

Phenotypic plasticity of the stem epidermis in the bluegrasses (*Poa* L.) of section *Stenopoa* Dumort. (*Poaceae*). I. Mesomorphic species

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Abstract

Section *Stenopoa* Dumort. is one of the largest representatives of the bluegrass genus (*Poa* L.). Despite relative antiquity, *P. palustris* L. and *P. nemoralis* L. have not been preserved in original states. Their ongoing evolution and hybridization has increased their diversity and has complicated the system. This obligate to search for new morphological characters, suitable for taxa discrimination, as well as for phylogenetic relationships. It is well known, that studying of grasses is difficult, bluegrass in particular. The reasons for this are next: their vegetative and reproductive organs structure is extremely uniform; the number of characters used in taxonomy is small as well as the number of these characters states. Meanwhile, characters of epidermis structure are widely used in the systematics and diagnostics of grasses. These characters consist of a presence or an absence of pubescence along the veins, lower lemmas keel and callus, and an rachilla. The main goal of the current work is to assess the variability of epidermis sculptural features, that determine the degree of stems and sheaths roughness of mesomorphic bluegrasses in *Stenopoa* section; and to assess the possibility of using these characters in taxonomy. Anatomical surfaces' study of stems and lower leaf sheaths was carried out with a Biolam-1 binocular light microscope (Russia) and a SEC SNE-4500M (SEM) scanning electron microscope (South Korea). Studies of diversity of stem and leaf epidermis structure on mass and serial herbarium materials showed that the change in the roughness degree has partly continual, partly discrete character. Sculptural formations are represented by a variety of crown cells, pricles, and bristles, that in fact are short stiff hairs. Thus, the characters of epidermis structure cannot be used as discriminators

for mesomorphic bluegrasses of the *Stenopoa* section. These characters can act as additional ones and mark the evolutionary branches of *P. palustris* and *P. nemoralis* along with such morphological features as the length of the ligule and the rachilla pubescence.

Keywords

Plant anatomy, scanning electron microscope, *Poa palustris* L., *P. nemoralis* L.

Introduction

The section *Stenopoa* Dumort., numbering up to 100 species, is one of the largest in the genus (*Poa* L.) according to Keng (1959), Tzvelev (1976), Liu (2003), Tzvelev and Probatova (2019). Its representatives play a significant role in the phytocoenosis, and frequently they are the dominants and edificators of plant communities in extratropical Asia. Evolution in sect. *Stenopoa* Dumort. followed the path of xerophilization (Serebryakova 1965; Tzvelev 1972). N.N. Tzvelev (1976) proposed to divide all species of this section into 4 groups according to the degree of xeromorphism, where each group represents a new evolutionary stage. In this case, the marker is an uppermost node position on the stem; additional characters include the leaf blade length, the ratio between the length of the flag leaf blade and its sheath, the length of panicle branches, and the ratio between the length of the panicle and its longest branch. Mesomorphic species *P. palustris* L. and *P. nemoralis* L. are attributed to the most ancient and poorly specialized species. They are the most common and widespread species in the section. Being most ancient in origin, *P. palustris* and *P. nemoralis*, nonetheless, currently differ in very high polymorphism caused by a general tendency of the genus to hybridization and apomixis (Stebbins 1941). They also have the highest and most diverse chromosome numbers among the species of this section (Takhtajyan 1993; Probatova 1985, 2007; Probatova et al. 2007). All this indicates that despite their relative antiquity, the species have not stabilized or stopped evolving, like, for example, *P. remota* Forsell. Their evolution continues in mesophilic conditions, and these species are no longer as primitive as their ancestors that probably gave rise to most of the species of the section.

Poa palustris and *P. nemoralis* are well distinguished by two qualitative characters. The first species has glabrous rachilla and uppermost ligula exceeding 2 mm, and the second one has pubescent rachilla and its flag leaf ligule does not exceed 1 mm. Nevertheless, the shift in the range boundaries of these species occurred in the Pleistocene and paved the way for hybridization of these species (Tzvelev 1974). In the territory of Northeastern Europe and Siberia, it resulted in formation of numerous forms, which exhibit the characters of both species in various combinations. The polymorphism caused by these events is reflected in the taxonomy: *P. palustris*, *P. nemoralis*, and presumably hybridogenic populations, considered as *P. intricata* Wein, are represented by numerous morphotypes and sometimes form isolated races. Some of them are regarded as species (Tzvelev 2009); however, due to

poor morphological isolation or insufficient data, it seems more appropriate to consider them as aggregates: Aggr. *P. nemoralis*, Aggr. *P. palustris*, and Aggr. *P. intricata* (Olonova 2010, 2016).

The tendency of species to hybridize enriches the gene pool, leads to noticeable anatomical and morphological changes, and, ultimately, increases both morphological and genetic diversity. Along with this, there is a blurring of morphological boundaries between species. All this stimulates the search for new characters suitable for both taxa discrimination and phylogenetic constructions.

