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THE CHALLENGE OF A SIBERIAN BLUEGRASS (*POA*) PHYLOGENY

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ABSTRACT

In Siberia, the bluegrass genus (*Poa*) comprises 43 species and 61 subspecies in 12 sections. Diverse modes of speciation, including polyploidy and hybridization, have led to reticulate evolution and adaptive radiation. Cladistic methods that ignore hybridization and reticulate evolution may not be appropriate for morphological data. The number of morphological characters suitable for bluegrass analysis is limited, a majority does not have clear adaptive significance, and the character states cannot be readily polarized, rendering phylogenetic reconstruction very difficult in this group. Other methods of estimating phylogenetic relationships should be used to test hypotheses about relationships and hybridization. Biochemical and molecular data, as well as karyological, phytogeographical, and other lines of evidence should be combined to establish an explicit and testable hypothesis of the sequence of character state changes acquired during biotic differentiation.

Key words: cladistics, morphology, phylogeny, *Poa*, Poaceae, Siberia, speciation.

INTRODUCTION

Poa L. (bluegrass) is one of the largest and most polymorphic genera of the Siberian flora, credited with between 35 and 84 species, depending on the source. For the purpose of this paper, I distinguish 43 species and 61 subspecies in 12 sections (Olonova 1998). *Poa* plays a vital part in Siberian phytocenoses [plant associations] and is economically important, for example, for grazing livestock. Research on the evolution of this genus over the vast territory of Siberia, an area of some 10 million square kilometers, would make a contribution both to grass taxonomy as a whole and to floristic studies of this region. The variable number of accepted species reflects mainly the differential interpretation of microspecies by different authors. There are both monomorphic and polymorphic species that contain numerous chromosomal races and generate hybridizing apomictic complexes; there are old and young species; and there are relatively few diploids. The genus is well represented in Russia, and 12 of the 14 sections growing in Eurasia (Tzvelev 1976; Edmondson 1978) are present in Siberia. Therefore, the Siberian material is suitable for preliminary phylogenetic reconstructions.

The goal of this research was to formulate preliminary hypotheses concerning the taxonomy and phylogeny of *Poa* in Siberia, and to provide a testable framework for more detailed future work using modern analytical methods. A second goal was to determine whether cladistic methods can be used for Siberian bluegrass phylogeny reconstruction using morphological characters.

For the reconstruction of scenarios of evolution, taxonomists use a range of methods, but an analysis of the recent literature reveals an increasing number of articles devoted to the construction of phylogenetic hypotheses using cladistic methods. Cladistic methodology was proposed by Hennig (1966) as a means of relationship estimation that is not only dependent on formal morphological similarity, as evaluated by phenetic methods (Baum 1987; Barkworth 1992), but also takes into account the initial (plesiomorphic) and derived (apomorphic) states of characters. The cladistic approach

has come to enjoy a high degree of popularity among taxonomists due to its significant advantages: characterized by logical rigor, it simplifies the creation of algorithms essential for computer-based data analysis, allowing us to consider a large number of attributes and to analyze large numbers of taxa. Molecular analysis of large data sets would be impossible without the use of computer programs. Nonetheless, this approach suffers from some disadvantages: specifically, the classic model of Hennigian cladistics recognizes only dichotomous branching but ignores hybridization and evolutionary or adaptive radiation. It reduces all the diverse paths of speciation that exist in nature to a bifurcating model that postulates the termination of the parental lineage as a result of the formation of two new ones (Pavlinov 1996; Baykov 1999). Successful application of cladistics is believed to require a large number of characters, including—whenever possible—those that are morphologically qualitative. The greater the number of characters, and the more states expressed within them, the better the chance of correctly recognizing homologies.

MATERIALS AND METHODS

The present study was based on herbarium specimens that were studied at KW, LE, MHA, MW, NS, NSK, SSBG, TK, and VLAD or borrowed from LD, O, UPS, and US.

Collecting expeditions and population studies of the most difficult species were made in the following Siberian provinces: Altai, Baikal, Dauria, Kolyma, Kuznetsk Alatau, and Sayan. The taxonomic study was based on classical morpho- and phenogeographical methods. Cluster analysis was used for the preliminary bluegrass phylogeny. Ward's method (1963) is known to maximize the differences between clusters, while minimizing the differences within clusters, making this method more suitable than others dealing with complex reticulate relationships (Duran and Odell 1977; Weir 1995). The characters used in this analysis are listed in Table 1. Hypotheses on putative evolution within sections were based on a preliminary assessment of species variability and distribution and on available chromosome numbers.

