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ENZYME VARIABILITY AND PHYLOGENETIC RELATIONSHIPS IN THE GRASS GENERA *AGROPYRON* GAERTN. AND *ELYMUS* L.

II. THE GENUS *ELYMUS* L.

The genera *Agropyron* Gaertn. s. lat. and *Elymus* L. s. lat. are diagnostically distinguished mainly on the basis of the number of spikelets at the node. The species with solitary spikelets are referred to the genus *Agropyron* while those carrying two or more spikelets at each node are placed in the genus *Elymus*.

Such a division has repeatedly been suspected to be purely artificial and not reflecting real phylogenetic relationships in this species group. To overcome the inadequacy of this classification, S. Nevski (Невский, 1933, 1936) has proposed to subdivide the two traditional large genera into smaller ones, which could be combined more appropriately to construct a taxonomic system reflecting the phylogeny of the tribe *Triticeae* Dum. (*Hordeae* Benth.). Thus, he separated from the genus *Elymus* s. lat. the genera *Clinelymus* (Griseb.) Nevski (correct name *Elymus* L.), *Asperella* Humb. and *Terrella* Nevski, placing them in the subtribe *Clinelyminae* Nevski. Similarly, from the genus *Agropyron* s. lat. he separated caespitose species with green, soft leaves and small anthers to the genera *Roegneria* C. Koch and *Anthosachne* Steud., which form the subtribe *Roegneriinae* Nevski.

In his works S. Nevski repeatedly (Невский, 1933, 1941) expressed the view that the species grouped in the subtribes *Roegneriinae* and *Clinelyminae* are phylogenetically much more closely related with each other than with the remaining species belonging to the genera *Agropyron* Gaertn. s. str., *Elytrigia* Desv., *Leymus* Hochst. (treated as *Elymus* L. s. str. by Nevski), etc. The phylogenetic concepts of S. Nevski have found further elaboration by N. Tzvelev (Цвелев, 1968, 1970, 1972) who found it justified, for phylogenetic reasons, to unite the species treated by S. Nevski as belonging to the genera *Roegneria*, and *Clinelymus* in the single genus *Elymus* L., separating from it the genus *Leymus* Hochst. Recent cytogenetic studies carried out by D. Dewey (1966a, 1967) provide further biosystematic evidence in favour of a need for analogous taxonomic revision in the North American group of wheatgrasses.

The approach of S. Nevski has been followed and supported by several systematists (Hylander, 1953; Melderis, 1950; Löve and Löve, 1961; etc.). However, there is substantial disagreement concerning the taxonomic status of the groups established, and S. Nevski's treatment of the *Elymus-Agropyron* group of the tribe *Triticeae* has not been unanimously accepted (Bowden, 1965; Runemark, Heneen, 1968, etc.).

The characters of the external morphology on which the splitting in the genera and species was based by S. Nevski, such as caespitose or rhizomatous nature of plants, the size of anthers, the shape of caryopses, palea and glumes, etc., vary widely within natural populations and none of them could be used unambiguously to establish distinct limits between the taxa. The taxonomic position of many species remains questionable and their treatment depends on the characters taken into account and considered to be more important by a systematist.

This indicates the need for continuing search for further characters which could be used to delimitate the taxa in the *Elymus-Agropyron* group and establish real phylogenetic relationships between them.

In this paper we have studied polyacrylamide gel electrophoretic patterns of seedling acid phosphatases and esterases in the species of the genus *Elymus* L. s. str. as compared with those for a group of wheatgrass species separated by S. Nevski in the genus *Roegneria*. It will be shown that many of the caespitose wheatgrass species belonging to the *Roegneria* group are phylogenetically, judging by isoenzyme data, much more closely related to *E. sibiricus* L., the type species of the genus *Elymus* L., than to the *Elytrigia* or *Eu-Agropyron* groups of the genus *Agropyron*, and should be treated as belonging to the genus *Elymus* L.

It will also be shown that caespitose wheatgrasses in North America are more closely related to *Elymus canadensis* L. than to Eurasian caespitose wheatgrasses of the *Roegneria* group. Three major sub-groups can tentatively be distinguished in the genus *Elymus* L. on the basis of the esterase electrophoretic patterns, while a part of species should be removed from the genus *Elymus* L. and treated as belonging to the genera *Leymus* Hochst. and *Psathyrostachys* Nevski.

Materials and methods

Plant material. The taxa and seed accessions involved in the present study and their origin are listed below. Plants have been grown in a field nursery for all the seed accessions received in a condition not allowing their identification. The accessions studied have been identified with the aid of available monographs. The botanical names are given in accordance with the results of the present study, i. e. the caespitose wheatgrasses of the *Roegneria* group are treated as belonging to the genus *Elymus* L. However, the old, more common synonyms are also presented to avoid any confusion.

1. *Elymus sibiricus* L., 1753: accession R 16/71, a reproduction of seeds originating from South-East Altai, received from the Arcto-Alpine Botanical Garden in Kirovsk (USSR); accession R 19/71, a seed reproduction of Siberian origin, received from the Botanical Garden of Novosibirsk (USSR); accession R 40/71 — a reproduction of seeds collected in Japan (Hokkaido, 1957), received from Dr. S. Sakamoto (Kyoto, Japan).

2. *Elymus dahuricus* Turcz. ex Griseb., 1852, s. l., incl. var. *excelsus* (Turcz.) Roshev., 1923, based on *E. excelsus* Turcz. ex Griseb., 1852: accession R 33/71, a reproduction of seeds collected in the Krasnoyarsk Krai, (USSR) received from the Botanical Garden of Novosibirsk; accession R 36/71, a reproduction of unspecified Siberian origin, received from the Botanical Garden of Novosibirsk; accession LP 3/71 — original seeds collected in the Primorsk Krai (foot-hills in the region of the mountain Sugan) by Dr. Nina Probatova (Vladivostok), accession LP 4/71 — original seeds collected in the Primorsk Krai (at the river Saifun) by Dr. Nina Probatova.

3. *Elymus tangutorum* (Nevski) Hand.-Mazz., 1936: accession R 69/71, a seed reproduction of unknown origin, received from the Botanical Garden in Vacratot (Hungary).

4. *Elymus canadensis* L., 1753: accession RL 1/70, a reproduction of seeds collected at the Ontario Province, Canada (banks of the Mississippi River), received from the Canadian Department of Agriculture (Ottawa, Canada); accession R 3/72, a reproduction of unspecified Canadian origin, received from the Botanical Garden of Montreal (Canada); accession RD-10, a reproduction of seeds originating from the state Montana (USA), received from the United States Department of Agriculture (Washington, Pullmann, USA) under the P. I. 232249 via Dr. D. Dewey (Utah, USA).

5. *Elymus glaucus* Buckl., 1862: accession R 71/70, a reproduction of unspecified Canadian origin, received from the USDA (P. I. 236811); accession RD-13, a reproduction of seeds originating from the state Idaho (USA), received from the USDA (P. I. 232263) via Dr. D. Dewey.

6. *Elymus virginicus* L., 1753, syn. *Terrella virginica* (L.) Nevski, 1932: accession RL 5/70, a reproduction of seeds collected by T. F. Adams in Canada (District Ontario), received from the Canadian Department of Agriculture (Ottawa, Canada); L 9/71 seeds collected in Canada (District Q. Riviere Ouelle), received from the City of Montreal Botanical Garden (Canada): R 94/70, a reproduction of unknown origin from the USDA (P. I. 315864).

7. *Elymus caninus* (L.) L. 1755, based on *Triticum caninum* L., 1753, syn. *Agropyron caninum* (L.) Beauv., 1812, *Roegneria canina* (L.) Nevski 1934: accession L 5/71, seeds collected in the Estonian SSR (District Räpina); accession L 42/72, seeds collected in the Armenian SSR (near Dilidjan); accession RL 35/69, seeds collected in Denmark (North-West Seeland), received from the Botanical Garden of Copenhagen (Denmark); accession RL 2/71, seeds collected in Sweden (Öemevalla, Halland), received from the Botanical Garden of Lund (Sweden); accession R 7/71, seeds collected in Finland (Tvärminne) by A. Saarisalo, received from the Botanical Garden of Helsinki (Finland); accession R 18/70 a reproduction derived from Italy, received from the USDA (P. I. 252044) via Dr. D. Dewey, accession R 20/70, a reproduction from Yugoslavia, received from USDA (P. I. 251417); accession R 22/70, a reproduction from Turkey, received from the USDA (P. I. 172346).

