

## Two new species of *Poa* (Poaceae) from the Altai Mountains, southern Siberia

Nikolai N. Nosov\*, Elizaveta O. Punina & Alexander V. Rodionov

Komarov Botanical Institute, Professor Popov Street, 2, St. Peterburg 197376, Russia  
(\*corresponding author's e-mail: nnosov2004@mail.ru)

Received 18 Oct. 2013, final version received 17 Dec. 2013, accepted 19 Dec. 2013

Nosov N.N., Punina E.O. & Rodionov A.V. 2015: Two new species of *Poa* (Poaceae) from the Altai Mountains, southern Siberia. — *Ann. Bot. Fennici* 52: 19–26.

Two new putative hybrid species of *Poa*, *P. navashinii* Nosov and *P. levitskyi* Nosov are described and illustrated. They were found in the southeastern Altai Mountains (southern Siberia, Russia), on a riverbank and in dry mountain steppe. Both of them resemble the species of sect. *Stenopoa* (a xerophytic group) but have some traits that suggest hybridization with species of other sections, presumably sect. *Poa* or *Malacanthae*. Intersectional reticulation with formation of new taxa occurs in mountain regions though species of the sect. *Poa s. stricto* and sect. *Stenopoa* cross rather rarely. Our data add support to a significant role of hybridization in the phylogeny of *Poa* and the Poae tribe in general.

*Poa* is the largest genus in the Poaceae, comprising about 575 species, extrapolated from recent data (Gillespie & Soreng 2005, Soreng *et al.* 2010). *Poa* is widespread on both hemispheres, including the subantarctic islands and Antarctic Peninsula (Chwedorzewska 2008, Molina-Montenegro *et al.* 2012) and Ellesmere Island, the most northern island of the Canadian arctic archipelago (Aiken *et al.* 2007). Some species of *Poa* are nearly cosmopolitan, with a wide ecological amplitude (e.g., *P. pratensis*). However, there is also regional endemism in *Poa* (Tzvelev 1976, Connor 2002, Soreng 2007)

Demonstrated allopolyploidy in the greater portion of the genus (even among widely divergent lineages), as well as frequent apomixis and hybridization complicate the taxonomy of *Poa*. Some researchers have even suggested that all European species (or some of the sections) might belong to a single polyploid complex (Steb-

bins 1950, Olonova 2001). These facts render the genus an interesting object for phylogenetic studies.

Several researchers have suggested that some of the sections have arisen from intersectional hybridization. Nannfeldt (1935) thought that the sections *Subbulbosae* (= *Alpinae*), *Stoloniferae* (= *Poa*), *Abbreviatae*, *Homalopoa*, and *Oreinos* were natural groups, within and among which hybridization was common. He proposed two possible hypotheses: the section *Stoloniferae* (= *Poa*, including e.g. *P. pratensis*) either is a primitive taxon ancestral to all the rest, or it was formed through multiple serial hybridizations. The latter hypothesis was considered by Nannfeldt more plausible from the morphological point of view. *Poa trivialis* as one of the parental taxa for *P. pratensis* was first proposed by Kiellander (1942). These notions were supported by other *Poa* researchers, e.g., Probatova (2007),

who considered that *P. pratensis* and its relatives could have originated from hybridization of the sect. *Homalopoa* and *Triviales* (incl. *P. trivialis*) species. Subsequent studies partly support that suggestion. For example, a molecular phylogenetic analysis of the nuclear ribosomal DNA repeat (nrDNA), ITS1-5.8S rDNA-ITS2 sequences of the nuclear genome (Rodionov et al. 2010, Soreng et al. 2010) and *trnL-trnF* sequences of the chloroplast genome (Soreng et al. 2010) showed that the species closest to polyploid species in the widespread sect. *Poa* are diploids in sections *Homalopoa* and *Macropoa*. *Poa trivialis* from the sect. *Triviales* is more distant from the sect. *Poa*; either the genome of *P. trivialis* did not contribute to the formation of the *P. pratensis* genome or it was mostly deleted from the nrDNA repeats through concerted evolution. Partly similar results were obtained by analysis of the low-copy genes from nuclear genome. Cultivars of *P. pratensis* (sect. *Poa*) from the USA contain four different genomes close to the genomes in the sections *Homalopoa*, *Stenopoa*, *Secundae* and *Macropoa*. The members of sect. *Stenopoa*, comprising caespitose species, with published chromosome numbers are polyploids, and thus they could have originated from intersectional hybridization themselves (Patterson et al. 2005).