It is known that grasses, bluegrasses in particular, are difficult to study, since the structure of their vegetative and reproductive organs is extremely uniform, and the number of taxonomic characters and character states is not sufficient. The qualitative characters are of the greatest taxonomic value, and they are often indicators of the genetic relationship (Davis 1977). Meanwhile, structural characters of the epidermis are widely used in the systematics and diagnosis of grasses (Clifford and Watson 1977; Ortúñez and Fuente 2010; Romaschenko et al. 2012), bluegrass in particular, both in the Russian Federation and in the world. (Tzvelev 1976; Soreng 2007; Tzvelev and Probatova 2019). These characters mainly concern the presence or absence of pubescence along the veins, the keel, the lemma callus and the rachilla surface. The characters of the stem and leaf epidermis are used for discrimination of xeromorphic species *Stenopoa* by many scientists (Rozhevitz 1934; Tzvelev 1976; Edmondson 1980, Rajbhandari 1991). Nevertheless, the characters of the stem surface below the panicle and the characters of lower stem nodes are also used as additional discriminators for *P. nemoralis*, *P. palustris*, and for closely related species: *P. sichotensis* Probatova, *P. selemdzhensis* Probatova, and *P. arsenjewii* Probatova (Probatova 1985, 2006); *P. austrouralensis* Tzvel (Tzvelev 2010), *P. probatovae* Olonova et Chepinoga, (Olonova and Chepinoga 2021). It is the stem epidermal structure that distinguishes two morphologically similar species – *P. nemoralis* and *P. sichotensis*. The discrimination of three Far Eastern species, *P. vorobievii* Probat., *P. zhirmunskii* Probat., and *P. verae* Probat., which compose the *P. vorobievii* aggregate, is also based on the epidermis characters (Probatova 2006). It should be noted that data on the surface of stems and sheaths in *P. nemoralis* and *P. palustris* are often contradictory. For example, some taxonomists suggest that *P. nemoralis* has a smooth stem under the panicle, and *P. palustris* has a rough one (Ovchinnikov and Chukavina 1957; Rajbhandari 1991; Peshkova 1979; Soreng 2007). K. Rajbhandari admits both smooth and slightly rough stems for *P. palustris*. At the same time, many floristic reports, from France to Tomsk region and Tajikistan, include *P. nemoralis* var. *rigidula* Mert. et W.D.J. Koch that differs in rough stems and sheaths (Krylov 1928; Podpéra 1925; Ovchinnikov and Chukavina 1957; Portal and Loiseau 2005, etc.). Other scientists report a rough stem under the panicle for a typical variety of *P. nemoralis* (Liu 2003). The description of the leaf sheath surface also differs: for example, according to P.N. Krylov (1928), K. Rajbhandari (1991), R. Soreng (2007). A. P. Gamayunova (1956), and N. S. Probatova (1985), *P. nemoralis* (with the exception of var. *rigidula*) has

smooth sheaths; L. Liu (2003) notes slightly rough lower leaf sheaths along with smooth ones, whereas N. L. Bor (1970) reports rough sheaths for this species.

Roughness of the stem and sheaths cannot be evaluated by touch; however, roughness depends on specific aspects of the epidermal structure. In order to objectively assess this character as the discriminator, a comparative anatomical study of the stem and leaf epidermis is required.

These are the sculptural elements (crown cells, pricles, bristles) that impart roughness to leaves and stems of grasses. The roughness degree of the stem and leaves depends on their numbers and length. Moreover, the epidermis of the stem and leaf sheaths is of most interest for taxonomy, since it is much less prone to modification variability compared with the epidermis of the leaf blade. The degree of taxon roughness is generally very individual and depends on many factors. Nevertheless, the roughness degree of *Stenopoa* bluegrasses often depends on xeromorphism (Tzvelev 1976; Edmondson, 1980): xeromorphic species are generally more scabrid.

The purpose of this study was to assess the variability of sculptural structure characters of the epidermis, which determine the roughness degree of the stem and sheath for mesomorphic bluegrass of sect. *Stenopoa*, and to evaluate the potential of these characters for taxonomic systematization. Undoubtedly, other epidermal cells such as stomata, short cells, and silicified and paired cells are also of great systematic interest, yet this study focuses on sculptural structure characters of the epidermis and their use in the keys. In addition, a differential amount of available material does not allow analysis and investigation of all mesomorphic bluegrasses of the section. Therefore, our study is limited to continental species. Narrowly endemic species of the southern Primorsky region require a different approach and will be studied and analyzed in detail in further research.

Material and methods

The materials for the study were the collections of AA, ALTB, C, E, HAL, INEP, IRKU, K, KUZ, LE, MAG, MHA, MO, MW, NS, NSK, O, PE, TK, TASH, US, UUH, UUDE, VLAD, and the collections kindly provided by Dr. R. Soreng (USA), Prof. G. Miede (Germany), Dr. E.B. Pospelova, Dr. I.N. Pospelov and Dr. N.M. Reshetnikova (Russia), Dr. B. Dickore and Dr. N. Tkach (Germany). Other materials used were collected by the authors in Russia, Middle and Central Asia, and in Chinese Xinjiang Uygur Autonomous Region (2009, 2010, and 2013) and Sichuan (2014, 2015).

Preliminary studies of the leaf epidermis of mesomorphic grasses with a light microscope revealed a very high variability of the following characters: length and shape of short and long cells, both above the veins and between them; shape and sinuosity of walls; the presence and frequency of pricles on the abaxial side, even within the same species (Olonova 1997, 2016). These results were confirmed by re-

peated studies and, therefore, further studies were performed only for the epidermis of lower leaf sheaths which turned out to be much more conservative.

The anatomical study of the stem and lower leaf sheath surfaces was carried out using a Biolam-1 binocular light microscope (Russia) and a SEC SNE-4500M (SEM) scanning electron microscope (South Korea).

For electron microscopy, sections of the stem about 5 mm long were cut out at a distance of 1–2 cm from the panicle and then fixed with a conductive carbon adhesive tape on a metal table. To reduce the impact of the charge and obtain improved secondary electron emission from the sample surface, each sample was coated with a thin layer (10 nm) of gold using an exhaust cart Quorum Q150R S. To study the leaf sheath epidermis, sections of about 25 mm² were cut out from the lower part above the node. The samples were examined in a high vacuum mode; the surface was scanned at accelerating voltage of 20 kV. The structure of the stem epidermis was determined at x110 and x300 magnification.