8. *Elymus caninus* var. *behmii* (Meld. in Hyl.) Jaaska, comb. nov., basionym: *Roegneria behmii* Meld. in Hylander, Nordisk kärlväxtflora I, 1953, syn. *A. caninum* var. *behmii* (Meld. in Hyl.) B. Nord., 1972: accession R 9/71, a reproduction of seeds of unspecified Swedish origin, received from the Botanical Garden of Vacratot (Hungary).

9. *Elymus caninus* var. *donianus* (F. B. White) Jaaska, comb. nov., basionym: *Agropyron donianum* F. B. White, Proc. Perthsh. Soc. Nat. Sci. 1893, I, p. 41, syn. *Roegneria doniana* (F. B. White) Meld., 1950: RL 8/72 and RD-5, reproductions of seeds derived from Scotland (England).

10. *Elymus fibrosus* (Schrenk) Tzvel., 1970, based on *Triticum fibrosum* Schrenk, 1845, syn. *Agropyron fibrosum* (Schrenk) Nevski, 1930 and *Roegneria fibrosa* (Schrenk) Nevski, 1934: accession R 126/70, a reproduction of unspecified Siberian origin, received from the Botanical Garden of Novosibirsk (USSR).

11. *Elymus kronokensis* (Kom.) Tzvel., 1968, s. lat., based on *Agropyron kronokense* Kom., 1915, non *Elymus borealis* Scribn., 1900.

11a. *Elymus kronokensis* var. *borealis* (Turcz.) Tzvel., 1968, based on *Triticum boreale* Turcz., 1856, syn. *Agropyron boreale* (Turcz.) Drob., 1916, *Roegneria borealis* (Turcz.) Nevski, 1934: accession R 17/72, seeds

collected in North Sweden (Torna, Lappmark), the Botanical Garden of Uppsala (Sweden); accession LP 8/71, collected in Kamtchatka (District Olyutorsk) by Dr. Nina Probatova, the diagnostic characters of the plants: glumes glabrous, abruptly contracted toward tip into a short (up to 1 mm) awn, lemmas also glabrous, short-awned, longer than glumes;

11b. *Elymus kronokensis* var. *alascanus* (Scribn. et Merr.) Jaaska, comb. nova, basionym: *Agropyron alascanum* Scribn. et Merr., 1910 (in Contrib. U. S. Nat. Herb., 13:85): accession LP 7/71, collected in Kamtchatka near Petropavlovsk, received from Dr. Nina Probatova. The plants had the following diagnostic characters: glumes glabrous, with broad hyaline-scarious margin, abruptly contracted toward tip into a short (up to 1 mm) awn; lemmas longer than glumes (10—12 mm and 6—8 mm, respectively), short-awned (2—3 mm), backs densely short-pubescent.

12. *Elymus confusus* (Roshev.) Tzvel., 1968, based on *Agropyron confusum* Roshev., 1924, syn. *Roegneria confusa* (Roshev.) Nevski, 1934: accession LP 6/71, seeds collected in Kamtchatka (District Olyutorsk), received from Dr. Nina Probatova (Vladivostok).

13. *Elymus czimganicus* (Drob.) Tzvel., 1968, based on *Agropyron czimganicum* Drob., 1923, syn. *Roegneria czimganica* (Drob.) Nevski 1934: accession R 123/70, a seed reproduction of Central Asian origin (collection place unknown), received from the Central Botanical Garden in Moscow (USSR).

14. *Elymus transhyrcanus* (Nevski) Tzvel., 1972, based on *Roegneria transhyrcana* Nevski, 1934, syn. *Agropyron transhyrcanum* (Nevski) Bond., 1968; incl. *Roegneria leptoura* Nevski, 1934, syn. *Agropyron leptourum* (Nevski) Grossheim, 1939: accession R 64/70, a seed reproduction of unspecified Iranian origin, received from the USDA (P. I. 229520), accession RD-6, a seed reproduction of unknown USSR origin, received from the USDA (P. I. 314199) via Dr. D. Dewey; accession LT 1/72, seeds collected near Ashkhabad (Turkmenian SSR), received from Dr. P. Tshopanov (Ashkhabad).

15. *Elymus trachycaulus* (Link) Gould et Shinners, 1954, based on *Triticum trachycaulon* Link, 1833, syn. *Elymus pauciflorus* (Schwein.) Gould, 1947, non Lam. 1791, based on *Triticum pauciflorum* Schwein., 1824, syn. *Agropyron pauciflorum* (Schwein.) Hitchcock, 1934, non Schur, 1859, *Roegneria pauciflora* (Schwein.) Nevski, 1932, *Agropyron trachycaulum* (Link) Malte ex. H. F. Lewis: accessions RL 7/70 and RL 38/71, both collected in Canada (Mackenzie District) by W. J. Cody, received from the Canadian Department of Agriculture: accession R 50/70, a reproduction of unspecified Canadian origin, received from the USDA (P. I. 183009); accession RD-20, a reproduction of seeds derived from Utah (USA), received from Dr. D. Dewey.

16. *Elymus nipponicus* Jaaska, nom. nov., basionym: *Agropyron yezoense* Honda, in Bot. Mag. Tokyo, 1929, 43, p. 292, non *Elymus yezoensis* Honda, 1930 (in J. Fac. Sci. Univ. Tokyo, sect. III 1, p. 16): accession R 8/72, a reproduction of seeds from Japan (Hokkaido), received from Dr. S. Sakamoto (Kyoto, Japan).

17. *Elymus ciliaris* (Trin.) Tzvel., 1972, based on *Triticum ciliare* Trin. 1833, syn. *Agropyron ciliare* (Trin.) Franchet, 1884, *Roegneria ciliaris* (Trin.) Nevski, 1934: accession LP 10/71, seeds collected by Dr. Nina Probatova near Vladivostok (Primorsk Krai).

18. *Leymus arenarius* (L.) Hochst., 1848, based on *Elymus arenarius* L., 1753: L 1/71, seeds collected at sandy sea-shore dunes near the village of Kabli (District Pärnu, Estonian SSR).

19. *Agropyron cristatum* (L.) Beauv., 1812, s. lat, based on *Bromus cristatus* L., 1753: a) ssp. *cristatum*: RB 4/69, a reproduction of unspecified Siberian origin, received from the Botanical Garden of Novosibirsk; b) ssp. *pectinatum* (Bieb.) Tzvel., 1970, based on *Triticum pectinatum* Bieb., 1808, syn. *Agropyron pectinatum* (Bieb.) Beauv., 1812: accession L 43/72, seeds collected at the foot-hills of the mountain Kara-Dag in the Crimea; accession L 51/72, seeds collected south-east of Yerevan (Armenian SSR).

20. *Agropyron repens* (L.) Beauv., 1812, based on *Triticum repens* L., 1753, syn. *Elytrigia repens* (L.) Desv. 1810: accession L 17/72, seeds collected in Estonia (Pangodi, District Tartu); accession L 20/72, seeds collected in the Crimea (cape Kiik-Atlama, District Feodossia).

Biochemical methods: Light-grown green or dark-grown etiolated 6 to 12-day-old seedlings (or stems and leaves separately) were individually crushed each in 0.2 ml of cold homogenization buffer, containing 0.25 M sucrose, 0.05 M tris-hydroxymethylaminomethane (Tris), 0.035 M ascorbic acid, 1 mM EDTA-Na_2Mg and 5 mM cysteine.

After removal of cell debris about 3—5 mg of Sephadex G-200 were mixed to the homogenates which were immediately subjected to electrophoresis in a polyacrylamide gel slab (60×45×3 mm) made in a vertical plexiglas cathode chamber by photopolymerizing between two fluorescent lamps of a freshly prepared mixture composed of 10 per cent acrylamide, 0.15 per cent N,N'-methylene-bisacrylamide, 0.25 M Tris, 0.075 M HCl, 0,2 per cent triethanolamine and 0.5 mg per cent riboflavine-5-phosphate. The upper cathode buffer contained 0.01 M Tris and 0.08 M glycine, whereas the lower anode buffer was 0.1 M Tris-acetate at a pH of about 8.9. Six enzyme extracts were layered in the sample slots on the top of the small-pore gel, and electrophoresis was carried out in a plexiglass-made refrigerated apparatus at about 15—20 mA per cm^2 of gel surface for about 2 hours, until the marker dye, bromophenol blue, reached the end of the gel.

After electrophoresis, the gels were removed from plexiglass chambers and incubated for 30 min. in 0.2 M maleate buffer, pH 5.2, to reduce pH in the gel matrix. The gels were then stained histochemically to locate acid phosphatase and esterase activities by incubating in reaction mixtures containing 0.5 mg/ml 1-naphthyl phosphate or 1-naphthyl acetate, respectively, as substrates, and 0.02 M freshly hexa-azotized basic fuchsin (or tetra-azotized *o*-dianisidine) as the dye coupler in 0.1 M maleate buffer at a final pH of about 5.2—5.4 (for phosphatases) or 6.0—6.2 (for esterases).

