the species in the sections Roegneria, Eremopyrum and Eu-Agropyron. (One unit = 0.72μ.)

Short arm	1	1	1	1	1	2	2	2	2	2	2	3	3	3	3	3	3	4	4	4	4	4	4	5	5	5	5	5	6	6	6	6	7	7
Long arm	6	7	8	9	10	3	4	5	6	7	8	3	4	5	6	7	8	4	5	6	7	8	9	5	6	7	8	9	6	7	8	9	7	8
Name	How many times represented																																	
Roegneria																																		
A. caninum							1		3			1	1	2	1			1	2	1														
A. latiglume														2	2			1	3	1	1			1	2									
A. panormitanum															1				1	2	1	1		1	2				1	1				1
A. pseudorepens													1		1	1		2	2	2	1			1		1								
A. semicostatum													3	2				2	3					2	3				2	2				
A. subsecundum							1						3	2	1			1						1	1	3								
A. trachycaulum									1				1					2	2					2	3					2				
Eremopyrum																																		
A. orientale	1	1	1	1			1			1	1		2		1				1			1												
A. triticeum		1	2		1				1	1	1																							
Eu-Agropyron																																		
A. agropyroides													1	1		1		1	3	1	2			2	3	2				2				
A. brachyphyllum																			2	1	2	1		1	2	1		1	1	3	1	1	2	1
A. ciliatiforme																	1		1	2				2	2	1	1		1				2	
A. cristatum															1	1			1		1			1	1	1								
A. desertorum															1	1			2			1			1	3	1		1	2			1	
A. kosanini						1		1		1		1	2	1	1			2	3	2	3			2	2	2			1	1				1
A. squarrosum														1	1	1			1	3	3	2		1	3	2	1	1		1				

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Table IV. Lengths of chromosome arms (excluding the satellite chromosomes) of the species in the section Elytrigia. (One unit = 0.72 μ.)

Short arm	2	2	2	2	2	3	3	3	3	3	3	4	4	4	4	4	4	5	5	5	5	5	6	6	6	6	7	7	8	8
Long arm	4	5	6	7	8	3	4	5	6	7	8	4	5	6	7	8	9	5	6	7	8	9	6	7	8	9	7	8	8	10
Name	How many times represented																													
A. acutum		1				1	1	1	1			1	2	2	1			1	3	1	1		1	1				1		
A. arizonicus						1	1	2				3	2					2	1											
A. caespitosum								1	1			3	1	3		1	1	1	1	2			1	1	1		2			
A. dasystachyum							1		1	1		1	2	2	1			1	1					1						
A. elongatiforme			1			1	1			2		1	2	2	1	1		4	1	1	1		2	2			2	1	1	
A. elongatum (2n=14)									1	1				1	1					1										
A. elongatum (2n=42)		1				1	2	1		1		3	2	1	1			2	2				1				1			
A. inerme													2		1			1	1											
A. intermedium						2	3	1	1				1					2	2	1			2	1	1		1	1		
A. lolioides			1			2	3	6				1	5	2				3	4				1							
A. popovi	1					2	2	1	1	1	1	1	4	1	2			1					1	1						
A. riparium			1			1	1	2		1			3	3	2	1		1	2				1	1						
A. spicatum						1		1	1			1	3	1	1			1	1											
A. strigosum						2	2	2	2			3	1						1											
A. subulatum				1			1	1		1	1	2	3	2	1	1		3	2	2			1	1	1			1		1
A. trichophorum	1						2	2		1	1	1	3	1	2			1	2				1	1						
A. junceiforme							2	2				2	2						2				2	1						

Table V. Satellite chromosomes of 29 <u>Agropyron</u> species.
(One unit = 0.72 μ.)