Table 1. Characters and character states used in the cluster analysis.

(1) Life form	(a) rhizome (b) tufted
(2) Bulb on the base culm	(a) present (b) absent
(3) Sheath margin fusion	(a) 2/3–5/6 of the length (b) 1/4–2/3 of the length (c) <1/4 of the length
(4) Surface of rachilla	(a) smooth or scabrid (b) hairy
(5) Lemma callus	(a) without tuft of hair (b) with tuft of hair
(6) Surface of lemma on keel and marginal vein	(a) with hairs (b) without hairs
(7) Surface between lemma veins	(a) smooth (b) hairy
(8) Surface of palea keels	(a) mostly with hairs (b) with prickles only (c) scabrid only
(9) Anther length	(a) <1 mm (b) >1 mm

RESULTS AND DISCUSSION

The study of Siberian bluegrass based on classical methods (e.g., Olonova 1992, 1993) has shown that the evolutionary vectors (describing the series from the most plesiomorphic to the most apomorphic character) conventionally used for cladistic analysis of morphological data can be satisfactorily determined only for sect. *Stenopoa* Dumort. Evolution within this section mainly took the path of progressive xeromorphogenesis (Fig. 1) and accordingly the sequence of adaptive characters is well defined. Sequential changes are detailed for three morphological and five anatomical characters:

Changes in gross morphology:

- upper culm nodes gradually becoming lower on the stem; the most xeromorphic samples having the upper node at the base of stem
- panicles becoming narrower, which is caused in part by the shortening of branches and in part by a reduction in the angle of divergence from the rachis
- leaf blades becoming narrower and their length decreasing relative to that of the sheath

Changes in anatomical structure:

- increasing numbers of samples with trichomes on the epidermis

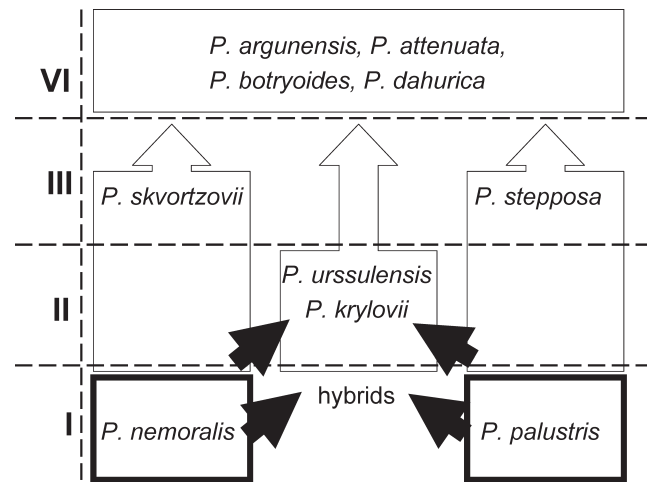


Fig. 1. Probable relationships among Siberian species of bluegrass (*Poa*) in sect. *Stenopoa*. Roman numerals I–IV refer to levels of xeromorphy (see text for details).

(b) decreasing vein number

(c) increasing amount of sclerenchyma above veins in the leaf blade, making the vein outline appear beaded when viewed in cross-section