The gels were fixed and stored in a mixture of ethanol-acetic acid-water (20 : 10 : 70) and photographed in a diffuse transmitting light for a permanent record. The enzyme electrophoretic patterns on polyacrylamide gels and their photographs will further be called enzymograms. Enzymograms were photographically enlarged to a convenient length, using enzyme bands for the type species, *Elymus sibiricus* L. on the same slab as standard markers. For convenience of description, the stained bands of enzyme activity will be designated by the distances of migration (D_m) from the origin toward the anode expressed in arbitrary units on the scale at the left side of the figure. Each enzymogram designated by an arabic number is obtained from the tissue extract of a single individual (seedling).

Results

Esterases. The enzymograms presented in Fig. 1 reveal the presence, in seedling tissues, of a series of electrophoretically distinct esterase fractions of different staining intensity. Electrophoretically discrete fractions (bands) represent multiple molecular forms of esterase and will be called isoesterases. Some isoesterases form clusters of closely-spaced bands and are seen as broad zones. The staining intensity of bands reflects enzymatic activity of individual isoesterases.

Esterase enzymograms of *Elymus sibiricus* L., the type species of the genus *Elymus* L., show the presence of 5—7 discrete fractions, i.e. isoesterases (enzymograms 1—6 in Fig. 1). The most characteristic of the esterase electrophoretic pattern of *E. sibiricus* are the bands at the D_m values of about 3.9, 3.5, 2.9 and 2.4. The isoesterase at the D_m of 2.4 appears as a densely stained band indicating its high enzymatic activity in the green leaves of the light-grown plants. In the etiolated seedlings this isoesterase is either totally lacking (in stems) or appears as a weak band (in leaves). Only a limited intraspecific individual variation restricted mainly to the isoesterases at the D_m values of 4.4 and 2.4 has been found in the three seed accessions of *E. sibiricus* of different geographic origin studied.

Esterase enzymograms of *Roegneria canina* (L.) Nevski, the commonest species of *Roegneria* in Europe, reveal considerable intraspecific variation in isoesterase fractions of medium electrophoretic mobility at the D_m values ranging from 2 to 3, and in fractions of high mobility ($D_m > 4$). However, isoesterases at the D_m values of 3.9 and 3.5, as a rule, proved to be invariant in *R. canina* and in common to *E. sibiricus*. The accession P. I. 252044 of Italian origin was the only exception among the collections of *R. canina* studied, showing only a scarcely distinguishable band at the D_m 3.9 and an additional band of slightly lesser mobility instead of it (enzymogram 16). The staining intensity of bands of intermediate electrophoretic mobility (D_m 2—3) was found to vary widely, depending on the age and growth conditions of the seedlings as well as on the genetic determinants. The observed intraspecific variation in the seedling esterases of *R. canina* needs a more detailed further study.

Many other Eurasian taxa (linneons) of the genus *Roegneria* revealed esterase electrophoretic patterns highly similar to those found in *E. sibiricus* and *R. canina*. Thus, the esterase enzymograms of the three taxa of *Roegneria* of various geographic origin known as *R. behmii* (endemic in Sweden), *R. doniana* (endemic in Scotland) and *R. fibrosa* (sporadically distributed in the European part of the USSR and in Western Siberia) showed the presence (enzymograms 17—22 in Fig. 1), in addition to the two diagnostic isoesterases at the D_m values 3.9 and 3.5, of a broad zone of highly active isoesterases of medium electrophoretic mobility, also characteristic of some collections of *R. canina* (enzymograms 9—12 in Fig. 1). The two short-awned taxa of arctic distribution, *R. borealis* and *R. alascana,* on the other hand, failed to form a high activity of isoesterases of medium electrophoretic mobility in the seedlings, and their esterase enzymogram proved very similar to that of *R. canina* of Armenian origin (not presented) with the two diagnostic isoesterases at 3.9 and 3.5 in common. Esterase enzymograms of the two *Roegneria* species, morphologically characterized by curved awns and over-all similarity to *E. sibiricus*, *R. czimganica* of Central Asian distribution and *R. confusa* of Eastern Asian distribution, proved almost identical with those of *E. sibiricus* (compare enzymograms 1—5 and 27—30 in Fig. 1). The esterase

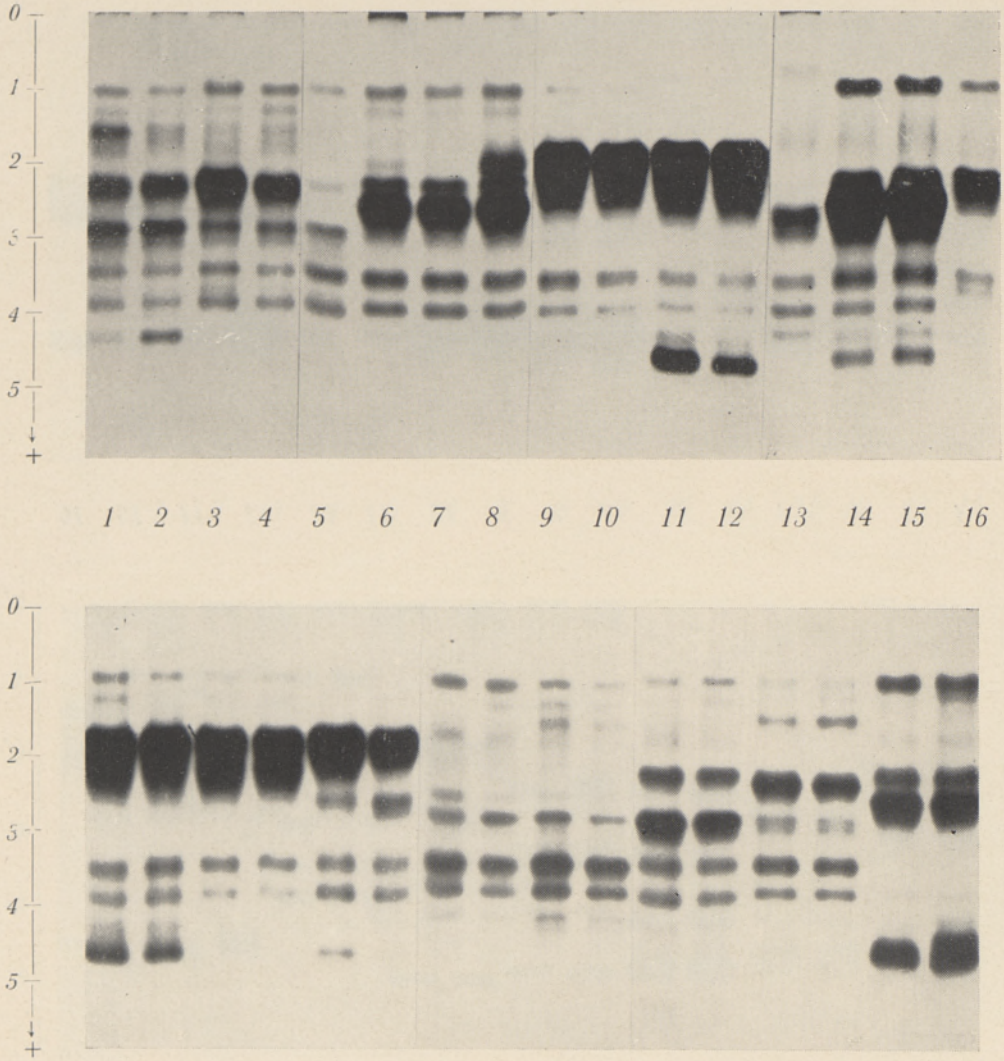


Fig. 1. Esterase enzymograms: *Elymus sibiricus* R 16/71 (*1—2*), R 19/71 (*3—4*) and R 40/70 (*5*), *Roegneria canina* RL 35/69 (*6—8*), L 5/71 (*9—10*), R 7/71 (*11—12*), R 22/70 (*13*), R 20/70 (*14—15*) and R 18/70 (*16*), *Roegneria behmii* R 9/71 (*17—18*), *Roegneria doniana* RD-5 (*19—20*), *Roegneria fibrosa* R 126/70 (*21—22*), *Roegneria borealis* R 17/72 (*23—24*), *Roegneria alascana* LP 7/71 (*25—26*), *Roegneria czimganica* R 123/70 (*27—28*), *Roegneria confusa* LP 6/71 (*29—30*), *Roegneria ciliaris* LP 10/71 (*31—32*).