The study employed the terminology suggested by Metcalfe (1960), T.S. Nikolaevskaia and L.R. Petrova (1989), Ellis (1979). To assess the potential of sculptural structure characters of the epidermis for the systematics of mesomorphic bluegrasses of sect. *Stenopoa*, we studied their variability in individual species and counted the state frequencies of these characters in populations. We considered sculptural formations of the epidermis – crown cells and prickles, and bristles. To analyze the frequencies of any given formations in populations, from 13 to 22 (27) individuals were studied. For mass research of the herbarium material and population studies, stems and sheaths were totally examined; however, the surface of the stem section under the panicle about 2 to 3 cm long was taken into account. When studying stem nodes, mainly the nodes located in the lower part of the stem were considered, since trichomes are usually most pronounced there. Samples of widely distributed *P. palustris*, *P. nemoralis*, and *P. intricata* were taken from different parts of their ranges; the studied samples included *P. zhirmunskii* Probatova, and *P. verae* Probatova endemics, and species with a relatively narrow range – *P. urssulensis* Trin., *P. sichotensis* Probatova – from 1 to 3 populations, respectively.

Results

A preliminary study of the epidermis of the stem and lower leaf sheaths revealed various structures: long and short integumentary cells, guard cells of stomata, and silicified cells. Sculptural formations are represented by a variety of crown cells, prickles and bristles, which are rather short stiff hairs on the sheaths above the nodes.

The studies of the diversity of the stem and leaf epidermal structure, based on the mass and serial herbarium materials, showed that the change in the roughness degree is of both continual and discrete nature. A slight roughness of the stems

and sheaths surfaces is caused by silicified crown cells, the density of which may range from a single one (complete absence is extremely rare and does not persist in populations) to numerous ones. The upper periclinal wall shape forms a continuous series of variability (from domed to pointed at the apex). Prickles bring qualitative changes, not always well distinguished by touch. A further increase in the density of crown cells and prickles or bristles makes increases the stem roughness, and in keys the surface is described as densely scabrous. To assess the roughness, the entire range of variability (revealed in mesomorphic bluegrasses of the section) was conditionally divided into 6 states (steps), which reflect both qualitative and quantitative changes. These states are as follows: a – surface with individual crown cells (rarely completely smooth), b – surface with numerous crown cells; c – individual prickles or bristles in addition to crown cells; d – prickles or bristles of medium density, often arranged in rows; e – dense prickles or bristles; f – very dense and frequently long prickles or bristles, sharply rough surface (Figs 1–3).

The studies showed that sculptural formations of the stem under the panicle are represented by crown cells and prickles, and sculptural formations under the node and leaf sheaths are represented by crown cells and bristles, rarely turning into short hairs.

The characters of the epidermis sculptural structure of individual species were studied, and stability tests of these characters in populations were performed after revealing the diversity of epidermis elements that determine its roughness.

Poa nemoralis is the most ancient, polymorphic, and widespread species of sect. *Stenopoa*. Species formed around this species are presumably of close genetics, and they are treated as *Aggr. P. nemoralis*. N.S. Probatova (Tzvelev and Probatova 2019) attributes eight species to this aggregate in the territory of Russia. Four of the eight species are narrow endemics of the Ural and the Far East regions. Five of these are assumed to be of hybrid origin: three species presumably originated from hybridization between *P. palustris* and *P. nemoralis*, and two species probably originated from hybridization with species of sect. *Homalopoa* Dumort. (Tzvelev and Probatova 2019). *Poa probatovii* collected at the foothills of the Tunka Alps in Buriatia and then described (Olonova and Chepinoga 2022) could also originate from hybridization between *P. nemoralis* and some possibly extinct species of sect. *Homalopoa*.

Based on morphological descriptions and identification keys, most of the authors report that *P. nemoralis* has smooth leaf sheaths and stems smooth along the entire length (Rozhevitz 1934; Tzvelev 1976; Koyama 1987; Soreng 2007), that is, they are supposed to have neither prickles nor bristles, only several silicified crown cells. As for other species of this aggregate, *P. arsenjevii* Probat. has stems rough in the lower part (Tzvelev and Probatova 2019), *P. austrouralensis* Tzvelev has rough or hispid (short-haired) stems, and *P. probatovii* exhibits densely scabrid stems and sheaths. This is due to the assumed origin of these species from hybridization with the species of sect. *Homalopoa*.