(d) decreasing length of the long cells in intercostal areas

(e) increasing waviness [undulation] of the long cell walls

Adaptations in *Poa* sect. *Stenopoa*

Two branches of evolution are recognized in *Poa* sect. *Stenopoa*, originating from *P. nemoralis* L. and *P. palustris* L., respectively (Fig. 1). These evolutionary branches, in their ancestral species, differ in rachilla pubescence and ligule length. In addition, all species in this section can be assigned to one of four xeromorphy levels that best reflect their expression of xeromorphic features. Levels 1 through 4 exhibit progressively stronger degrees of xeromorphy (see Olonova 2007; Fig. 1), with the upper node position serving as the main marker for a given xeromorphy level. The two species at the first level, *P. nemoralis* and *P. palustris*, have interhybridized. Some of their resulting hybrids are comparable to their parents in degree of mesomorphy and hence placed in the first level. Other hybrids, in the course of adapting to dry environments, developed xeromorphic features and are found at the second level, yet still combine the characteristics of both Level-I parents. Hybrids assigned to the second level are *P. krylovii* Reverd. and *P. urssulensis* Trin. The third xeromorphy level includes only a few species; the two Siberian species at this level are *P. skvortzovii* Prob. and *P. stepposa* (Krylov) Roshev., representing xeromorphic derivatives of *P. nemoralis* and *P. palustris*, respectively. They are closely related both to one another and to the species of the second and fourth levels. All species of the most xeromorphic fourth level (*P. argunensis* Roshev., *P. attenuata* Trin., *P. botryoides* (Trin. ex Griseb.) Kom., and *P. dahurica* Trin.) likely result from hybridization among species from the two branches.

Poa nemoralis and *P. palustris* are viewed as the most ancient of the extant species in sect. *Stenopoa* in Siberia and contain numerous chromosomal races. An abundance of

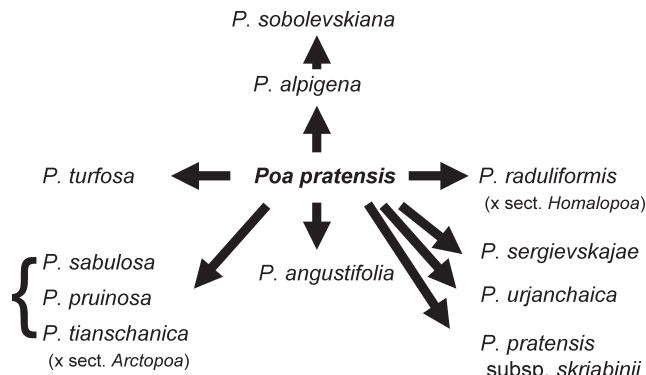


Fig. 2. Probable relationships among Siberian species of bluegrass (*Poa*) in sect. *Poa*.

chromosomal variation and polymorphism is presumably caused by hybridization and apomixis.

Character changes resulting from adaptation to increasingly xeromorphic habitats have been gradual in all species, rendering identification of the apomorphic state practically impossible. For instance, the character states exhibited by the xeromorphic species are already discernible in relatively mesomorphic species when grown in similarly xeromorphic conditions. This may be caused partly by phenotypic plasticity and partly by genetic variation within populations. At the same time, it is possible that the mesomorphic species (*P. nemoralis* and *P. palustris*), which are placed as the basal species in this system and are seen as giving rise to two evolutionary branches, may have undergone their own adaptive processes. They differ markedly from reputedly primitive ancestral species, which—according to Tzvelev (1972)—originated in the high mountains during the Tertiary period. Now *P. nemoralis* and *P. palustris* form apomictic complexes consisting of numerous chromosomal races (Olova 2000, 2001).

Hybridization processes are highly advanced in this section. Evolution, seemingly, has progressed at the tetraploid and hexaploid levels (Probatova 1991, 2007), which appear to be optimal for hybridization. These processes supposedly began in the Pleistocene and caused the blurring of boundaries between the species. The processes of hybridization discourage the use of cladistic methodology to infer phylogenetic relationships.

Adaptations in Poa sect. Poa

The evolution of the second largest Siberian section, *Poa* sect. *Poa* (Fig. 2), resembles that of mesomorphic species of sect. *Stenopoa*. Morphological analysis, field observation, and the available karyological data suggest that sect. *Poa* has undergone adaptive radiation and frequent hybridization.

Poa pratensis L., a very polymorphic and widely distributed species that has numerous chromosomal races and forms apomictic complexes, forms the nucleus of this group (Fig. 2). *Poa alpigena* (Blytt) Lindm. is likely to be its polyploid derivative, secondarily adapted to the high mountains and arctic tundras. One of the isolated populations of *P. alpigena* was described as *P. sobolevskiana* Gudoschn.