However, it has been noted that natural intersectional hybridization leading to formation of nothospecies is not very frequently suggested in *Poa*. A list of the named intersectional hybrids was presented by Knobloch (1969). Tzvelev (1976) mentioned a single named intersectional hybrid, *P. × herjedalica*, and thought it was a hybrid between two rather distant species, *P. pratensis* (sect. *Poa*) and *P. alpina* (sect. *Alpinae*). Additionally, he discussed numerous other occasional hybrids and possible hybrid origins of taxa, but those were mainly produced by intra-sectional reticulation. Soreng (2007) described three named intersectional hybrids, and said that *P. glauca* frequently hybridizes with the arctic species of other sections, including *P. laxa* (sect. *Oreinos*) and *P. hartzii* (sect. *Secundae*; Gillespie et al. 1997, Gillespie & Boles 2001). Some intersectional hybrids, due to introgression, are preserved in the parental section that they most closely resemble, e.g. *P. tolmatchewii*, a vivipa-

rous hybrid between the rhizomatous *P. arctica* (sect. *Poa* in broad sense, now sect. *Malacanthae*), and perhaps *P. glauca* (sect. *Stenopoa*) (Tzvelev 1976). *Poa abbreviata* was also identified as a hybrid between sections *Abbreviatae* and *Madropoa* (Soreng et al. 2010).

Probatova (2007) emphasized that natural hybrids between species of sect. *Poa s. stricto* and sect. *Stenopoa* are mostly unknown, but natural hybrids are rather frequent between representatives of the sections *Malacanthae* and *Stenopoa*. *Poa* species easily hybridize in crossing experiments, the hybrids having morphological features intermediate between the parental species (Grun 1954, Nygren & Åkerberg 1957, Hiesey & Nobs 1982). The largest number of hybrids was obtained with *P. pratensis*, which has a very interesting feature: an ability to accumulate other species' genomes, also from other sections (Clausen 1961, Patterson et al. 2005). Intersectional hybridization can reveal phylogenetic relationships of parental species, and so, the finding of new intersectional hybrids is significant for understanding the evolution of *Poa*.

The Altai Mountains in southern Siberia is one of the diversity centers of *Poa* (Hartley 1961). Hybrid speciation is the main means for the plants to colonize new and extreme habitats, such as mountains, especially at high altitudes (Tzvelev 2005a, 2005b). During field trips to the Altai we found some unusual *Poa* specimens. Those samples combine features of the species from different, unrelated sections and perhaps they are of hybrid origin (intersectional hybrids). Some of them could be occasional hybrids recently formed, others genetically stabilized and fertile species. Here we describe two new taxa of putative reticulate intersectional origins.

### *Poa × navashinii* Nosov, sp. nova (Figs. 1 and 2)

TYPE: Russia. "Russian Federation, Republic of Altai, Kosh-Agachsky District, the Chuyskaya steppe, locality Aktal, the bank of the Yustyt River, near the water edge, 49°55'N, 88°55'E, ca. 2000 m a.s.l., 27.VIII.2006. Coll. A. V. Rodionov, E. O. Punina, M. P. Rayko, S. A. Dyachenko" (holotype LE).