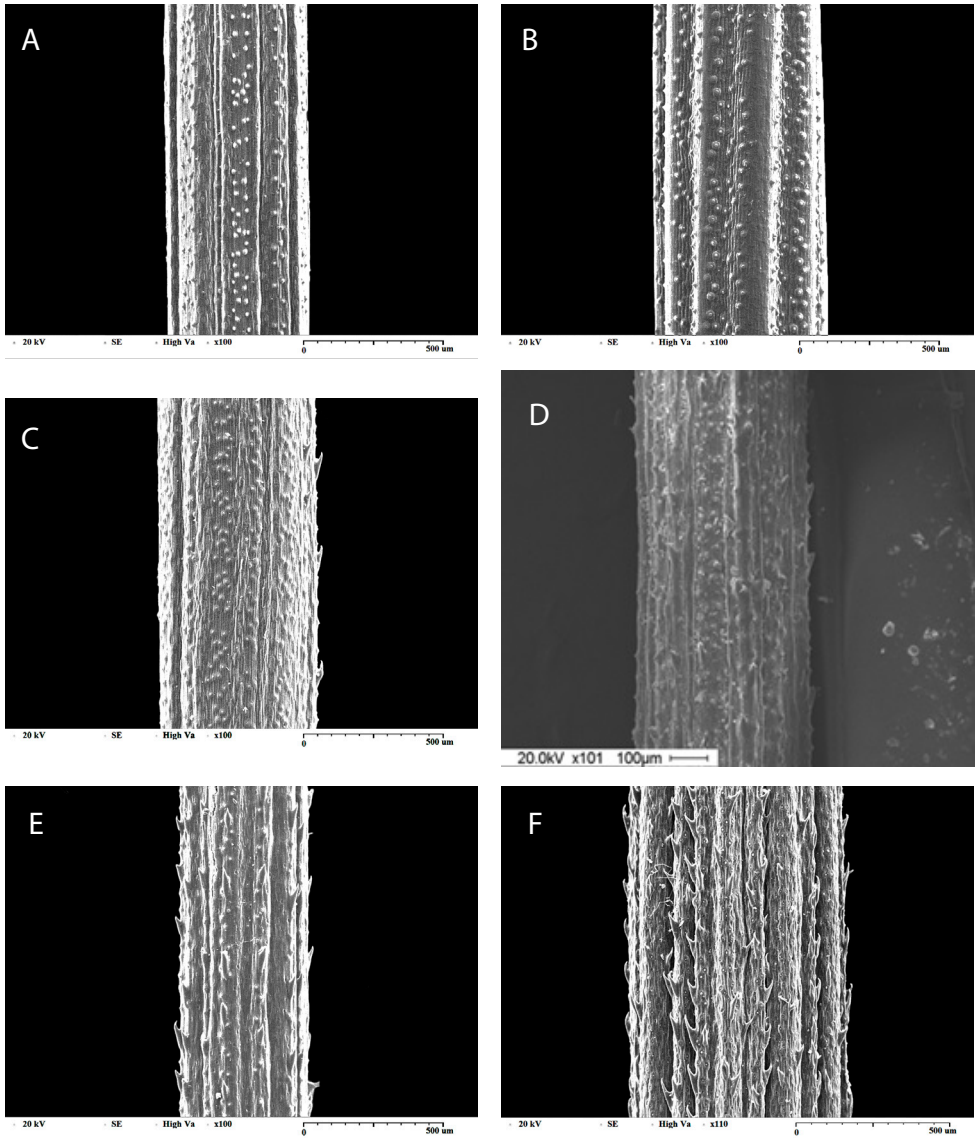


Figure 1. Different states of stems characters under the panicle within mesomorphic bluegrasses of sect. *Stenopoa*. **A, B** – with crone cells; **C** – with separate prickles; **D** – prickles in rows; **E** – dense prickles; **F** – very dense prickles.

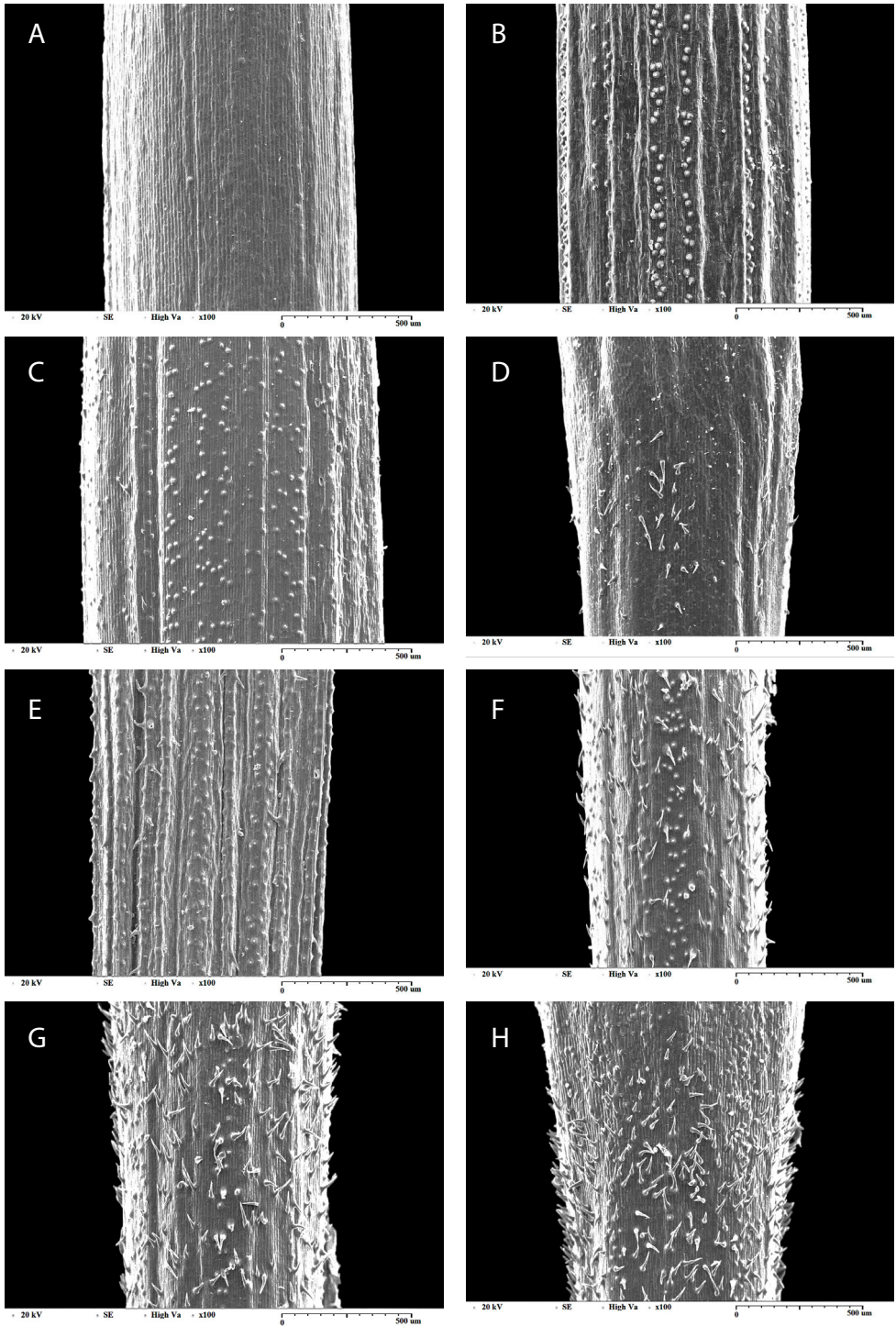


Figure 2. Different states of stems characters under the node within mesomorphic blue-grasses of sect. *Stenopoa*. **A** – with rare crown cells; **B** – with crone cells; **C** – with separate bristles; **D** – with scarce bristles; **E, F** – with dense bristles; **G, H** – very dense bristles.