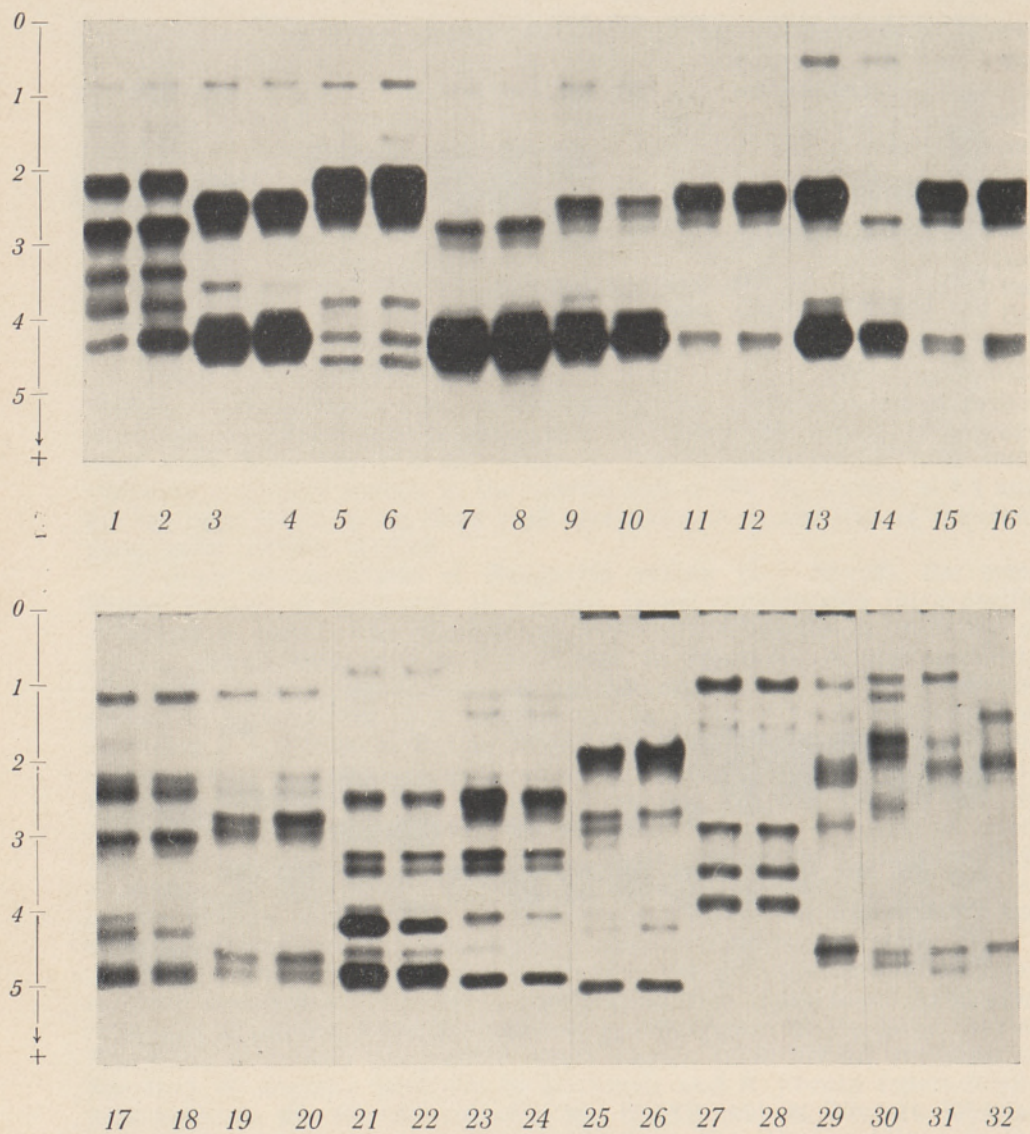


Fig. 2. Esterase enzymograms: *Elymus sibiricus* R 16/71 (*1—2*), *Elymus glaucus* RD-13 (*3—4*) and R 71/70 (*5—6*), *Elymus canadensis* RL 1/70 (*7—8*) and RD-10 (*9—10*), *Roegneria pauciflora* R 50/70 (*11—12*), RL 38/71 (*13—14*) and RL 7/70 (*15—16*), *Elymus dahuricus* LP 3/71 (*17—18*) and LP 4/71 (*19—20*), *Elymus tangutorum* R 69/71 (*21—22*), *Agropyron yezoense* R 8/72 (*23—24*), *Leymus arenarius* L 1/71 (*25—26*), *Elymus sibiricus* R 40/71 (*27—28*), *Elytrigia repens* L 17/72 (*29*) and L 20/72 (*30*), *Agropyron cristatum* RB 4/69 (*31—32*).

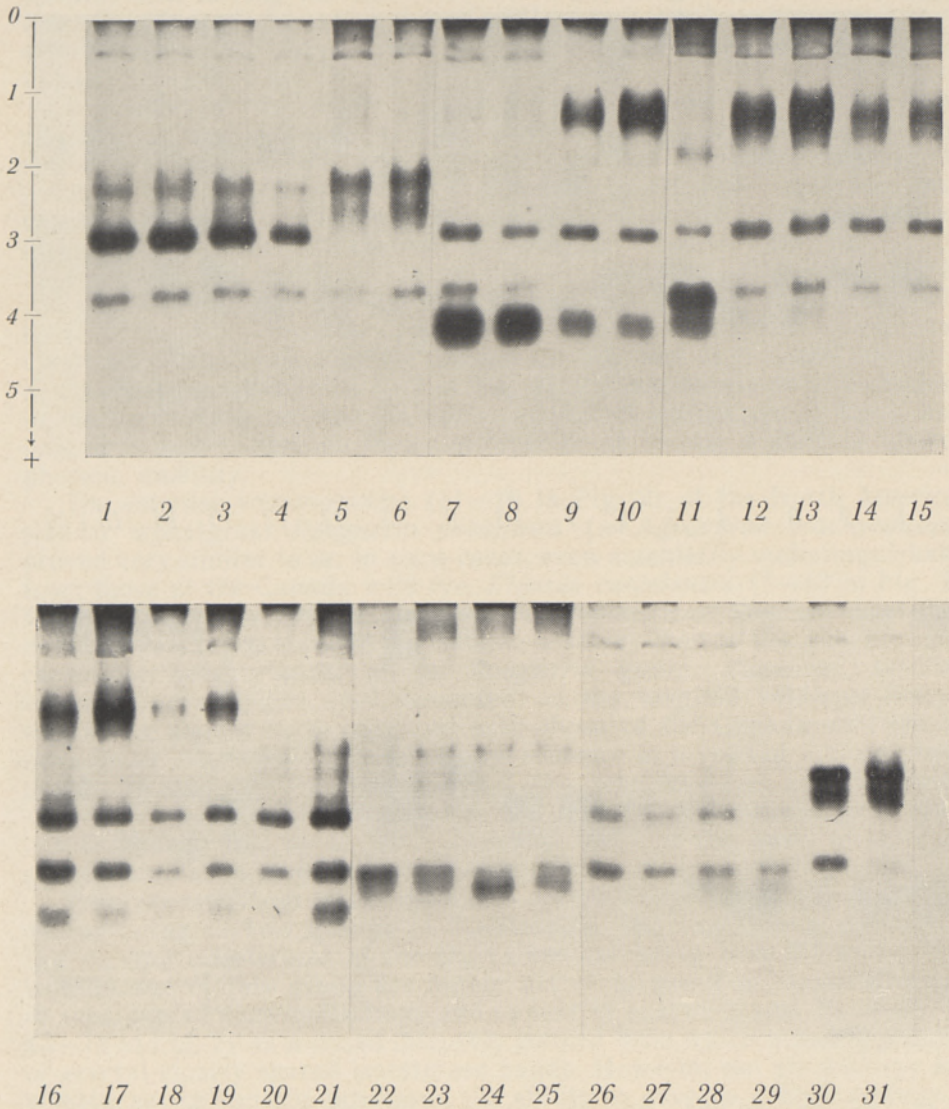
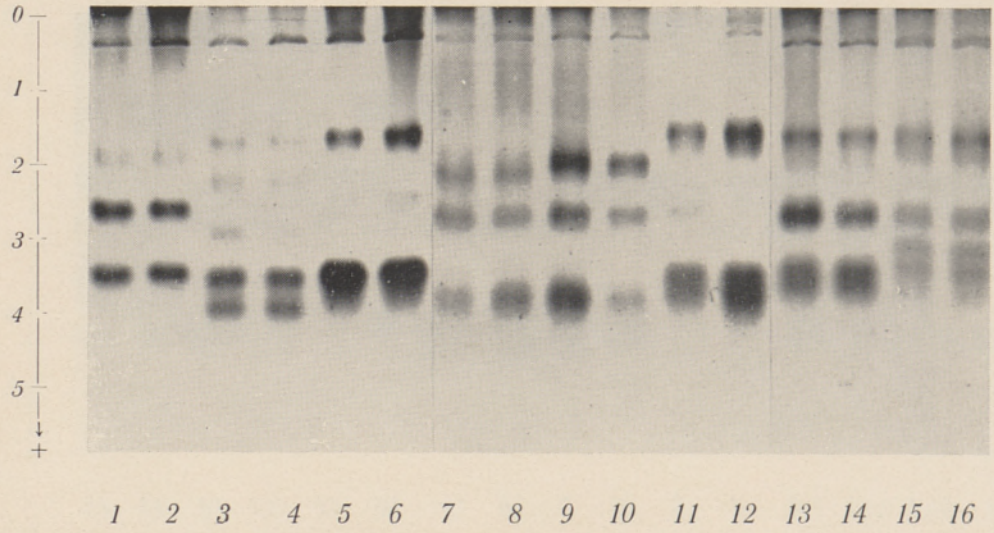