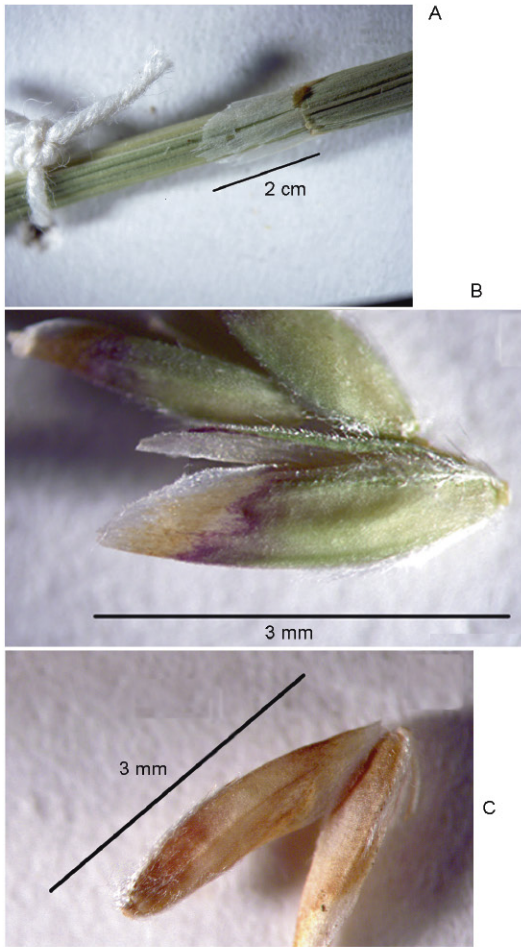
ETYMOLOGY: Named in honor of Mikhail S. Navashin (1896–1973), one of the first Russian plant cytogeneticists (Smocovitis 2009: 319–320).



**Fig. 1.** Holotype of *Poa* × *navashinii*.

Perennials, more or less loosely tufted, with few short rhizomes, glaucous. Shoots intra- and extravaginal, vegetative shoots numerous. Culms 28–46 cm tall, slightly scabrous in lower part. Nodes 3, upper node lower than 1/6 of culm. Uppermost leaf sheaths closed for 1/6 of their length. Panicles 6–8 cm long, contracted, spreading in age, panicle branches angled, scabrous, hooks more dense on little branches and near the places of spikelet attachment on big branches. Ligule of uppermost leaf 2–2.8 mm long, acute.

Leaf blades 1–1.5 mm wide, flat or slightly folded, rigid, long-acute. Spikelets 4–5 mm long, with 2–3 florets, broadly lanceolate. Rachilla internodes glabrous. Lower glume 2.5 mm long, slightly scabrous on keel from its middle. Upper glume 2.9–3 mm long, keels sometimes slightly scabrous from middle. Lemmas 3–4 mm long, lanceolate, pubescence on keel and marginal veins rather well developed on mature florets, between veins mostly short and sparse. Callus webbed, callus hairs well developed. Paleas



**Fig. 2.** *Poa* × *navashinii* (from the holotype). — **A:** Ligule of upper leaf. — **B:** Florets. — **C:** Pubescence between lemma veins.

3 mm long, shortly villous between keels, palea keels covered with spinules from base, in center of keels puberulent. Anthers ca. 1.8 mm long. Ovary light brown, glabrous, 1.7 mm long.

**DISTRIBUTION AND HABITAT:** Southeastern Altai (Chuyskaya steppe). Occurs on river banks, in meadows with *Elymus sibiricus*, *Arctopoa tibetica*, *A. schischkini*, and *Beckmannia syzigachne*. Probably also in Tuva and Buryatia Republics (southern Siberia, Russian Federation).

*Poa* × *navashinii* differs from *P. pratensis* by having a long acute blade of the upper leaf, acute ligules, lemma pubescence between veins, hair-like trichomes on the palea keels, and more open sheaths. From the species in the section

*Stenopoa* (e.g., *P. stepposa* aggr.) it differs by having spreading panicles, short subterranean shoots, more developed lemma keel pubescence, and hair-like trichomes on the palea keels.