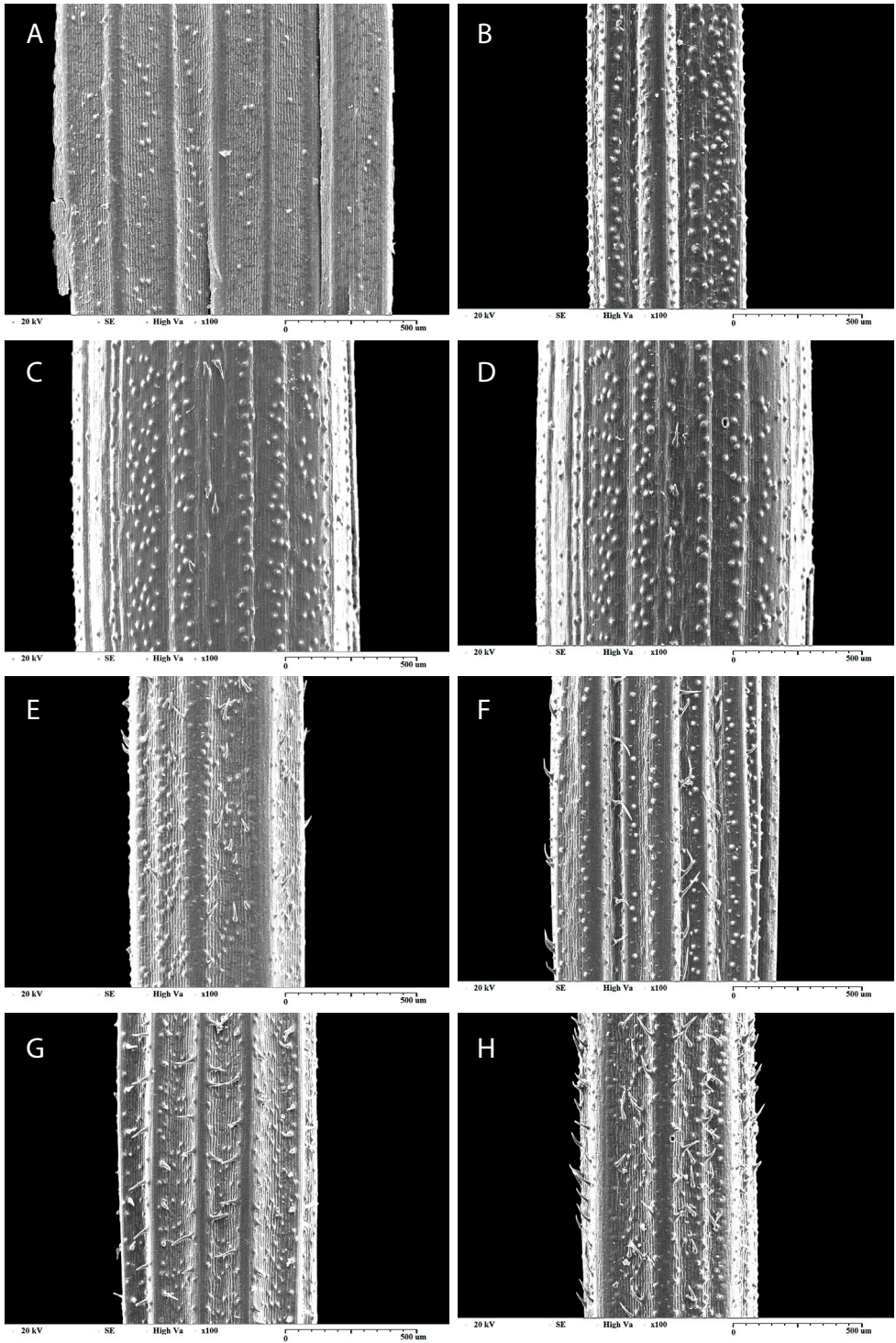


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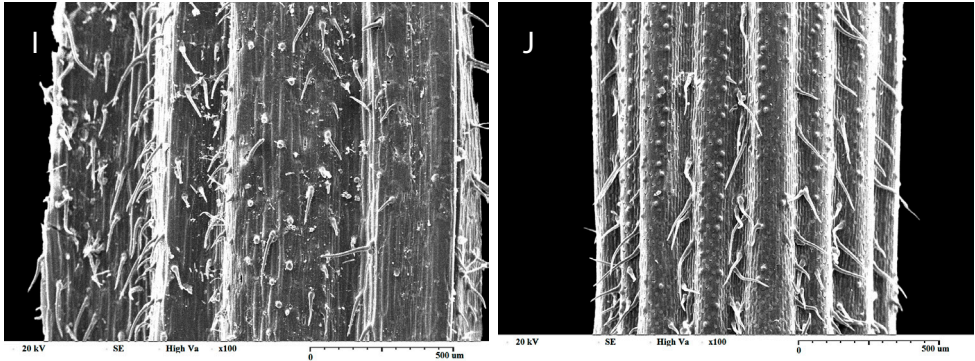


Figure 3. Different states of lower-leaf sheaths characters within mesomorphic bluegrasses of sect. *Stenopoa*. **A** – glabrous or with scarce crown cells; **B** – with crown cells; **C**, **D** – with separate bristles; **E**, **F** – with scarce bristles; **G**, **H** – dense pubescence; **I**, **J** – very dense pubescence.