Fig. 3. Phosphatase enzymograms: *Elymus sibiricus* R 16/71 (*1—2*), R 19/71 (*3—4*) and R 40/71 (*5—6*), *Roegneria canina* L 5/71 (*7—8*), R 7/71 (*9—10*), R 22/70 (*11*), R 20/70 (*12—13*) and R 18/70 (*14—15*), *Roegneria behmii* R 9/71 (*16—17*), *Roegneria doniana* RD-5 (*18—19*), *Roegneria fibrosa* R 126/70 (*20—21*), *Roegneria borealis* R 17/72 (*22—23*), *Roegneria alascana* LP 7/71 (*24—25*), *Roegneria czimganica* R 123/70 (*26—27*), *Roegneria confusa* LP 6/71 (*28—29*), *Roegneria ciliaris* LP 10/71 (*30—31*).



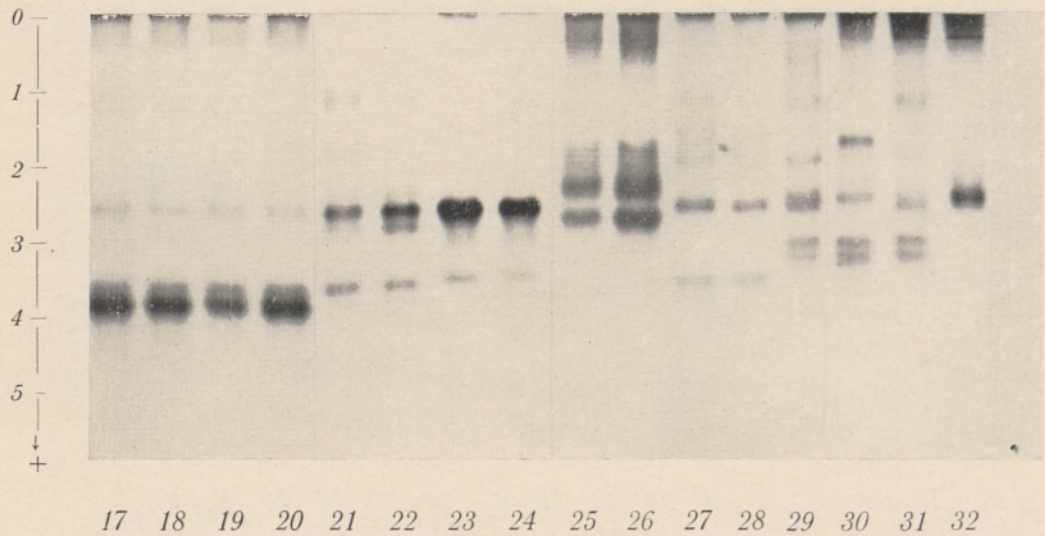


Fig. 4. Phosphatase enzymograms: *Elymus sibiricus* R 16/71 (*1—2*), *Elymus glaucus* RD-13 (*3—4*) and R 71/70 (*5—6*), *Elymus canadensis* RL 1/70 (*7—8*) and RD-10 (*9—10*), *Roegneria pauciflora* R 50/70 (*11—12*), RL 38/71 (*13—14*) and RL 7/70 (*15—16*), *Elymus dahuricus* LP 3/71 (*17—18*) and LP 4/71 (*19—20*), *Elymus tangutorum* R 69/71 (*21—22*), *Agropyron yezoense* R 8/72 (*23—24*), *Leymus arenarius* L 1/71 (*25—26*), *Elymus sibiricus* R 40/71 (*27—28*), *Elytrigia repens* L 17/72 (*29*), and L 20/72 (*30—31*), *Agropyron cristatum* RB 4/69 (*32*).

enzymogram of *R. ciliaris* (31—32 in Fig. 1), a Far-East Asian species, also having curved awns but morphologically more divergent from *E. sibiricus*, however, proved different from those previously considered by lacking the characteristic doublet of isoesterases at the D_m values 3.9 and 3.5.

In conclusion, the results presented in Fig. 1 show that a large group of Eurasian caespitose wheatgrass species and *E. sibiricus* L., the type species of the genus *Elymus* L., possess similar esterase electrophoretic patterns with two isoesterases in common to all taxa. Esterase enzymograms of the two wheatgrass species, *R. confusa* and *R. czimganica,* are essentially identical with those of *E. sibiricus.*

Enzymograms 1—10 in Fig. 2 compare esterases of the two North-American species of the genus *Elymus, E. glaucus* and *E. canadensis,* with those of the Asian species, *E. sibiricus.* It can be seen that, of the two diagnostic isoesterases at the D_m values 3.5 and 3.9 characteristic of *E. sibiricus* (enzymograms 1—2 in Fig. 2), the isoesterase at 3.5 is lacking in the North-American species, while the second isoesterase at 3.9 is, as a rule, less active than in Eurasian species or shows a shift in electrophoretic mobility.

The esterase enzymograms (11—16 in Fig. 2) of the North American slender wheatgrass *Roegneria pauciflora* (= *Agropyron trachycaulum*) proved very similar to or, in some cases, even essentially undistinguishable from those of the Canada wild-rye, *Elymus canadensis* (7—10 in Fig. 2). Indeed, esterase enzymograms of the North-American slender wheatgrass are more similar to those of the Canada wild-rye than to those of Eurasian caespitose wheatgrasses of the *Roegneria* group. Moreover, seedling esterase enzymograms (not presented) of the Virginia wild-rye, *Elymus virginicus,* proved to be identical with those of the Canada wild-rye, *E. canadensis.* These data provide a new evidence in favour of a close phylogenetic relationship between the North-American wild-ryes and the North-American caespitose wheatgrasses of the *Roegneria* group, the view which has been expressed by D. Dewey (1966a, 1967) on the basis of his cytogenetic studies of meiotic chromosome pairing in interspecific hybrids.

Esterase enzymograms of the North-American species can be considered as consisting of two groups of isoesterases. The first group consists of fast-moving isoesterases of the D_m values extending from 3.5 to 4.6. The isoesterases of this group are highly active in green or etiolated leaves of seedlings of some collections and appear in enzymograms (3—4, 7—10, 13—14 in Fig. 2) as a broad intensely stained zone which actually consists of several closely spaced isoesterase bands. However, not all wild-rye and wheatgrass collections possessed the ability to develop a high activity of fast-moving isoesterases in the leaf tissue (enzymograms 5—6, 11—12 and 15—16 in Fig. 2). In these cases esterase enzymograms of the leaf tissue remain similar to those of the stem tissue, and individual esterase isoforms could be better distinguished.

The second group of isoesterases possessing intermediate electrophoretic mobilities (D_m 2—3) also showed intraspecific variability in both the activity and electrophoretic mobility of individual isoesterases. The meaning of this variation remains to be elucidated.

Elymus dahuricus, a wild-rye species of Asian distribution pattern, revealed esterase enzymograms (17—20 in Fig. 2) different from all those considered above. The data presented exemplify significant differences in esterase enzymograms between different collections of *E. dahuricus* (s. lat.). This variation in isoesterase patterns, however, did not correspond with the division of *E. dahuricus* s. lat. into two morphological forms

previously related to separate linneons *E. dahuricus* s. str. and *E. excelsus* s. str.