This is probably a hybrid between a xerophytic *Stenopoa* species (it somehow resembles them in the glaucous culms and the long, acute, rigid leaves) and some species of the section *Poa*, related to *P. pratensis*. It can possibly be placed in sect. *Poastena*, but the species in that section are hybrids between relatives of *P. arctica* (sect. *Malacanthae*) and species of *Stenopoa* (presumably, *P. nemoralis* aggr. or *P. glauca* aggr.).

Interestingly, some herbarium specimens of south Siberian *Poa* in LE, and in particular a plant originally identified as *Poa reverdattoi* from Tuva (18.VII.1972 *E. Pen'kovskaya* & *L. Kupalova*; 7.VII.1970 *I. Krasnoborov* & *E. Dubrovina*) and Buryatia (coll. *H. H. Iltis*, *J. C. Coffey*, *M. F. Denton* & *I. M. Krasnoborov*) resembles our specimen in the more or less spreading panicles and wide, lanceolate spikelets. However, they are clearly distinct from the holotype of *P. reverdattoi* which has long, very compressed panicles and narrower spikelets. Those specimens might belong to *P. navashinii* although the specimens from Tuva differ from *P. navashinii* by not having web on the lemma callus.

### *Poa* × *levitskyi* Nosov, *sp. nova* (Figs. 3 and 4)

**TYPE:** Russia. "Russian Federation, Republic of Altai, Kosh-Agachsky District, southern slope of the Boshtu mountain, near the settlement Kokorya. 49°55'N, 89°01'E. 17.VIII.2010. Coll. A. V. Rodionov, E. O. Punina, A. A. Gnutikov" (holotype LE). — **PARATYPES** (both LE): "Russian Federation, Republic of Altai, Kosh-Agachsky District, right bank of the river Yustyt, downstream from the bridge. 49°55'N, 88°55'E. 16.VIII.2010. Coll. A. V. Rodionov, E. O. Punina, A. A. Gnutikov"; "Russian Federation, Republic of Altai, Kosh-Agachsky District, left bank of the river Kuskinnar, downstream from the winter hut. 49°58'N, 88°06'E. 22.VIII.2010. Coll. A. V. Rodionov, E. O. Punina, A. A. Gnutikov".

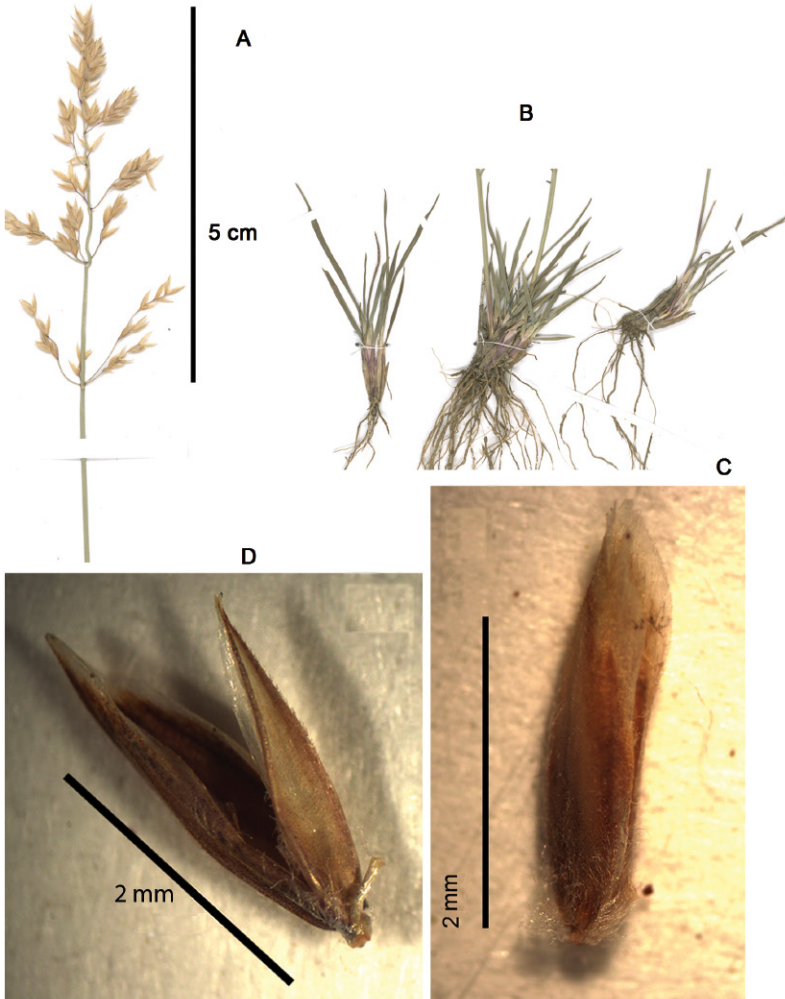
**ETYMOLOGY:** Named in honor of Grigorii A. Levitsky, a well-known Russian plant cytologist and geneticist, who introduced the term "karyotype" in its current definition as describing the characteristics of the particular chromosome complement of an individual or cell (Rodionov 2009).



