

ON THE ORIGIN OF SOME SPECIES OF THE GENUS *AGROSTIS* L. (POACEAE: AVENEAE) IN NORTHERN ASIA

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Critical revision of some species of the genus *Agrostis* L. (Poaceae: Aveneae) in Northern Asia was carried out. The paper considers the hybridization process within the genus. Suppositions about the kinship and origin of some species are made. New taxonomic rank *A. bodaibensis*, *A. korczaginii*, and *A. ussuriensis* is substantiated.

Key words: *Agrostis*, Poaceae, hybrids, kinship, Northern Asia.

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INTRODUCTION

The genus *Agrostis* L. includes about 150 species. It is one of the largest and most polymorphic genera of the tribe *Aveneae* Dumort., therefore it is considered taxonomically complex. Representatives of the genus are distributed almost in all extratropical areas of both hemispheres; they also occur at high altitudes of the tropics (Tsvelev 1976).

Taxonomic complexity of the genus is associated with considerable polymorphism of its representatives, which is due to the processes of polyploidization as well as intersectional and intrasectional hybridization of species, in particular. Significant role of these processes in formation of the genus has been covered many times by a number of authors when compiling various summaries and keys to plants.

In Northern Asia (Siberia, the Russian Far East, and Northern Mongolia) the genus is represented by 29 species, which belong to three sections, namely: sect. *Agrostis*, sect.

Agraulus (Beauv.) Tzvel., and sect. *Trichodium* (Michx.) Dumort.

Species of the first section are characterized by awnless (normally), less frequently aristate lemmas. Callus hairs are generally more than 6 times shorter than lemmas, more rarely are absent. Paleae are 1.5 – 2 times shorter than lemmas. Anthers are 0.8 – 1.5 mm long. This section includes predominantly tetraploid ($2n=28$), more rarely hexaploid ($2n=42$), species. Within the territory of Northern Asia 10 species belong to the section *Agrostis*, namely: *A. albida* Trin., *A. bodaibensis* Peschkova, *A. breviramea* (Roshev. ex. Tzvel.) Kurczenko, *A. gigantea* Roth, *A. capillaris* L., *A. jacutica* Schischkin, *A. divaricatissima* Mez, *A. sibirica* V. Petrov, *A. stolonifera* L., and *A. straminea* Hartman.

Species of the section *Agraulus* are aristate, more rarely without awns. Callus hairs are more than 4 times shorter than lemmas. Paleae are almost absent. Anthers are 0.6 – 1.5 (2) mm long. The section comprises diploid ($2n=14$), tetraploid, and more rarely octoploid ($2n=56$), species. In Northern Asia it is represented by *A. flaccida* Hackel, *A. kronokensis* Probatova, *A. kudoii* Honda, *A.*

sichotensis Probatova, *A. trinii* Turcz., *A. mertensii* Trin., and *A. vinealis* Schreber. The section *Trichodium* includes *A. alascana* Hulten, *A. anadyrensis* Soczava, *A. clavata* Trin., *A. exarata* Trin., *A. geminata* Trin., *A. pazuhetica* Probatova, and *A. scabra* Willd. These are generally awnless plants. Callus hairs are usually absent; if there are any, they are very short and visible only at high magnification. Paleae are almost absent. Anthers are 0.3 – 0.8 mm long. The majority of species of this section are characterized by hexaploid chromosome number ($2n=42$). Such number is the result of stabilization of hybrids by means of autopolyploidy when crossing diploids with tetraploids. Therefore the section *Trichodium* can be considered entirely hybridogenic.