The second wave of adaptive evolution resulted in the formation of the xeromorphic species *P. angustifolia* L., a third

formed *P. sergievskajae* Prob., which has adapted to birch woodlands, a fourth wave formed *P. turfosa* Litv., adapted to peat bogs, and *P. pratensis* subsp. *skrjabinii* Tzvelev is the result of adaptation to sandy substrate. The tendency of this section to produce species via hybridization has been of great significance for its evolution. *Poa raduliformis* Prob., *P. sergievskajae*, and *P. urjancaica* Roshev. are thought to be of hybrid origin. *Poa tianschanica* (Regel) Hack. ex O.Fedtsch., *P. pruinosa* Korotky, and probably *P. sabulosa* (Roshev.) Turcz. ex Roshev. appear to be the result of hybridization of the ancient populations of *P. pratensis* with members of the closely related genus *Arctopoa*.

A characteristic feature of most of the species in sect. *Poa* is their ability to grow under conditions of mild salinity. This property is rather rare in bluegrass as a whole, although it is also common in *Arctopoa* species.

These examples are evidence that hybridization is not unusual in this section and, consequently, cladistic analysis is not applicable to this group either, though some estimates of relationships among species can be made.

Species in the remaining ten sections of Siberian *Poa* exhibit insufficient variation to formulate hypotheses of relationships among these species.

The Challenge of Poa

Bluegrass has few characters suitable for analytical use because *Poa* species, like all grass species, constitute a highly specialized and streamlined group. The structure of their reproductive, and especially vegetative parts, is essentially invariant and yields few morphological character states. Moreover, a character state such as pubescence may be governed by several genes and may have evolved for very different reasons. As a result, if we compare two species having pubescence between lemma veins, it is practically impossible to establish whether the species inherited this state from a shared ancestor, whether the character arose independently as a result of homoplasious mutations, or whether it was introduced via introgressive hybridization with other species that have a completely different ancestry. Therefore, if we compare two species that have character states in common, we cannot treat these shared characteristics as resulting from the same evolutionary event. A step-by-step analysis of this group and the use of cladistic analysis for the reconstruction of phylogeny at the species level are thus very problematic.

As the number of analytical methods expands and as cladistic methodologies become more flexible, these difficulties will be overcome. Noteworthy is the SYNAP method (Baykov 1999) that is based on the Median Elimination Series (MES) method (Li 1990). It takes better account of the peculiarities of plant speciation than its predecessors, and makes provision for a much broader spectrum of processes, including speciation other than by simple bifurcation. Computer algorithms for the reconstruction of evolutionary trees developed by Posada and Crandall (2002) and Legendre and Makarenkov (2002) take into consideration reticulate evolution. For now, however, genus *Poa* cannot be legitimately studied via formal cladistic analysis of morphological characters, mainly due to hybridization and reticulate evolution.

The question of relationships within the sections of *Poa*—at least those in Siberia—basically can be resolved, whereas

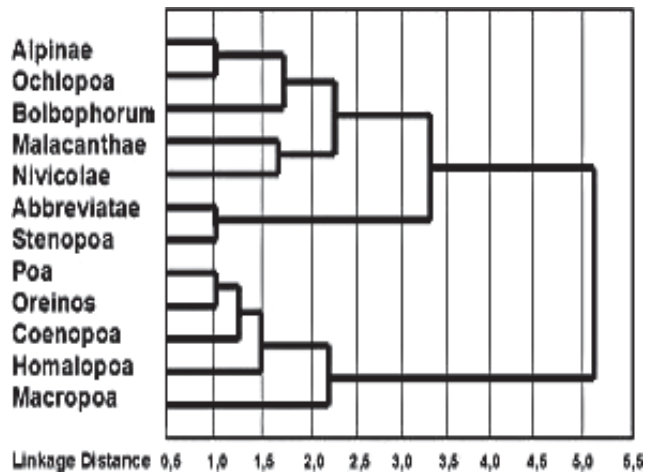


Fig. 3. Phenogram of the Siberian sections of *Poa* (Ward's method [1963], Euclidian distance).

relationships among sections are much more difficult to unravel. Following the scenario proposed by Tzvelev (1974), genus *Poa* arose in the high mountains (i.e., above the timberline or in alpine habitat), followed by dispersal from these higher elevations to all other zones and mountain belts. Today, almost all extant species, having adjusted to all kinds of environmental extremes, are to some degree or other specialized. Morphological studies and the available data on chromosome numbers allow us to assume an adaptive radiation in genus *Poa* and to assign its sections to only two or three evolutionary levels, depending on whether the characters in their member species are more ancient or more advanced. Following this system, sections *Stenopoa*, *Poa*, and probably *Homalopoa* and *Macropoa*, presumably each having a hybrid origin, belong to the more advanced level.