**Fig. 3.** Holotype of *Poa* × *levitskyi*.

Plants perennial, glaucous, 16–25 cm tall. Culms slightly scabrous. Branching intravaginal. Vegetative shoots developed. Nodes 2. Upper leaf sheaths closed for 1/6 of length. Vegetative and generative shoots enveloped by remnants of sheaths. Leaf blades of vegetative shoots flat, those of generative shoots folded. Generative shoot blades ca. 1 mm wide, apex shortly pointed, not naviculate. Ligules of upper leaves 3 mm long, slightly pointed. Panicle 3–5 cm long, more or

less spreading. Panicle branches densely scabrous. Spikelets lanceolate, 5–7 mm long, 5–7-flowered. Glumes subequal, 2.6–3 mm long, glabrous, or slightly scabrous on keels above middle. Lemmas 2.6 mm long, lanceolate. Callus webbed, web short, lemma pubescence short, between veins sparse and shorter than on keels. Paleas ca. 2 mm long, with short spinules on keels, between them poorly scaberulous. Anthers ca. 1.8 mm long. Ovary light brown, ca. 1 mm long.



**Fig. 4.** *Poa* × *levitskyi* (from the holotype). — **A:** Panicle. — **B:** Branching. — **C:** Lemma. — **D:** Palea.

**DISTRIBUTION AND HABITAT:** This species is a very rare endemic of SE Altai Mountains. It grows in dry mountain steppes with numerous *Artemisia* species, *Euphorbia tschuensis*, *Agropyron cristatum*, *Leymus secalinus* and *Psathyrostachys juncea*. Sometimes it occurs on riverside meadows.

*Poa* × *levitskyi* differs from *P. rangkulensis* by the panicle and spikelet shape and by having smaller spikelets and longer generative shoots.

*Poa* × *levitskyi* is reminiscent of other xerophytic members in section *Stenopoa* (mostly *P. attenuata* and *P. botryoides*), but clearly differs from them by having numerous short vegetative shoots, which is unusual in sect. *Stenopoa*. Only the central Asian *P. rangkulensis* has them, but in that species they are less well developed. In

addition, there are remnants of the sheaths enveloping the culm bases. This trait was not known in the section *Stenopoa*, it rather characterizes members of the section *Alpinae* and some species of the section *Poa* (such as *P. angustifolia*). The dense tufts of *P. × levitskyi* also resemble those of the members of sect. *Kolymenses*, such as *P. tzvelevii*. However, *P. × levitskyi* clearly differs from *P. tzvelevii* in the wider leaves and panicles, scabrous culms, and a more xerophytic habit. The panicle shape of *P. × levitskyi* does not agree with any of sect. *Kolymenses* species, which are closer to sect. *Abbreviatae* in this trait. This species can be an intersectional hybrid between species of the sect. *Stenopoa* and a yet unknown parent (sect. *Alpinae*, *Poa* or *Abbreviatae*). The intravaginal branching of *P.*

× *levitskyi* as well as the presence of numerous short vegetative shoots can be adaptations to the dry conditions of the mountain steppe.