Seven species of those, which occur in Northern Asia, (*A. bodaibensis*, *A. jacutica*, *A. kronokensis*, *A. pazuhetica*, *A. sibirica*, *A. sichotensis*, and *A. trinii*) do not go beyond its limits in their distribution. Three species (*A. alascana*, *A. exarata*, and *A. geminata* (= *A. ×kamtschatica* Probatova)) are predominantly North American. Three species more (*A. anadyrensis*, *A. kudoii*, and *A. scabra*) penetrate into North America. Three species are typical Euro-Siberian taxa, which reach the South Urals (*A. albida*), Yamal-Nenets Autonomous District (*A. straminea*) and Transbaikalia (*A. breviramea*) in the east. Two species are East Asian taxa: one of them (*A. flaccida*) is distributed mainly in the form of islands, and another one (*A. divaricatissima* (= *A. mongolica* Roshev.)) occurs from Transbaikalia to the Korean Peninsula and Japan. *A. gigantea* and *A. capillaris* (= *A. tenuis* Sibth.) have Eurasian areal. Four species (*A. clavata*, *A. mertensii* (= *A. borealis* Hartman), *A. stolonifera*, and *A. vinealis*) are circumpolar. Two of them (*A. mertensii* and *A. vinealis*) can be referred to the group of circumpolar scattered ones (species with discontinuous area). Six are considered spontaneous intrasectional and intersectional hybrids (Probatova, 1985): *A. × amurensis* Probatova (*A. scabra* × *A. trinii*), *A. × clavatifformis* Probatova (*A. clavata* × *A. flaccida*), *A. × kamtschatica* Probatova (*A. scabra* × *A. kudoii*), *A. × paramuschirensis* Probatova (*A. alascana* × *A. flaccida*), *A. × subclavata* Probatova (*A. clavata* × *A. kudoii*), and *A. × ussuriensis*

Probatova (*A. clavata* × *A. stolonifera*). Information about them is quite poor and fragmentary.

Representatives of the genus *Agrostis* have a low level of ploidy as compared to other gramineous plants (Kurchenko 2002). They are generally di-, tetra-, hexa-, and octoploids. Triploid hybrids with $2n=35$ are known. As a comparison, the ploidy level for species of the genus *Calamagrostis* Adans., which is close to bent grass, varies from $4x$ to $10x$ and more (Probatova 1993). Moreover, the number of karyological races in individual species of *Agrostis* is not so large as in *Calamagrostis*. Apparently, the process of morphogeny via a change of chromosome set in *Agrostis* is a rarer phenomenon, than in *Calamagrostis*. For instance, only two karyological races are known for Eurasian *A. gigantea*: $2n=28$ (Krogulevich 1978) and 42 (Sokolovskaya & Probatova 1974); while in *Calamagrostis langsdorffii* (Link) Trin. there are races $2n=28$, 42, 56, and 70 (Sokolovskaya & Probatova 1977). Some authors consider that in the low level of ploidy of the genus *Agrostis* there is a potentiality of further evolution through the increase of chromosome complex (Kurchenko 2002, Enushchenko 2010).

We do not deny that the process of hybridization also contributes greatly to the species weald of the genus. *A. × amurensis* Probatova (*A. scabra* × *A. trinii*) and *A. geminata* Trin. (*A. scabra* × *A. vinealis* s.l.) can be a good example of hybridization. In addition to morphological characters of the mentioned species, their chromosome numbers count in favor of their hybridogenic nature, i.e. they both have $2n=35$ (Sokolovskaya and Probatova, 1974; Probatova and Kharkevich, 1983). Such a number is obtained when crossing parental forms: *A. scabra* ($2n=42$, Sokolovskaya and Probatova 1974) with *A. trinii* ($2n=28$, Sokolovskaya & Probatova 1974) and *A. kudoii* ($2n=28$, Sokolovskaya & Probatova 1974).

However, some authors explain the origin of individual taxa, based only on their morphological similarity with some other taxon. With such an approach, hybridization is the simplest, but, unfortunately, not always objective variant to explain the origin of species. In the present

paper we examine in more detail some species of the genus *Agrostis*, which are traditionally considered hybrids.