Poa nemoralis has the widest distribution among all representatives of sect. *Stenopoa*. Its range extends from England and Spain to Kamchatka and Japan, from the coast of the Arctic Ocean to the Himalayas. This species has also been introduced to North America as a valuable pasture plant. However, its distribution is uneven: in Siberia and northeastern European Russia this species is relatively rare, being replaced by *P. intricata*, which is supposed to be of hybrid origin and shows the characters of *P. palustris* and *P. nemoralis* in various combinations, being generally similar to *P. palustris*. N.N. Tzvelev (1972) suggested that this hybridization took place at the end of the Pleocene due to geographic range shifts in response to changing climate conditions. In the southern part of its range, in the territory of Tajikistan, *P. nemoralis* populations also deviate from the type. P.N. Ovchinnikov (Ovchinnikov and Chukavina 1957) reported the intermediate forms between *P. nemoralis* and *P. nemoraliformis* Roshev., and between *P. nemoralis* and *P. relaxa* Ovcz. The study of *P. nemoralis* and *P. relaxa* populations from Tajikistan confirmed a close morphological similarity of these species (Olonova et al. 2012; Olonova and Khisoriev 2013).

Habitation in such a vast and diverse territory, and various natural disasters that caused migration, isolation, and hybridization over a long history of existence, affected the *P. nemoralis* gene pool and its genetic structure. A high diversity of chromosome numbers and the presence of several karyological races confirm a complex genetic structure of this species. An unprecedented number of intraspecific non-areal taxa described within the species, representing a wide variety of morphological deviations from the type material (Chase and Nils 1962; Soreng et al. 2004), indicates a high morphological variability of the species. Analysis of the literature data and the morphological and ecological-geographical studies suggest the presence of several geographical races.

To assess the significance of sculptural elements of the epidermis in the systematics of mesomorphic bluegrasses of sect. *Stenopoa*, species variability was studied across the entire range, and state frequencies were calculated in individual populations.

To reveal the variability of epidermal anatomical characters in *P. nemoralis* populations, the ratios of three character states were calculated: the epidermis surface under the panicle and under the lower nodes of the stem, and the epidermis surface of the sheath above the nodes of the lower leaves. The key morphological characters of the studied populations corresponded to *P. nemoralis*: pubescent rachilla, flag-leaf ligule length does not exceed 1 mm.

Studies into frequencies of various states in *P. nemoralis* populations across their range have shown that the epidermis anatomy in the studied populations is variable. It comprises not only silicified crown cells, which can be with a domed or pointed upper periclinal wall, but also prickles under the panicle and bristles under the lower nodes, which can impart a significant roughness to the organs (Fig. 4). On the histograms, the states with the roughest surfaces are plotted in the darkest tone. Meanwhile, most graminologists suggest that *P. nemoralis* has smooth stems and sheaths. In many populations, rough stems are not always combined with rough leaf sheaths. For the core part of the range (populations 18, 19), variability of the epidermal structure was not recorded. The studied herbarium specimens of *P. nemoralis* from the European part, including Central Russia, were predominantly smooth and had neither prickles nor bristles. All populations with the roughest surfaces (1, 2, 4, and 14) are located on the periphery of the range and contact with species that have rough stems and leaves. Most of the studied populations from the periphery of the range contained, to one degree or another, rough stems and lower leaf sheaths. Samples with prickles even under the panicle were found in populations 14 and 20 from Kamchatka and the Kola Peninsula, respectively. This may indicate past hybridization with different species, which likely altered the gene pool in some parts of the range. All of this might ultimately result in species diversification, and it is necessary to determine its degree at the genetic level.

Poa palustris is not as widespread as *P. nemoralis*. It belongs to a less ancient boreal floristic complex. However, its range is very extensive and stretches from Scandinavia to Japan. In the Middle and Central Asia, it is almost completely replaced by *P. nemoralis* and its derivatives. Species corresponding to the *P. palustris* morphotype are sometimes considered as *P. serotina* Ehrh. (Gamayunova 1956). Studies into the variability of the key morphological characters that mark the evolutionary branches of *P. palustris* and *P. nemoralis* showed that many Siberian populations include representatives with not only typical morphological characters (long, longer than 1.8 mm flag leaf ligule, and glabrous rachilla), but also with those inherent to *P. nemoralis*. This suggests that large-scale hybridizations in the late Pliocene – early Pleistocene that were mentioned by N.N. Tzvelev (1972, 1976) altered the *P. palustris* gene pool in the zone of probable hybridization.