Esterase enzymograms of *E. tangutorum* (21—22 in Fig. 2), a Central Asian species, reveal features of similarity to those of *E. dahuricus,* thus supporting previous indications (Цвелев, 1968) of a close phylogenetic relatedness of the two taxa based on the similarity of their morphological characters. It was, however, intriguing to find the esterase enzymogram of *A. yezoense* (23—24 in Fig. 2), a caespitose wheatgrass endemic in Japan, to be highly similar to that of *E. tangutorum.* Most isoesterases of the two species proved to be electrophoretically similar, thus indicating their genetic relatedness with several esterase loci in common. A more detailed study of esterase variation in the Far-East and Central Asian *Roegneria* species is in progress at present.

Enzymograms 25—32 in Fig. 2 compare seedling esterases of *Leymus arenarius* — the type species of the genus *Leymus*, of *Elymus sibiricus* — the type species of the genus *Elymus*, of *Elytrigia repens* — the type species of the genus *Elytrigia*, and of *Agropyron cristatum* — the type species of the genus *Agropyron* s. str. Considerable differences in the seedling isoesterase electrophoretic patterns of the type species of the four *Triticeae* genera are evident from the data. The two diagnostic isoesterases of *E. sibiricus* at the D_m values 3.9 and 3.5 are lacking in seedlings of other three type species. Esterase enzymograms of *Leymus arenarius*, *Elytrigia repens* and *Agropyron cristatum* are all divergent from each other as well as from those found for the wheatgrasses of the *Roegneria* group and for the wild-ryes of the genus *Elymus* s. str. From this evidence it clearly follows that the caespitose wheatgrass species of the *Roegneria* group which share the two diagnostic isoesterases, 3.9 and 3.5 in common with *E. sibiricus* are genetically divergent from the *Elytrigia* and *Eu-Agropyron* groups of the genus *Agropyron* Gaertn. s. lat. and, thus, should be preferentially treated as belonging to the genus *Elymus* L.

Acid phosphatases. Fig. 3 presents seedling phosphatase enzymograms of *Elymus sibiricus* L. as compared with those of Eurasian caespitose wheatgrasses referred to the genus *Roegneria* C. Koch. The data reveal general similarity of acid phosphatase enzymograms of *Elymus sibiricus* and of the *Roegneria* group wheatgrasses which all, as a rule, share two major isophosphatases characterized by the D_m values at about 3.6 and 2.8. The relative staining intensity of the two bands varied considerably, depending on the age and growth conditions of the seedlings. Occasionally, the band at 2.8 was lacking in seedlings of some collections. Variation among the taxa and accessions studied was observed in fractions of slower electrophoretic mobility with the D_m values ranging from 1.0 to 2.5. The intensity of this group of phosphatase bands was found to depend significantly on the seedling age and growth conditions, and their taxonomic value seems questionable.

Variation was also observed in the phosphatase band at the D_m value of about 4.0. Thus, in different collections of *R. canina* studied, the activity of this isophosphatase varied considerably — from a complete absence (enzymograms 5—6 and 14—15) to a dominant band (enzymograms 7—8). This isophosphatase band was lacking in the strains of *E. sibiricus* studied.

Three awnless (or short-awned) wheatgrasses known as *R. behmii*, *R. doniana* and *R. fibrosa* revealed highly similar phosphatase enzymograms with three major isophosphatases at 4.2, 3.6 and 2.8 in common. The seedling phosphatase patterns of the two curved-awned species, *R. czimganica* and *R. confusa,* are similar to those of *E. sibiricus* and *R. canina.* The third curved-awned species distributed in the far-east of Asia, *R. ciliaris*,

revealed the isophosphatase at the D_m 3.6 in common with other *Roegneria* species, but differed from them in possessing two closely spaced isophosphatase bands at the D_m values of about 2.6 and 2.4.

The North-American species, *E. glaucus*, *E. canadensis* and *R. pauciflora*, reveal overall similarity of their seedling acid phosphatase enzymograms (3—16 in Fig. 4) with those of *E. sibiricus* (enzymograms 1—2 in Fig. 4). The two isophosphatases at the D_m 3.6 and 2.8 characteristic of *E. sibiricus* as well as of Eurasian *Roegneria* species (see Fig. 3) were also present, although not always, in the seedlings of *E. glaucus* and *R. pauciflora* (enzymograms 3—4 and 11—16 in Fig. 4). The staining intensity of this isophosphatase band is low in enzymograms of *E. canadensis* presented in Fig. 4, and an isophosphatase of slightly higher electrophoretic mobility also encountered in seedlings of *E. glaucus* and *R. pauciflora* is evident. The isophosphatase band at 2.8 was also found in most collections studied, although its staining intensity varied considerably. It should be noted that the relative staining intensity of the individual isophosphatase fractions reflecting their activity varied considerably, depending not only on the collection studied but also on the seedling age and growth conditions, as well as on the pH of the reaction mixture for the histochemical stain. In addition, shifts in the electrophoretic mobility of isophosphatase bands from the standard values are evident from the data in Fig. 4.

Acid phosphatase pattern of *E. virginicus* (not presented) proved to be identical with that of *E. canadensis*, with major isophosphatase bands in common to both species.

Seedlings of *E. dahuricus* (s. lat.) were found (enzymograms 17—20 in Fig. 4), to contain the same major isophosphatases judging by the similarity of their electrophoretic mobilities, in common with other species of *Elymus* and *Roegneria* considered above. Enzymograms of *Elymus tangutorum* and *Agropyron yezoense* (21—24 in Fig. 4) were found to be of the same type.

Enzymograms 25—32 in Fig. 4 compare seedling acid phosphatase electrophoretic patterns of type species of four *Triticeae* genera — *Leymus arenarius* (L.) Hochst., *E. sibiricus* L., *Elytrigia repens* (L.) Desv. and *Agropyron cristatum* (L.) Beauv. Enzymograms of *Leymus arenarius* reveal two closely spaced major isophosphatase bands which are electrophoretically distinctly different from those characteristic of *E. sibiricus*. No isophosphatase band was found in common to the two species. This evidence strongly supports the removal from the genus *Elymus* L. of a group of species comprising the section *Psammelymus* Griseb. in Ledeb. with *Elymus arenarius* L. as the sectional lectotype into a separate genus *Leymus* Hochst. with *Leymus arenarius* (L.) Hochst. as the type species.

The three type species, *Elymus sibiricus*, *Elytrigia repens* and *Agropyron cristatum*, were found to share one isophosphatase band of similar electrophoretic mobility at about 2.8. They were, however, found to differ with respect to isophosphatases of higher electrophoretic mobility.

Discussion

The results of the present study derived from esterase and phosphatase electrophoretic patterns provide strong experimental evidence in support of the view expressed by S. Nevski (Невский, 1933, 1941), N. Tzvelev (Цвелев, 1964, 1968, 1970, 1972) and D. Dewey (1966, 1967) that the caespitose wheatgrass species attributed by S. Nevski to the genus

Roegneria C. Koch are phylogenetically much more closely related to the genus *Elymus* L. s. str. than to the wheatgrasses grouped in the genera *Agropyron* Gaertn. s. str. and *Elytrigia* Desv., and, thus, should be taxonomically treated as belonging to the genus *Elymus* L. s. lat. On the basis of esterase electrophoretic patterns, the species of *Elymus* L. s. str. and *Roegneria* C. Koch studied were found to form three major clusters of genetically closely related species which can be taxonomically treated as sections of the genus *Elymus* L. s. lat., involving the taxa studied as follows:

1. Section *Elymus*, involving *E. sibiricus* L. (type species), *E. confusus* (Roshev.) Tzvel., *E. czimganicus* (Drob.) Tzvel., *E. caninus* (L.) L. var. *caninus*, *E. caninus* var. *behmii* (Meld. in Hyl.) Jaaska (comb. nov.), *E. caninus* var. *donianus* (F. B. White) Jaaska (comb. nov.), *E. fibrosus* (Schrenk) Tzvel., *E. kronokensis* (Kom.) Tzvel. var. *borealis* (Turcz.) Tzvel., *E. kronokensis* var. *alascanus* (Scribn. et Merr.) Jaaska (comb. nov.), *E. transhyrcanus* (Nevski) Tzvel.

2. Section *Turczaninovia* (Nevski) Tzvel., 1968, involving *Elymus dahuricus* Turcz. ex Griseb., s. lat. (type species), *E. tangutorum* (Nevski) Hand.-Mazz., *E. nipponicus* Jaaska (nom. nov.), *E. ciliaris* (Trin.) Tzvel.

