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

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Two new putative hybrid species of *Poa*, *P. navashinii* Nosov and *P. levitskii* 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 *Mala-canthaec*. 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 Poeae 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 (Stebbins 1950, Otonova 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 cespitose 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 distinct 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 intrasectional 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. tolmachewii_, a viviparous 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 Chuyyskaya steppe, locality Aktal, the bank of the Yusty 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).
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
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*, *Arcetoapoa tibetica*, *A. schischkinii*, 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. Itlis, 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)


**ETYMOLOGY:** Named in honor of Grigoriy 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 × levitskii.

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.
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 tschuenensis, Agropyron cristatum, Leymus secalinus and Psathyrostachys juncea. Sometimes it occurs on riverside meadows.

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

**Poa × levitskii** 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. × levitskii* also resemble those of the members of sect. *Kolymenses*, such as *P. tzvelevii*. However, *P. × levitskii* clearly differs from *P. tzvelevii* in the wider leaves and panicles, scabrous culms, and a more xerophytic habit. The panicle shape of *P. × levitskii* 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.
\textit{Poa} \textit{levitskii} 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, Hisey & Nobs 1982) showed that \textit{P. pratensis} \textit{s. lato} readily hybridizes with members of other sections (e.g., with \textit{P. secunda} \textit{s. lato} of sect. \textit{Secundae}, which is a relative of sect. \textit{Stenopoa}). One of the American species, \textit{P. arida}, which also has frequently crossed with \textit{P. pratensis}, is thought to be an intersectional hybrid \textit{P. pratensis} \textit{x} \textit{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 \textit{Poa} \textit{s. stricto} and \textit{Stenopoa}. Members of sect. \textit{Stenopoa} may have contributed to the formation of sect. \textit{Poa} (Patterson \textit{et al.} 2005) and so they can hybridize with species of sect. \textit{Poa} (back-crossing). The specimens found by us add lend support to the central role of hybridization in the phylogeny of \textit{Poa}, and of the Poaceae tribe in general.

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