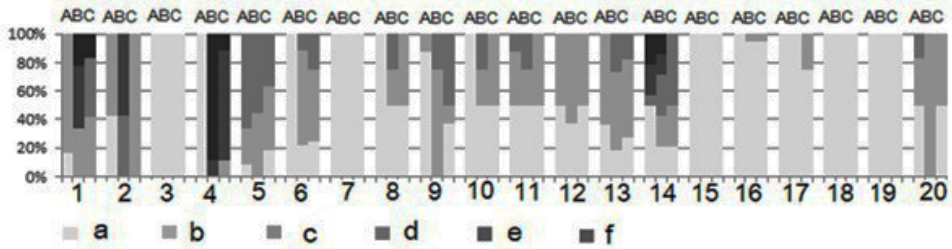


Figure 4. Anatomical structure of the stem and leaf (lower leaf sheaths) epidermis *Poa nemoralis*. **A** – stem under the panicle; **B** – stem under the node (in lower part); **C** – lower leaf sheaths. Geographic location of the studied populations: **1** – Magadan region, **2** – the Republic of Khakassia, **3, 4** – Lake Baikal, **5** – Kemerovo region (Kuznetsk Alatau), **6** – the Republic of Uzbekistan (Western Tian Shan mountains), **7** – the Republic of Tajikistan (Hissaro-Alay mountain system), **8** – the People’s Republic of China, Xinjiang (Eastern Tian Shan mountains), **9** – the People’s Republic of China, Xinjiang (Northern Tian Shan mountains), **10, 11** – the People’s Republic of China, Xinjiang (Eastern Tian Shan mountains), **12** – the Republic of Kazakhstan (Altai), **13–15** – the Kamchatka Peninsula, **16** – the Republic of Kazakhstan (Northern Tian Shan mountains), **17** – Krasnodar, **18** – France, **19** – Switzerland, **20** – the Kola Peninsula. Character states: **a** – surface with separate crown cells; **b** – surface with numerous crown cells; **c** – separate prickles and bristles, including crown cells; **d** – prickles or bristles of medium frequency arranged in rows; **e** – dense prickles or bristles; **f** – very dense prickles or bristles.

As mentioned above, many scientists report that *P. palustris* has bristles, hairs, or prickles under the lower nodes, in contrast to smooth nodes of *P. nemoralis*. The study of the herbarium material across the entire range and the population study were carried out to determine the ratio of various states of the roughness characters within *P. palustris* populations.

The studies revealed significant intra- and interpopulation variability among both *P. palustris* and hybridogenous *P. intricata*. The graphs show that, despite the majority of keys, not only numerous silicified crown cells, but also more or less developed prickles under the panicle are quite common within *P. palustris* populations. In general, the graphs plotted for *P. palustris* are dominated by a darker tone than those of *P. nemoralis*, which indicates a greater development of sculptural elements of the epidermis, and, consequently, a greater roughness of samples within the populations of these species (Fig. 5). In this case, there is no visual difference between *P. palustris* and *P. intricata*: populations of both species include practically smooth individuals (8 and 33) and rather strongly rough ones (12, 14, 15, 18, 25, 28, 32, 35, 36, and 43); in most cases, bristles located under the nodes of lower stems are oriented downwards. Less frequently, if they are thick, they can be directed both upwards and downwards. The populations with dense trichomes are widely distributed – from the Kola Peninsula to Lake Baikal and Primorye, from the taiga zone to

the forest-steppe and steppe zones. Therefore, these features are most likely caused by different reasons.

For comparison, several populations of a more xeromorphic species *P. urssulensis* Trin. were analyzed. The species was considered as a more xeromorphic variety of *P. nemoralis* for some period, but its status was soon restored. It differs morphologically from *P. nemoralis* in more xeromorphic features, and somewhat tends to *P. palustris*, which suggests its hybrid origin and mixed nature: some populations morphologically related to *P. palustris* may simply be more xeromorphic representatives of *P. intricata*, which is known to be of high modificational variability. Other populations have undergone evolutionary, genetically determined changes caused by adaptation to drier conditions. Preliminary studies of various epidermal characters within populations of *P. urssulensis* revealed more prominent sculptural elements than those within populations of *P. palustris*. This applies to the stem and leaf epidermis (Fig. 5), and generally indicates a greater xeromorphism of this species compared to *P. nemoralis*, *P. palustris*, and *P. intricata*. However, many individuals have thick or very thick bristles, at least under the lower nodes.

Poa sichotensis, a Far Eastern endemic, is somewhat isolated from other mesomorphic species of the section, but according to main morphological characters (rachilla and ligule length), it can be considered a derivative of *P. nemoralis*. Nevertheless, it differs in strongly rough stems and lower leaf sheaths, which was confirmed by herbarium materials and our own collections. The anatomical studies within *P. sichotensis* population have shown significant differences from *P. nemoralis* (Fig. 6). Thus, verification by molecular genetic methods is required in order to confirm their affinity or difference.

The preliminary study of a very interesting endemic group of mesomorphic *Stenopoa* was initiated in the southern part of Primorye. Unlike other mesomorphic species of the section with upper node approximately in the middle of the stem, these nodes are located between 1/3–1/5 of the lower part of the stem, sometimes occurring almost at the base. Moreover, these plants are quite mesomorphic, with thin and long withering leaves and wide lax panicles. The ratio of sculptural elements of the stem and leaf epidermis of *P. verae* and *P. zhirmunskii* (Fig. 6) was preliminary studied at the population level. Our studies have shown a significant scatter of frequencies within *P. verae* population and more aligned characters in *P. zhirmunskii*. This species has quite stable states of sculptural elements of the epidermis in the 27 samples studied; the observed variability did not exceed 2 steps. This group of rare endemic species growing in the very south of the Russian Pacific coast requires a more detailed analysis in our further research.

The sculptural elements of the stem and leaf epidermis were studied within populations and across the entire range. The study showed that the populations represented by common morphotypes of *P. nemoralis* (mesomorphic individuals with short, less than 1 (1.2) mm, ligules and pubescent rachilla) and the populations located in the core part of the range predominantly exhibited stems and leaf sheaths that were smooth along the entire length, and sculptural formations were

represented only by silicified cells. This confirms data reported by R.Yu. Rozhevits (1934), N.N. Tzvelev (1976), T. Koyama (1987), R.J. Soreng (2007), etc.

Poa nemoralis samples collected on the periphery of their range combine the characters of *P. palustris* and *P. nemoralis* in different proportions, and their epidermal structure (types and frequency of trichomes) brings them closer to *P. palustris*. There were samples with prickles and bristles not only under the lower nodes, but also under the panicle, which was probably due to hybridization between *P. nemoralis* and other species.

These findings, apparently, explain the assumption made by N.L. Bor, Liu Liang and N.S. Probatova that in Iran, China, and the Far East the stem and/or sheaths of *P. nemoralis* are rough.