MATERIAL AND METHODS

Herbarium funds of the V.L. Komarov Botanical Institute RAS (St. Petersburg, LE), Central Siberian Botanical Garden SB RAS (Novosibirsk, NS, NSK), Institute of Biology and Soil Science FEB RAS (Vladivostok, VLA), Irkutsk State University (Irkutsk, IRKU) and Institute of Biological Problems of the North FEB RAS (Magadan, MAG) served as materials for the present work. Short titles of the large herbaria of the RF (acronyms) are given according to the electronic version of the edition "Index Herbariorum" P.K. Holmgren & N.H. Holmgren (1998: [http://swetgum.nybg.org/ih/...](http://swetgum.nybg.org/ih/)). When it is necessary to specify storing places of particular samples after a tag an acronym of the corresponding Herbarium is cited in the text of the article.

Karyological data used in the work were obtained as a result of our research and processing of literary sources. Material for the determination of chromosome numbers (young rootlets of plants, germinated seeds) was fixed in Clark's fixative (simplified Carnoy's fixative), consisting of three parts of ethanol and one part of glacial acetic acid. Chromosomes were colored with hematoxylin; numbers were determined on squash preparations under the microscope Biomed-2.

RESULTS AND DISCUSSION

Since the date of disclosure *A. anadyrensis* has been considered endemic of the Anadyr river basin (Shishkin 1934, Khokhryakov 1985), where it was described (type: «the Belaya river basin (left tributary of the Anadyr), on the sand shore at the Bitcho upland, 4 VII 1929, V.B. Sochava» - LE). More recently this species was indicated for different regions of the Russian Arctic and the Far East as well as for Alaska (Tsvelev 1976, Probatova 1985).

A great number of *A. anadyrensis* sites within the territory of Tuva was recorded by M.N. Lo-

monosova (1984). In «Flora of Siberia» (1990) G.A. Peshkova indicated two more previously unknown sites, namely: in the Irkutsk region (Murino station, on the southeastern shore of Baikal) and in Buryatia (the Kotelnikovskiy cape on the northwestern shore of Baikal). When examining the herbarium material for *A. clavata*, we found four more sites of *A. anadyrensis* in different parts of Southern Siberia (the Western Sayan, the Barun-Khemchinsk district, the Ak-Sug river valley, meadow bog, 5 VIII 1975, G.A. Peshkova (NSK); the Irkutsk region, the Kachug district, the Sr. Ilikta and Bol. Tarel watershed, the Pavlik stow, thawed patches, bog-ledum cedar woodland, 11 VIII 1960, № 1960, Galkin (IRKU); the same place, the Mamsko-Chuisk district, Sagdiondon village, 640 m above mean sea level, upper part of forest belt, waterlogged birch forest on the village edge, 5 VII 1977, № 1019, M. Ivanova, Solovyev (NSK); Buryatia, the Chikoy river valley, the Selenga river tributary, meadow, 11 VII 1913, № 2146, V.I. Smirnov (IRKU)).

When describing *A. anadyrensis*, V.B. Sochava (in: Shishkin 1934:746) pointed to the closeness of this species with *A. trinii*. Later the authors of floristic summaries (Tsvelev 1964, 1976, Probatova 1985, Lomonosova 1984, Kurchenko 2002, and others) traditionally underlined the hybridogenic nature of *A. anadyrensis* (*A. clavata* × *A. trinii*), apparently, relying on the feature of beardedness of lemmas. Generally, the presence of awns in the majority of spikelets of the head of this species is the only characteristic, distinguishing it from the hypothetical parental species *A. clavata*. It was also mentioned by N.S. Probatova (1984). Indeed, all samples of *A. anadyrensis* from Yakutia, Tuva, Buryatia, the Irkutsk and Magadan regions, and the Russian Far East, examined by us, are, in a great measure, habitually similar to *A. clavata*. It is also worth noting that the degree of awns maturity of individual samples of *A. anadyrensis* is diverse. Even in different spikelets of the head of one plant this feature is pronounced irregularly. It is especially characteristic of the South Siberian samples. In northern populations of the species the feature of beardedness is more strictly determined and stable.