3. Section *Macrolepis* (Nevski) Jaaska, comb. nov., (basionym: gen. *Clinelymus* Nevski, sect. *Macrolepis* Nevski, 1932, in Bull. Jard. Bot. Acad. Sci. URSS, 637), based on the type species *E. canadensis* L. includes *E. trachycaulus* (Link) Gould et Shinners and *E. virginicus* L.

The most important synonymy for the taxa considered is given in the chapter "Material and methods" of the present paper.

Our data derived from esterase enzymograms give no reason to separate the wheatgrass species grouped by S. Nevski (1934) in the section *Cynopoa* Nevski of the genus *Roegneria,* such as *Elymus caninus* (=*R. canina*), *E. kronokensis* (= *R. borealis*) and *E. fibrosus* (= *R. fibrosa*), from the section *Elymus* of the genus *Elymus* for which *E. sibiricus* is the type species neither into the section *Turczaninovia* (Nevski) Tzvel. (Цвелев, 1968) nor into the section *Goulardia* (Husn.) Tzvel. (Цвелев, 1970).

The subdivision of the enlarged genus *Elymus* L. s. lat. presented above should be considered only as a tentative one, and further more detailed studies of additional taxa are expected to add important adjustments. Thus, our preliminary study of a single collection of the type species of the genus *Roegneria*, *R. caucasica* C. Koch, from Armenia, has revealed its esterase electrophoretic pattern to be qualitatively distinct from any of the three types of esterase enzymograms reported in the present study. More detailed study is needed to decide conclusively if *R. caucasica* should be maintained in the genus *Roegneria* or should be included in a separate section of the genus *Elymus* L. The same problem has arisen from the preliminary investigation of *Roegneria panormitana* (Bertol.) Nevski and *Elymus nutas* Griseb. whose esterase patterns were also found to be different from those of *Elymus sibiricus* L.

No firm conclusion has been reached with respect to the position of *Elymus ciliaris* (Trin.) Tzvel., syn. *Roegneria ciliaris* (Trin.) Nevski, in the system of the genus *Elymus* L. Extensive cytogenetic studies of S. Sakamoto (Sakamoto, 1964; Sakamoto, Muramatsu, 1966) have demonstrated a high degree of homology of the tetraploid genomes of *Agropyron ciliare* (Trin.) Franchet and *Agropyron yezoense* Honda. Our electrophoretic enzyme studies, however, revealed considerable genetic differences between a stain of *A. ciliare* from the Primorsk Krai and a Japanese strain of *A. yezoense*. These differences may result from intraspecific enzyme

variation which remains to be elucidated for the two species. Since esterase and phosphatase enzymograms of *Agropyron yezoense* proved highly similar to those of *Elymus tangutorum*, we are inclined to involve the two Far-East wheatgrass species in the section *Turczaninovia* (Nevski) Tzvel. of the genus *Elymus* L. as *E. nipponicus* Jaaska (=*A. yezoense*) and *E. ciliaris* (Trin.) Tzvel. (=*A. ciliare*).

The North-American wild-rye species, *E. virginicus* L. has been separated by S. Nevski (Невский, 1932) in the genus *Terrella* Nevski as *Terrella virginica* (L.) Nevski. Although this species, indeed, is morphologically different from the Canada wild-rye, *E. canadensis* L., esterase and phosphatase enzymograms of the two species proved highly similar, providing no evidence of considerable genetic differences in their genomes. Our data, thus, do not support a separation of *E. virginicus* in the genus *Terrella* Nevski, and they also provide no evidence for its placing in a separate section *Terrella* (Nevski) L. and L., as it was proposed by A. Löve and D. Löve (1961). Instead, our results suggest a close similarity of genomes of *E. virginicus* L. and *E. canadensis* L., despite the existing differences between them in certain characters of external morphology. This is in one line with the results of cytogenetic studies by C. Church (1958), who has produced vigorous, although sterile, F_1 plants from crosses between *E. canadensis* and *E. virginicus* with essentially normal meiotic division and chromosome pairing. Similar data have also been reported by W. Brown and G. Pratt (1960). The cytogenetic and biochemical data, thus, support the preferential inclusion of the two taxa in the same section of the genus *Elymus* L.

Considerable disagreement exists concerning the place of the North-American blue wild-rye *E. glaucus* Buckl. in the system of the genus *Elymus* L. It has been placed by S. Nevski (Невский, 1932) in a separate section, *Strictisetum* Nevski, of his genus *Clinelymus* Nevski, while W. Bowden (1964) included it in the same section with *E. sibiricus* L. A wide range of variability in morphological characters accompanied by the existence of intraspecific genetic barriers of various extent has been reported (Snyder, 1950) for this species. With respect to the position of *E. glaucus* in the genus *Elymus*, our data proved inconclusive, due to observed variation in the enzyme patterns of the two accessions available, indicating the need for a more detailed study.

The genus *Elymus* L. in the classical sense is treated by many systematists (Bowden, 1964; Hitchcock, Chase, 1951, etc.) as including the North-European littoral species *E. arenarius* L. s. str. and its relatives grouped in the section *Psammelymus* Griseb. in Ledeb., as well as several North-American species, such as *E. triticoides* Buckl., *E. cinereus* Scribn. et Merr. and some other related taxa. Our data which demonstrate distinctness of both esterase and phosphatase enzymograms of *E. arenarius* from those of *E. sibiricus, E. dahuricus* and *E. canadensis* which represent sectional lectotypes of the genus *Elymus* L., support its removal from the genus *Elymus* in a separate genus *Leymus* Hochst. as *L. arenarius* (L.) Hochst. Similarly, our preliminary studies have revealed that esterases and phosphatases of *E. cinereus* and *E. triticoides* differ distinctly from those characteristic of the three sectional lectotype species of the genus *Elymus*, while being electrophoretically much more similar to those of *Psathyrostachys juncea* (Fisch.) Nevski. This is in agreement with the results of recent cytogenetic studies by D. Dewey (1970a), whose data suggest that the tetraploid genomes of *E. triticoides* and *E. cinereus* involve a composite genome which is closely homologous with the diploid genome of *Psathyrostachys juncea*. At the same time, the composite genomes of

E. canadensis were found (Dewey, 1966b, 1970b) to be distinctly different from those of *E. triticoides* and *E. cinereus* with little if any chromosome homology. The available cytogenetic and biochemical data, thus, seem to argue in favour of a removal of *E. triticoides* and *E. cinereus* from the genus *Elymus* L. either into the genus *Leymus* Hochst. s. lat. or into the genus *Psathyrostachys* Nevski. The latter point, however, remains to be specified.

Enzyme electrophoretic patterns proved unsuitable for the delimitation of the species level in the genus *Elymus*, and only clusters of phylogenetically related species and taxa could be distinguished according to the data. When treating the two endemic wheatgrass taxa, *Roegneria behmii* Meld. and *Roegneria doniana* (F. B. White) Meld. as reduced to a variety level of *E. caninus* (L.) L., we proceeded from the recent important investigation of B. Nordenstam (1972). *Roegneria behmii* Meld. — a rare local endemic known from a single population in Central Sweden was found (Nordenstam, 1972) to form fertile natural hybrids of morphologically intermediate type with occasional individuals of *Elymus caninus* (L.) L. in the same population. It seems possible that awnless and short-awned, narrowly endemic forms of *Roegneria* described as *R. behmii* in Sweden, *R. doniana* in Scotland, *R. doniana* var. *stefanssonii* in northern Iceland and *R. doniana* var. *virescence* in southern Greenland (Melderis, 1950) might have arisen autochthonically from local forms of *E. caninus* s. str. as a result of independent mutational events and were maintained as local populations due to the domination of self-pollination combined with the founder effect. Indeed, some collections of *E. caninus* s. str. were characterized by esterase enzymograms undistinguishable from those found for the two local endemics. It is thus suggested that *E. caninus* var. *behmii*, *E. caninus* var. *donianus* and similar taxa are neoendemics of post-Pleistocene origin, which have not yet reached the species level of evolutionary development rather than archaic remnants of the mesophytic Tertiary flora which have survived the Pleistocene glaciations in local refugia.

Although significant intraspecific variation in some seedling esterases was found among geographically different populations of *E. caninus*, the extent of the observed variation within the limits of the section *Elymus* consisting of species distributed over the whole Eurasian continent was astonishingly low. Thus, the two collections of the short-awned Arctic species *E. kronokensis* s. lat. (= *R. borealis* s. lat.), one from northern Sweden (var. *borealis*) and the other from Kamtchatka (var. *alascanus*), proved indistinguishable by their esterase enzymograms. *Elymus sibiricus*, *E. confusus* and *E. czimganicus* were found to possess highly similar seedling esterases.