In the current phase of investigation, the problem is thus not in reconstructing a phylogenetic species tree for the whole Siberian bluegrass group, but in establishing the relationships among sections. There are no clear-cut directions of evolution discernable here, and affinities cannot be inferred from the available morphological characters.

Initial Progress Toward a Phylogenetic Understanding

While the abovementioned obstacles do not allow application of cladistic analysis based on the sum of morphological characteristics to this group, it is nevertheless possible to take some initial steps in the direction of a phylogenetic understanding of the genus and to try to determine possible relationships between sections using other methods, notably cluster analysis (Weir 1995). Such an approach differs from the phenetic one employed by Barkworth (1992), in which a small number of characters was used to generate preliminary phenograms that could then be used as the basis for further reconstruction of the phylogeny by taking into account ecological and karyological data.

Nine characters were chosen, collectively represented by 20 states conventionally used for the characterization of sections (Table 1). Diagrams and a distance matrix were constructed from a matrix of character states. The phenogram produced using Ward's method (1963) shows the degree of morphological similarity among sections (Fig. 3).

Comparison of the preliminary phenogram with the system proposed by Tzvelev (1976), who used classical methods, and with the cladogram produced by Gillespie and Boles (2001) using molecular (chloroplast DNA) characters, reveals similar relationships for many groups. In particular, sects. *Alpinae*, *Bolbophorum* and *Ochlopoa* are united in the same cluster, and sects. *Abbreviatae* and *Stenopoa* also form a cluster.

However, there are also some points of disagreement, which in this phase of my investigation are likely explained by an insufficient number of characters involved in the analysis. There are numerous other characters that might be used (e.g., epidermal characters and the surface microstructure of pollen grains and stamens), but these need further study. Preliminary data on distinctions between sections based on these anatomical characters have been gathered, but at present the sampling is insufficient to allow for their use in the analysis. Increasing the number of additional attributes will raise the accuracy of the analysis and will lower the risk of artifactual coincidence. Better methods of data processing and inclusion of species from other localities could improve the results as well. The system of bluegrasses constructed recently (Gillespie and Soreng 2005; Gillespie et al. 2007) is a splendid example of how classical morpho-geography and molecular genetics can be combined to reconstruct a phylogeny.

CONCLUSION

In summary, it is possible to conclude that:

- (1) Bluegrass (*Poa*) exhibits diverse modes of speciation, including polyploidy and hybridization; reticulate evolution and the application of cladistic methods to morphological data therefore may not be valid, at least at the species level.
- (2) Phylogenetic reconstruction based on morphological characters in pooid grasses suffers from a limited number of characters suitable for analysis; a majority of morphological characters cannot be polarized and does not have clear adaptive significance.
- (3) Hypotheses about phylogenetic relationships and hybridization should be tested using biochemical and molecular data, as well as karyological, phyto-geographical and other available lines of evidence.
- (4) A system of relationships among taxa constructed in this manner utilizes available methods in an attempt to establish an evolutionary scenario, recreated by a stepwise sequence of modifications during biotic differentiation, and to provide an explicit and testable hypothesis of relationships.

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This article is the English version of a similar Russian article by the same author, published in *Botanicheskii Zhurnal* **91**(2): 297–306 (2006), Problema filogenii festukoidnykh zlakov na primere roda *Poa* [the problem of a phylogeny of festucoid grasses with genus *Poa* as an example].