It is interesting to mention the fact that *A. anadyrensis* is one of two aristate species of Northern Asia, which are characterized by the largest chromosome number among the representatives of the genus *Agrostis* ($2n=56$, Sokolovskaya and Probatova, 1974). The second aristate octoploid species is East Asian-North American *A. mertensii*, which is a doubtless hybrid between one of the species of the section *Agraulus* (Beauv) Tzvel. with $2n=14$ and *A. clavata* with $2n=42$ of the section *Trichodium* (Michx.) Dumort. (Tsvelev, 1976). E.I. Kurchenko (2002) consider this species autopolyploid from *A. flaccida* with $2n=14$, (Sokolovskaya and Probatova, 1974), inasmuch as it has much closer resemblance with the latter, than with *A. clavata*. The probability of the origin of *A. anadyrensis* by means of autopolyploidy of the hexaploid parental form (*A. clavata*) is almost excluded. Even if we assume that there is an unequal chromosome disjunction of *A. clavata* during the meiotic division, with formation of gametes $n=14$ and 28 , in the first generation octoploids amount to only 25%. However, the supposition about its origin from crossing *A. clavata* \times *A. trinii* is also doubtful. These species are characterized by hexa- ($2n=42$, Sokolovskaya and Probatova, 1974) and tetraploid ($2n=28$, Sokolovskaya and Probatova, 1974) chromosome sets, respectively. It is obvious that the hybrid from crossing these two species cannot have $2n=56$. It is more likely that *A. anadyrensis* is a result of ancient introgressive hybridization of *A. clavata* \times *A. flaccida*. It is proved in the best way possible by the fact that in the Arctic regions of the Far East (ancient part of the areal) *A. anadyrensis* replaces *A. clavata*, which is almost absent there (Probatova 1985). It is evident that diploid *A. flaccida* had vaster area formerly. Currently, this species occurs only in southern Kamchatka, Sakhalin Island, Kuril Islands and Japan, i.e. in places, where hybridisation with *A. clavata* was avoided.

However, the location of *A. anadyrensis* at a considerable distance from the main ancient area as well as different degrees of awn maturity in heads of Siberian samples of the species are difficult to associate with the processes of hybridization or invasion. Possibly, in this case we deal with

some other process of local race formation within *A. clavata*.

Among awnless species of the nominal section *Agrostis* formation of awns on back sides of lemmas is also registered. And in some instances such aristate forms are treated as independent species, resulting from crossing of awnless parental forms with aristate ones. They have no well-defined area and occur discretely throughout the area of awnless parental species, which they differ from only based on the presence of awns. Moreover, awns have different degree of intensity even within one head of these «species» up to the total absence.

Thus, *A. bodaibensis*, described from the Irkutsk region (type: «Khomolkho village, 174 km from Bodaibo along the tract via Kropotkin, 800 m above mean sea level, weakly marshy meadow near the road, 27 VII 1987, M. Ivanova, L. Belousova» (NSK)), and *A. ussuriensis*, described from the Ussuri river basin (type: the Primorye Territory, the Chuguevsky district, Verkhne-Ussuriiskiy research station, along the track approximately 1 km from the research station base, 31 VII 1975, T. Bezdeleva, S. Nesterova (VLA)) in a great measure habitually deviate, similar to *A. anadyrensis*, towards their awnless parental forms: *A. sibirica* and *A. stolonifera*, respectively (Peshkova 1990, Probatova 1984). To date, only three sites are known for *A. bodaibensis*, therefore it is considered endemic.