Satellite	0.1	0.1	0.1	0.1	0.1	0.5	0.5	0.5	1	1	1	1.5	2	2	2	2	2	2	2	2
Short arm	3	3	3	4	4	3	3	3	1	3	3	3	1	1	2	2	2	2	3	3
Long arm	5	6	7	5	7	6	7	10	5	5	6	5	4	5	4	5	6	7	5	6
Name	How many times represented																			
Section <u>Roegneria</u>																				
<u>A</u>. <u>caninum</u>																1				
<u>A</u>. <u>latiglume</u>																1				
<u>A</u>. <u>panormitanum</u>			1													1				
<u>A</u>. <u>pseudorepens</u>						1									1					
<u>A</u>. <u>semicostatum</u>															2					
<u>A</u>. <u>subsecundum</u>															1					
<u>A</u>. <u>trachycaulum</u>																	1			
Section <u>Eremopyrum</u>																				
<u>A</u>. <u>orientale</u>			1		1															
Section <u>Eu-Agropyron</u>																				
<u>A</u>. <u>agropyroides</u>									1									1		
<u>A</u>. <u>brachyphyllum</u>																	1			
<u>A</u>. <u>ciliatiforme</u>																	1			
<u>A</u>. <u>kosanini</u>																1				
Section <u>Elytrigia</u>																				
<u>A</u>. <u>acutum</u>																			1	
<u>A</u>. <u>arizonicus</u>																2				
<u>A</u>. <u>caespitosum</u>				1																
<u>A</u>. <u>dasystachyum</u>									1							1				
<u>A</u>. <u>elongatiforme</u>														1		1				
<u>A</u>. <u>elongatum</u> (2n=14)								1			1									
<u>A</u>. <u>elongatum</u> (2n=42)							1				1									
<u>A</u>. <u>inerme</u>						1										1				
<u>A</u>. <u>intermedium</u>										1		1								
<u>A</u>. <u>lolioides</u>																1				
<u>A</u>. <u>popovi</u>	1																			
<u>A</u>. <u>riparium</u>																1				
<u>A</u>. <u>spicatum</u>					1											2				
<u>A</u>. <u>strigosum</u>															1					
<u>A</u>. <u>subulatum</u>													1	1						
<u>A</u>. <u>trichophorum</u>						1														1
<u>A</u>. <u>junceiforme</u>						1														

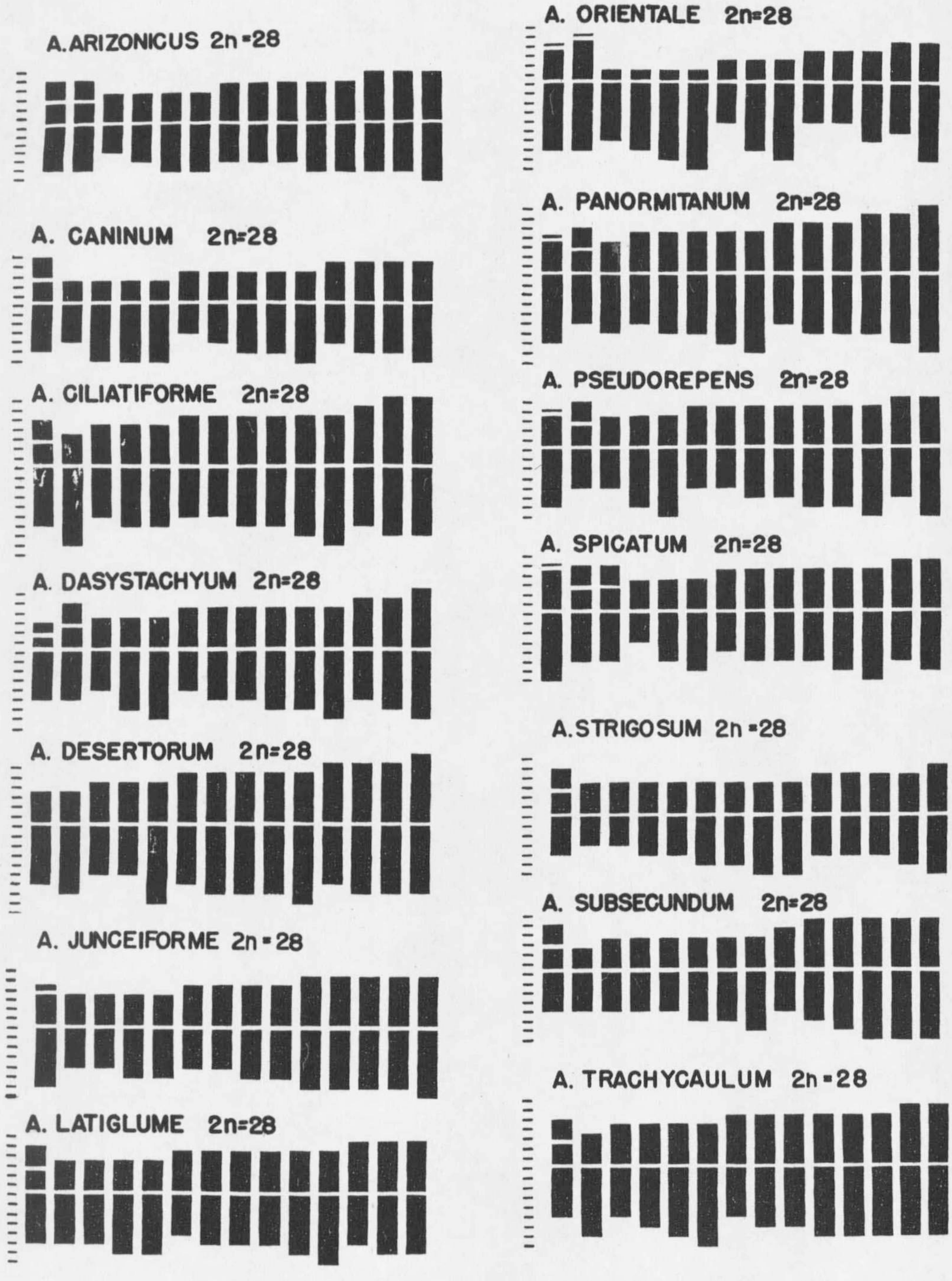

Figure 1. Idiograms showing several Agropyron species with 2n=28 chromosomes. Scale : one unit = 0.72μ.