Numerous crossing experiments (Grun 1954, Clausen 1961, Hiesey & Nobs 1982) showed that *P. pratensis* s. lato readily hybridizes with members of other sections (e.g., with *P. secunda* s. lato of sect. *Secundae*, which is a relative of sect. *Stenopoa*). One of the American species, *P. arida*, which also has frequently crossed with *P. pratensis*, is thought to be an inter-sectional hybrid *P. pratensis* × *P. secunda* (Soreng 2007). There is however very little morphological data (Knobloch 1969) and no published DNA sequence data concerning hybridization between species of the sections *Poa* s. stricto and *Stenopoa*. Members of sect. *Stenopoa* may have contributed to the formation of sect. *Poa* (Patterson *et al.* 2005) and so they can hybridize with species of sect. *Poa* (back-crossing). The specimens found by us add lend support to the central role of hybridization in the phylogeny of *Poa*, and of the Poeae tribe in general.

## Acknowledgements

The authors are grateful to Dr. Nikolai N. Tzvelev for his opinions and kind help in the herbarium work, and to Drs. Robert J. Soreng and Nina S. Probatova for thorough discussions. Also we thank Dr. Alexander I. Shmakov, Dr. Sergei A. Dyachenko, Alexander P. Shalimov, Dr. Mike P. Rayko and Alexander A. Gnutikov for their assistance in the field studies and in collecting of the material. This study was financially supported by the Russian Fund for Basic Research (RFBR), projects 12-04-01470, 12-04-31524, 14-04-01416 A and by the Program of the Russian Academy of Sciences “Dynamics of the Gene Pools”.

## References

- Aiken S.G., Dallwitz M.J., Consaul L.L., McJannet C.L., Boles R.L., Argus G.W., Gillett J.M., Scott P.J., Elven R., LeBlanc M.C., Gillespie L.J., Brysting A.K., Solstad H. & Harris J.G. 2007: Flora of the Canadian Arctic Archipelago: descriptions, illustrations, identification, and information retrieval. — NRC Research Press, National Research Council of Canada, Ottawa. [Available at <http://nature.ca/aafloora/data/index.htm>].
- Chwedorzewska K.J. 2008: *Poa annua* L. in Antarctic: searching for the source of introduction. — *Polar Biol.* 31: 263–268.
- Clausen J. 1961: Introgression facilitated by apomixis in polyploid *Poas*. — *Euphytica* 10: 87–93.
- Connor H.E. 2002: Regional endemism in New Zealand grasses. — *New Zealand J. Bot.* 40: 189–200.
- Gillespie L.J., Consaul L.L. & Aiken S.G. 1997: Hybridization and the origin of the arctic grass *Poa hartzii* (Poaceae): evidence from morphology and chloroplast DNA restriction site data. — *Canad. J. Bot.* 75: 1978–1997.
- Gillespie L.J. & Boles R. 2001: Phylogenetic relationships and infraspecific variation in Canadian Arctic *Poa* based on chloroplast DNA restriction site data. — *Canad. J. Bot.* 79: 679–701.
- Gillespie L.J. & Soreng R.J. 2005: A phylogenetic analysis of the bluegrass genus *Poa* based on cpDNA restriction site data. — *Syst. Bot.* 30: 84–105.
- Grun P. 1954: Cytogenetic studies of *Poa* L. chromosome numbers and morphology of interspecific hybrids. — *Am. J. Bot.* 41: 671–678.
- Hartley W. 1961: Studies on the origin, evolution and distribution of the Gramineae. IV. The genus *Poa* L. — *Aust. J. Bot.* 9: 152–161.
- Hiesey W.M. & Nobs M.A. 1982: *Experimental studies on the nature of species. VI. Interspecific hybrid derivatives between facultatively apomictic species of bluegrasses and their responses to contrasting environments*. — Carnegie Inst. Washington Publ., Washington.
- Kiellander C.L. 1942: A subhaploid *Poa pratensis* L. with 18 chromosomes and its progeny. — *Svensk Bot. Tidskr.* 36: 200–220.
- Knobloch I.W. 1969: *A checklist of crosses in the Gramineae*. — Privately published.
- Molina-Montenegro M.A., Carrasco-Urra S., Rodrigo C., Convey P., Valladares F. & Gianoli E. 2012: Occurrence of the non-native annual bluegrass on the Antarctic mainland and its negative effects on native plants. — *Conserv. Biol.* 26: 717–723.
- Nannfeldt J.A. 1935: Taxonomical and plant-geographical studies in the *Poa laxa* group. A contribution to the history of the North European mountain floras. — *Symbolae Botanicae Upsalienses* 1: 1–113.
- Nygren A. & Åkerberg E. 1957: Studies in species and hybrid derivatives of *Poa* new to practical work. — *Annales Academiae Regiae Scientiarum Upsalienses* 1: 53–69.
- Olonova M.V. [Олонова М.В.] 2001: [Study of the *Poa glauca* complex (Poaceae) in Siberia]. — *Bot. Zh.* 86: 18–27. [In Russian].
- Patterson J.P., Larson S.L. & Johnson P.G. 2005: Genome relationships in polyploid *Poa pratensis* and other *Poa* species inferred from phylogenetic analysis of nuclear and chloroplast DNA sequences. — *Genome* 48: 76–87.
- Probatova N.S. [Пробатова Н.С.] 2007: [Chromosome numbers in the Family Poaceae and their significance for systematics, phylogeny, and phytogeography (the Russian Far East)]. — *Komarov Memorial Lectures (Vladivostok)* 55: 9–103. [In Russian].
- Rodionov A.V. 2009: Grigorii Andreevich Levitsky (1878–1942) — *Russian Journal of Genetics* 45: 1261–1266.
- Rodionov A.V., Nosov N.N., Kin E.S., Machs E.M., Punina E.O. & Probatova N.S. 2010: The origin of polyploid