In addition to the territory, from which *A. ussuriensis* was described, it was also registered in the Khabarovsk Territory (Probatova 1985) as well as in the Chita and Tyumen regions (Peshkova 1990). In the herbarium funds of Novosibirsk (NSK) we discovered a bent grass from the Kurgan region (the Shadrinsky district, surroundings of Peschano-Tavolzhnovo village, sand shore of Lake Tavolzhnoye, 9 VII 1984, № 1487, Krasnikov), defined as a hybrid *A. gigantea* \times *A. trinii*. However, based on the presence of above-ground creeping stems, we defined it as *A. ussuriensis*. One more sample from the territory of Buryatia (Buryatia, the Zaigraevsky district, the Uda river, surroundings of Onokhoy settlement, marshed

bank of the flood plain, 25 VII 1987, N. Frizen (NSK)) was found by us in the bunch *A. sibirica*. Indication of *A. ussuriensis* for the territory of the Irkutsk region (Peshkova 1990) is incorrect and refers to the aristate form *A. capillaris*. Similar samples from the Mezen and Pechora bassins as well as from the middle Urals were described as an endemic hybridogenic (*A. capillaris* × *A. trinitii*) species *A. korczaginii* Senjan.-Korcz. In view of the considerable breaking away of the aristate *A. capillaris*, found by us, from the basic area of the latter, we examined the discovered form as an independent species *A. innominata* Enustschenko (Enushchenko 2010).

The phenomenon of beardedness is registered also for *A. gigantea* (Probatova 1985; Peshkova 1990). We found an aristate sample of this species in the herbarium funds NSK (the Irkutsk region, Katangsky district, Yerbogachen settlement, floodplain meadow, 15 VII 1977, N. Vodopyanova, S. Tretyakov, R. Krogulevich). Awns of these forms are very weak and thin, often short. We also recorded an aristate form for *A. divaricatissima*, close to the species *A. gigantea*, (the Irkut river basin, Tunkinskaya depression, surroundings of Kharbyaty settlement, hummocky moist meadow, 3 IX 1931, V.I. Smirnov (IRKU); the same place, the Tunkinsky district, Torskaya depression, surroundings of Tory settlement, meadow, VII 1931, V.I. Smirnov (LE)).

It should be noted that just as the phenomenon of awns appearance is registered in awnless species of the genus *Agrostis* (section *Agrostis*), the phenomenon of their reduction is observed among aristate ones (section *Trichodium*). Thus, in addition to the typical variety *A. canina* L. (with well-developed awns), var. *pudica* Doell, 1843, Rhein. Fl.: 108 with underdeveloped awns and var. *mutica* Sinclair, 1816, Hort. Gram. Woburn.: 266 without awns are distinguished. In another species of this section – *A. vinealis* Schreb. (with very underdeveloped awns) two varieties are also distinguished, namely: awnless var. *mutica* (Lavr.) Tzvel., 1976, Gramineous plants of the USSR: 337 (= *A. syreistschikovii* var. *mutica* Lavr. 1940, in Flora of Ukrainian SSR, 2: 153) and var. *arida* Schlecht., 1823, Fl. Berol. 1: 45

with well-developed kneed awns.

CONCLUSION

Using large herbarium material, we traced a tendency of appearance of aristate forms in populations of awnless species, growing in ecotopes with increased moisture content of a substrate. Hence, it is possible to assume that manifestation of beardedness among the species of the section *Agrostis* is a response to a certain environmental factor or their complex, which are in general unnatural for awnless parental species.

Beardedness in the tribe *Aveneae*, which includes the genus *Agrostis*, is a primary feature with respect to awnless. Therefore, the appearance of awns in awnless species as well as their reduction in aristate species can be a result of somatic mutation and is a demonstrative example of the N.I. Vavilov's law of homologous series.

Based on the abovementioned, we suggest considering *A. bodaibensis*, *A. korczaginii*, and *A. ussuriensis* in the rank not above the varieties *A. sibirica* var. *bodaibensis* (Peschkova) Enustschenko, *A. capillaris* var. *korczaginii* (Senjan.-Korcz.) Enustschenko (= *A. innominata* Enustschenko), and *A. stolonifera* var. *ussuriensis* (Probatova) Enustschenko (Enushchenko 2011).

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