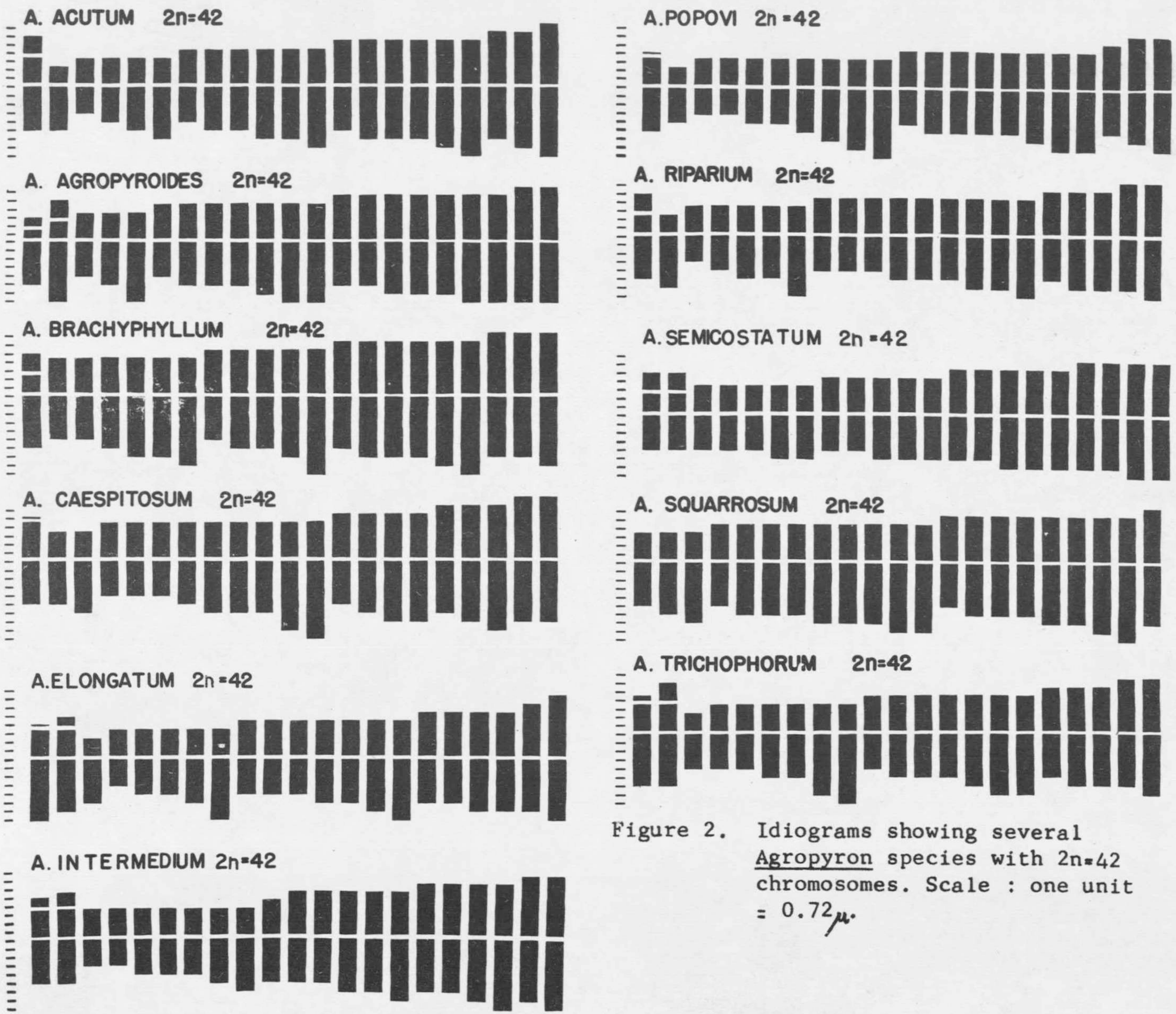

Figure 2. Idiograms showing several <u>Agropyron</u> species with 2n=42 chromosomes. Scale : one unit = 0.72μ.