Only a limited genetic variation in isoesterases was observed among individuals of the same local population of *E. caninus*, although differences between geographically isolated populations were more pronounced. This is in sharp contrast with the extensive intrapopulational genetic polymorphism of the same enzyme, esterase, previously found (Jaaska, 1972) in the wheatgrass species of the *Elytrigia* group — *Agropyron intermedium* (Host) Beauv.

Of special interest is the result that the three major phylogenetic groupings established in the genus *Elymus* on the basis of seedling esterase enzymograms are of a distinct phytogeographic distribution pattern. The boreal species of predominantly Eurasian distribution form the section *Elymus* which is differentiated from the North-American boreal species referred to the section *Macrolepis* by genes controlling seedling

esterases. The third section, *Turczaninovia*, involves species distributed in East and Central Asia.

The observed distinct hiatus between the North-American and Eurasian sections of the genus *Elymus*, both involving species distributed over wide continental territories, in the esterase genes suggests prolonged independent evolution within the two groups. This has presumably resulted from the breaking up of the Bering landbridge which has led to phytogeographical isolation of the two continents. Thus, it seems probable that contemporary species of *Elymus* have arisen autochthonically on each continent as a result of independent differentiation and speciation events.

The species of both sections are known to be exlusively tetraploid plants. Two alternative hypotheses about their independent origin on each continent can be suggested: (i) origin from different diploid precursors as a result of independent polyploidisation events, or (ii) differentiation from a common tetraploid precursor.

Recent cytogenetic studies of D. Dewey (1968) have shown that the North-American *Elymus canadensis* can successfully be crossed with the European species *Elymus caninus* to form viable hybrids of a morphologically intermediate type which, although sterile, show fairly good chromosome pairing. The data show that both genomes of *E. canadensis* are closely homologous with those of *E. caninus*. Overall similarity in seedling acid phosphatase enzymograms of all sections of the genus *Elymus* also suggests that divergence of the basic genomes has not been very extensive and that they have retained considerable homology.

Available evidence seems to favour the hypothesis according to which contemporary species of the genus *Elymus* have been diverged autochthonically on each continent from genetically more closely related tetraploid precursors, which, presumably, have arisen from the diploids before the breaking up of the Bering landbridge and were members of the Mesophytic forest flora widely distributed on both continents in the Late Cretaceous and Early Tertiary.

Summary

Polyacrylamide gel electrophoretic patterns (enzymograms) of seedling esterase and phosphatase show that a large group of caespitose wheatgrass species previously referred to the genus *Roegneria* C. Koch sensu Nevski are phylogenetically much more closely related to the genus *Elymus* L. s. str. than to the wheatgrasses of the genera *Agropyron* Gaertn. s. str. and *Elytrigia* Desv. On the basis of esterase enzymograms, the species of *Elymus* L. s. str. and *Roegneria* C. Koch studied were found to fall into three major clusters of phylogenetically closely related species which were taxonomically treated as sections of the genus *Elymus* L. The basic section *Elymus* with *E. sibiricus* L. as type species involves Eurasian boreal wheatgrass species such as *E. confusus* (Roshev.) Tzvel., *E. czimganicus* (Drob). Tzvel., *E. caninus* (L.) L. s. lat., *E. fibrosus* (Schrenk) Tzvel., *E. kronokensis* (Kom.) Tzvel. s. lat. and *E. transhyrcanus* (Nevski) Tzvel. The North-American boreal species *E. virginicus* L. and *E. trachycaulus* (Link) Gould et Shinners, together with *E. canadensis* as the sectional type, are regarded in the section *Macrolepis* (Nevski) Jaaska, comb. nov. The section *Turczaninovia* (Nevski) Tzvel. with *E. dahuricus* Turcz. ex Griseb. s. lat. as type species combines *E. tangutorum* (Nevski) Hand.-Mazz., *E. nipponicus* Jaaska, nom. nov. and *E. ciliaris* (Trin.) Tzvel.

Electrophoretic enzyme data substantiate the removal from the classical genus *Elymus* L. of a part of species in the genus *Leymus* Hochst. s. lat.

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ENSÜÜMIDE VARIEERUVUS JA FÜLOGENEETILISED SEOSED KÕRRELISTE PEREKONDADES *AGROPYRON* GAERTN. JA *ELYMUS* L.
II. Perekond *ELYMUS* L.

Resümee

Idandite esteraasi ja happelise fosfataasi polüakrüülamiidgeelelektroforeetilise uurimise andmed (ensümogrammid) näitavad, et suur rühm orasheina liike, mis seni olid koondatud perekonda *Roegneria* C. Koch sensu Nevski, on märksa lähemas fülogeneetilises suguluses perekonnaga *Elymus* L. s. str. kui perekondadega *Agropyron* Gaertn. s. str. ja *Elytrigia* Desv. Esteraasi ensümogrammide alusel jagunesid uuritud *Elymus* L. s. str. ja *Roegneria* C. Koch liigid kolme põhilisse fülogeneetilisse liikide rühma, mida käesolevas töös käsitletakse perekonna *Elymus* L. sektsioonidena.

Tüüpliigil *E. sibiricus* L. baseeruv põhisektsioon *Elymus* hõlmab *Euraasia* boreaalseid orasheinaliike *E. confusus* (Roshev.) Tzvel., *E. czimganicus* (Drob.) Tzvel., *E. caninus* (L.) L. s. lat., *E. fibrosus* (Shrenk) Tzvel., *E. kronokensis* (Kom.) Tzvel. s. lat. ja *E. transhyrcanus* (Nevski) Tzvel. Sektsioon *Macrolepis* (Nevski) Jaaska, comb. nov., mis on loodud tüüpliigi *E. canadensis* L. baasil, hõlmab Põhja-Ameerika boreaalseid liike *E. virginicus* L. ja *E. trachycaulus* (Link) Gould et Shinners. Sektsiooni *Turczaninovia* (Nevski) Tzvel., mille aluseks on tüüpliik *E. dahuricus* Turcz. ex Griseb. s. lat., koondati Kesk-Aasias ja Kaug-Idas levinud liigid *E. tangutorum* (Nevski) Hand.-Mazz., *E. nipponicus* Jaaska, nom. nov. ja *E. ciliaris* (Trin.) Tzvel.

Ensüümide elektroforeetilise uurimise tulemused kinnitavad seisukohta, et perekonnast *Elymus* L. tuleb osa liike üle viia perekonda *Leymus* Hochst. s. lat.

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Велло ЯАСКА

ИЗМЕНЧИВОСТЬ ФЕРМЕНТОВ И ФИЛОГЕНЕТИЧЕСКИЕ СВЯЗИ В РОДАХ ЗЛАКОВ *AGROPYRON* GAERTN. И *ELYMUS* L.
II. Род *ELYMUS* L.

Резюме

Сравнительное изучение эстеразы и кислой фосфатазы проростков методом электрофореза в полиакриламидном геле показало, что большая группа дернистых пыреев, ранее отнесенных к роду *Roegneria* C. Koch sensu Nevski, филогенетически намного ближе к роду *Elymus* L. s. str., чем к пыреям родов *Agropyron* Gaertn. s. str. и *Elytrigia* Desv. По энзимограммам эстеразы изученные виды *Elymus* L. s. str. и *Roegneria* C. Koch (sensu Nevski) подразделялись на три основные группы филогенетически близкородственных видов, которые были признаны как секции рода *Elymus* L. Основная секция *Elymus* с *E. sibiricus* L. в качестве типа включает бореальные виды Евразии

E. confusus (Roshev) Tzvel., *E. czimganicus* (Drob.) Tzvel., *E. caninus* (L.) L. s. lat., *E. fibrosus* (Schrenk) Tzvel., *E. kronokensis* (Kom.) Tzvel. s. lat. и *E. transhyrcanus* (Nevski) Tzvel. Североамериканские бореальные виды *E. virginicus* L. и *E. trachycaulus* (Link) Gould et Shinners вместе с *E. canadensis* L. в качестве типа включены в секцию *Macrolepis* (Nevski) Jaaska, comb. nov. В секцию *Turczaninovia* (Nevski) Tzvel. с типом *E. dahuricus* Turcz. ex Griseb. S. lat. включены *E. tangutorum* (Nevski) Hand.-Mazz., *E. nipponicus* Jaaska, nom. nov. и *E. ciliaris* (Trin.) Tzvel.

Электрофоретические признаки эстераз и фосфатаз проростков подтверждают обоснованность выделения из классического рода *Elymus* L. части видов в род *Leymus* Hochst. s. lat.

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