LITERATURE CITED

- BARKWORTH, M. E. 1992. Taxonomy of the Triticeae: a historical perspective. *Hereditas* **116**: 1–14.
- BAUM, B. R. 1987. Numerical taxonomic analyses of the Poaceae, pp. 334–342. In T. R. Soderstrom, K. W. Hilu, C. S. Campbell, and M. E. Barkworth [eds.], Grass systematics and evolution. Smithsonian Institution Press, Washington, D.C., USA.
- BAYKOV, K. S. 1999. Basis for phylogenesis modeling with the SYNAP method. Central Siberian Botanical Garden, Novosibirsk, Siberia, Russia. 95 p. [In Russian].
- DURAN, B. S. AND P. A. ODELL. 1977. Cluster analysis, a survey. Statistica, Moscow, Russia. 128 p. [In Russian].
- EDMONDSON, J. R. 1978. Infrageneric taxa in European *Poa* L. *Bot. J. Linn. Soc.* **76**: 329–334.
- GILLESPIE, L. J. AND R. BOLES. 2001. Phylogenetic relationships and infraspecific variation in Canadian arctic *Poa* based on chloroplast DNA restriction site data. *Canad. J. Bot.* **79**: 679–701.
- AND R. J. SORENG. 2005. A phylogenetic analysis of the bluegrass genus *Poa* based on cpDNA restriction site data. *Syst. Bot.* **30**: 84–105.
- , A. ARCHAMBAULT, AND R. J. SORENG. 2007. Phylogeny of *Poa* (Poaceae) based on *trnT-trnF* sequence data: major clades and basal relationships. *Aliso* **23**: 420–434.
- HENNIG, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, USA. 263 p.
- LEGENDRE, P. AND V. MAKARENKOV. 2002. Reconstruction of biogeographic and evolutionary networks using reticulograms. *Syst. Biol.* **51**: 199–216.
- LI, C. L. 1990. A new method for cladistic analysis: median elimination series (MES). *Acta Phytotax. Sin.* **28**: 34–53.
- OLONOVA, M. V. 1992. Materials for studying Siberian species of *Poa* (sect. *Stenopoa*). *Sibirsk. Biol. Zhurn.* **3**: 51–56. [In Russian].
- . 1993. Chorological study of the taxonomical structure of *Poa* section *Stenopoa* in Siberia. *Bot. Zhurn.* **78**: 50–59. [In Russian].
- . 1998. The system and the list of Siberian species of *Poa* (sect. *Stenopoa*). *Turczaninovia* **4**(1): 3–17. [In Russian].
- . 2000. The morphological study of hybridous populations of *Poa palustris* × *nemoralis* (Poaceae) in the South of Tomsk province, pp. 161–163. In N. Kolchanov, D. Furman, E. Borovskikh, N. Glazkova, D. Gruzdev, Y. Shavrukov, A. Zhuravlev, N. Omelianchuk, and S. Lavrushev [eds.], Biodiversity and dynamics of ecosystems in northern Eurasia, vol. 2. Institute of Cytology & Genetics, Novosibirsk, Russia.
- . 2001. The populational study of hybridogenous complexes *Poa palustris* L.–*P. nemoralis* L.–*P. urssulensis* Trin. in the south of western Siberia, pp. 13–33. In A. N. Kupriyanov [ed.], Botanical research of Siberia and Khazakhstan, vol. 7. Altai State University, Barnaul, Russia. [In Russian].
- . 2007. Variability of bluegrass (*Poa*) in Siberia. *Aliso* **23**: 435–449.
- PAVLINOV, I. Y. A. 1996. A word about the modern systematics. *Archivy Zoologicheskogo Muzeya Moskovskogo Universiteta* **34**: 5–53. [In Russian].
- POSADA, D. AND K. A. CRANDALL. 2002. The effect of recombination on the accuracy of phylogeny estimation. *J. Molec. Evol.* **54**: 396–402.
- PROBATOVA, N. S. 1991. Chromosome numbers and systematics of USSR grasses, pp. 92–93. In N. N. Tzvelev, A. K. Skvortzov, and V. F. Semikhov [eds.], Systematics and evolution of grasses. Kuban State University, Krasnodar, Russia. [In Russian].
- . 2007. Chromosome numbers in Poaceae family and their significance for systematics, phylogeny and phytogeography (illustrated by grasses of Russian Far East). *Komarovskiye chteniya* **55**: 9–103. [In Russian].
- TZVELEV, N. N. 1972. Towards meadow grass (*Poa* L.) systematics of the European part of the USSR. *Novitates Systematicae Plantarum Vascularium* **9**: 47–54. [In Russian].
- . 1974. About meadow grass (*Poa* L.) in the USSR. *Novitates Systematicae Plantarum Vascularium* **11**: 24–41. [In Russian].
- . 1976. Grasses of the USSR. Nauka, Leningrad, Russia. 788 p. [In Russian].
- WARD, J. H. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* **58**: 236.
- WEIR, B. S. 1995. Genetic data analysis: methods for discrete population genetic data. Mir, Moscow, Russia. 400 p. [In Russian].