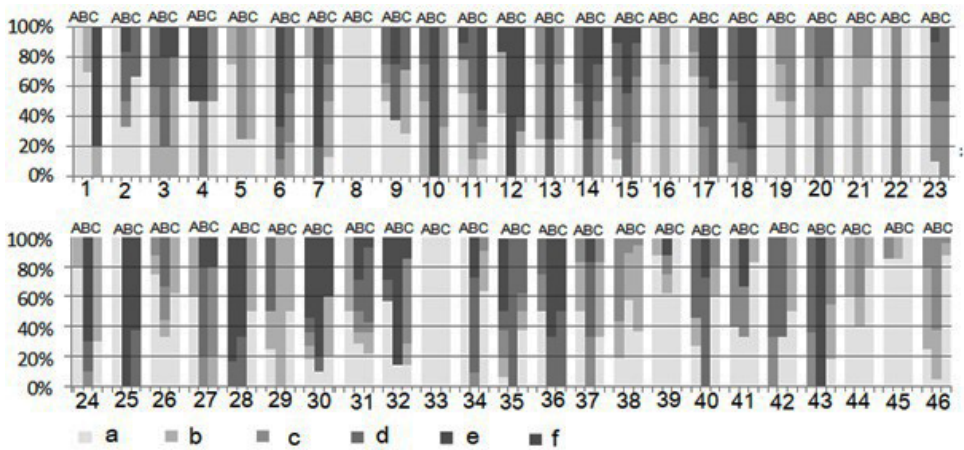


Figure 5. Anatomical structure of the stem and leaf (lower leaf sheaths) epidermis: *Poa palustris* (populations 1 – 30) and *P. intricata* (populations 31 – 46). **A** – the stem under the panicle; **B** – the stem under the node (in lower part); **C** – lower leaf sheaths. Locality of the studied populations: 1 – the Republic of Khakassia, 2 – Sakhalin, 3 – Magadan region, 4 – the Republic of Khakassia, 5 – Lake Baikal, 6 – Gorny Altai, 7 – Kuznetsk Alatau, 8 – Primorye, 9 – Tyumen region, 10 – Kuznetsk Alatau, 11 – Tyumen region, 12 – Omsk region, 13 – Novosibirsk region, 14 – Altai region, 15–16 – Lake Baikal, 17–18 – Primorye, 19 – Magadan region, 20, 21 – the Republic of Kazakhstan (Altai), 22 – Tomsk region, 23–24 – the Kamchatka Peninsula, 25 – Kemerovo region, 26–29 – the Kola Peninsula, 30 – Omsk region, 31 – the Kamchatka Peninsula, 32 – Sakhalin, 33–34 – The Republic of Khakassia, 35 – Chita region, 36 – Lake Baikal, 37 – Novosibirsk region, 38–42 – the Kola Peninsula, 43–44 – Tyumen region, 45 – the Republic of Kazakhstan (Altai), 46 – Tomsk region. Character states: **a** – surface with separate crown cells; **b** – surface with numerous crown cells; **c** – separate prickles and bristles including crown cells; **d** – prickles or bristles of medium frequency, arranged in rows; **e** – dense prickles or bristles; **f** – very dense prickles or bristles.

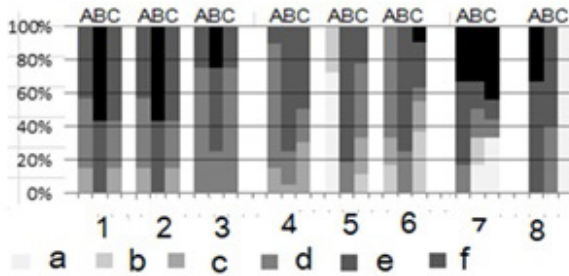


Figure 6. Anatomical structure of the stem and leaf (lower leaf sheaths.) epidermis: *P. urssulensis* (populations 1–3), *P. sichotensis* (populations 4–6), *P. verae* (population 7), *P. zhirmunskii* (population 8). A – the stem under the panicle; B – the stem under the node (in lower part); C – lower leaf sheaths. Locality of the studied populations: 1 – Omsk region, 2 – Novosibirsk region, 3 – the Republic of Buryatia, 4 – the Kamchatka Peninsula, 5–8 – Primorye. Character states: a – surface with separate crown cells; b – surface with numerous crown cells; c – separate prickles and bristles including crown cells; d – prickles or bristles of medium frequency, arranged in rows; e – dense prickles or bristles; f – very dense prickles or bristles.

Within populations of *P. palustris*, the composition and density of trichomes vary in a relatively wide range, from almost completely smooth to those covered with dense trichomes. *Poa intricata*, which presumably arose from hybridization between *P. palustris* and *P. nemoralis*, has the stem and leaf epidermal structure that is similar to that of *P. palustris*. Moreover, quite dense prickles were frequently found in *P. palustris* representatives. They were found not only under the lower nodes, but also under the panicle, which brings them closer to a more xeromorphic aggregate *P. urssulensis*.

The study of the Far Eastern mesomorphic endemic *P. sichotensis*, as well as *P. verae* and *P. zhirmunskii*, which can be attributed by morphological characters to a separate aggregate, showed that they differ from other mesomorphic species of the section in sculptural elements of the epidermis.

This study has shown that the characters of the epidermal structure cannot be used as discriminators for mesomorphic bluegrass of sect. *Stenopoa*, only as additional characters. Moreover, characters of the epidermal structure can mark the evolutionary branches of *P. palustris* and *P. nemoralis* along with such morphological characters as ligule length and rachilla pubescence. At the same time, the results of the study of the stem epidermis may indirectly indicate the hybridization processes occurring in individual populations of *P. nemoralis*.

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