- genomes of bluegrasses *Poa* L. and gene flow between Northern Pacific and Sub-Antarctic Islands. — *Russian Journal of Genetics* 46: 1407–1416.
- Smocovitis V.B. 2009: The “Plant *Drosophila*”: E. B. Babcock, the genus *Crepis*, and the evolution of a Genetics Research Program at Berkeley, 1915–1947. — *Historical Studies in the Natural Sciences* 39: 300–355.
- Soreng R.J. 2007: *Poa* L. — In: Flora of North America Editorial Committee (eds.), *Flora of North America North of Mexico*: 486–610. Oxford University Press, New York.
- Soreng R.J., Bull R.D. & Gillespie L.J. 2010: Phylogeny and reticulation in *Poa* based on plastid trnTLF and nrITS sequences with attention to diploids. — In: Seberg O., Petersen G., Barford A.S. & Davis J.I. (eds.), *Diversity, phylogeny, and evolution in the monocotyledons*: 619–643. Århus University Press, Århus.
- Stebbins G.L. 1950: *Variation and evolution in plants*. — Columbia University Press, New York.
- Tzvelev N.N. [Цвелёв Н.Н.] 1976: [*Grasses of the USSR*]. — Nauka Publishers, Leningrad. [In Russian].
- Tzvelev N.N. [Цвелёв Н.Н.] 2005a: [Hybridization as one of the factors increasing biological diversity and genome criterion of the higher plants genera] — In: Tzvelev N.N. [Цвелёв Н.Н.] (ed.), [*Problems of the theoretical morphology and evolution of higher plants*]: 141–148. KMK Press, Moscow. [In Russian].
- Tzvelev N.N. [Цвелёв Н.Н.] 2005b: [About significance of the hybridization in evolution of higher plants]. — In: Tzvelev N.N. [Цвелёв Н.Н.] (ed.), [*Problems of the theoretical morphology and evolution of higher plants*]: 149–154. KMK Press, Moscow. [In Russian].