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RESEARCH ARTICLE

# Phenotypic plasticity of the stem epidermis in the bluegrasses (*Poa* L.) of section *Stenopoa* Dumort. (*Poaceae*). II. Xeromorphic species

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## Abstract

Section *Stenopoa* is one of the most significant among the bluegrasses, and its proper identifying is important task. The epidermal characters, which determine the degree of roughness of the bluegrasses, are used widely in botanical literature, but the information on bluegrasses characters is controversial frequently. This work is devoted to the study of xeromorphic representatives of the section. The aim of this work was to assess the variability of the sculptural features of the epidermis, which determine the degree of roughness of the stems within xeromorphic bluegrass of the *Stenopoa* section, and the possibility of using these characters in taxonomy. The types of epidermal trychomes and their variability and frequencies within the populations of 12 species were researched using SEM and light microscope. As a result of the study, no species-specific types of epidermal structure were revealed. In all the studied species, with the exception of the Central Asian hybridogenic species *Poa psilolepis*, the epidermis of the stem and leaf sheaths contained crown cells and pricles or bristles in varying proportions. Under the panicle only crown cells or pricles directed upwards were observed. The most species showed high interpopulation and intrapopulation variability. At the same time, the Central Asian species were distinguished by less polymorphism and a small number of deviated individuals in the populations.

The conducted studies cast doubt on the possibility of widespread use of epidermal sculpture as a discriminator for xeromorphic *Stenopoa* species, including for distinguishing between the Siberian *P. stepposa* and the European *P. erythropoda*.

**Keywords**
Asia, plant anatomy, *Poa versicolor* aggr., populations, SEM

## Introduction

The section *Stenopoa* Dumort. is rightfully considered to be one of the most problematic among the difficult genus of bluegrasses (*Poa* L.). As in grasses in general, the structure of their vegetative and generative organs is uniform. There are no bright markers of evolutionary branches, and there are very few discriminator characters. Therefore, the search for additional systematic features is of great practical importance.

This work is a continuation of the study of the variability of the sculptural features of the epidermis, which determine the degree of roughness of the stems and sheaths in bluegrasses of the *Stenopoa* section, and the assessment of the possibility of using these features in taxonomy. This work is devoted to the study of xeromorphic representatives of the section (ecological-evolutionary group III, uniting moderately xeromorphic species, the upper node of which is located between the lower 1/3 and 1/6 of the stem).

With the cooling and drying of the climate in the Pleistocene, the centers of species and form diversity arose both in Europe and in the mountain systems of Asia. Therefore xeromorphic bluegrass of the section are much more numerous and diverse than the mesomorphic ones, and the characters of roughness of stems and leaf sheaths is used to distinguish between species much more often, acquiring much more weight. Features of the stem surface under the panicle and lower nodes are widely used in keys as additional discriminators for xeromorphic *Stenopoa* species (Chung, 1965; Prokudin, 1977; Edmondson, 1980; Koyama, 1987; Liu, 2003; etc.). Special studies were also carried out to study the possibility of using these characters to distinguish between closely related species (Serbanescu, 1968). In the English-language literature, when defining xeromorphic *Stenopoa*, two alternative states are usually used – glabrous and scabrous (scabrid), whereas in Russian-language keys they distinguish between smooth, finely rough, rough, and strongly rough (Rozhevitz, 1934). N.N. Tzvelev (1976) distinguished not only smooth, almost smooth, rough and strongly rough, but indicated the anatomical details of the structure of the stem and leaf epidermis. He noted the stems and sheaths strongly rough because of rather large pricles (*P. versicolor* subsp. *stepposa*), pricles under the nodes facing only upwards (*P. versicolor* subsp. *araratica*) and partially facing downwards (*P. versicolor* subsp. *versicolor* and *P. versicolor* subsp. *erythropoda*). Characters of the surface of the stem and sheaths were widely used to distinguish between Sibe-

rian xeromorphic *Stenopoa*. So, L.P. Sergievskaya (1961) distinguished the following related species according to the degree of stem roughness: *P. stepposa* (glabrous and smooth) and *P. botryoides* (rough), *P. argunensis* Roshev. (slightly rough) and *P. reverdattoi* Roshev. (smooth or rough under the inflorescence). V.V. Reverdatto (1964) used more detailed characterization: *P. stepposa* (covered with blunt crown cells), *P. botryoides* (rough) and *P. transbaicalica* (sharply rough); *P. argunensis* Roshev. (rough) and *P. reverdattoi* Roshev. (sharp).

The most detailed description of the stem surface and sheaths structure can be found in N.N. Tzvelev and N.S. Probatova work (Tzvelev, Probatova, 2019). In addition to smooth, slightly rough and slightly rough surfaces of stems and leaf sheaths, they used such states of the surface character, as slightly rough because of pricles, rough from numerous pricles, rough from pricles and short hairs, pricles predominantly directed downwards, pricles predominantly directed upwards.

At the same time, it should be noted that there are discrepancies in the assessment of the degree of roughness by different authors. Thus, the surface of the stem of *P. argunensis* that N.N. Tzvelev (1976), N.S. Probatova (Tzvelev, Probatova, 2019 evaluated as smooth, were described as slightly rough by L.P. Sergievskaya (1961, 1969). V.V. Reverdatto (1964) described them as more or less rough, and G.A. Peshkova (1979) and Liu Liang (2003) as rough ones; in a closely related species *P. reverdattoi* L.P. Sergievskaya (1961) noted a smooth or rough stem under the inflorescence, but the majority of taxonomists (Reverdatto, 1964; Tzvelev, 1968, 1976; Liu, 2003; Tzvelev and Probatova, 2019) indicated the rough stems for this species. In his protologs R.Yu. Rozhewitz (1934) indicated that the stem of *P. argunensis* is rough, while that of *P. reverdattoi* is sharply rough.

R.Yu. Rozhevitz (1934) considered *P. stepposa* and *P. transbaicalica* as separate species, indicating more or less sharply rough stems under the panicle for both. At the same time, the protolog of *P. stepposa* (Rozhevitz, 1934, p. 754) indicates "caulis … glaber". In the morphological description in the Flora of the USSR (Rozhevitz, 1934, p. 401) he indicates "the stems are more or less sharply rough", and in the key (Rozhevits, 1934, p. 374) – "the stem under the panicle is finely rough or almost smooth". V.V. Reverdatto (1964), who also considered *P. stepposa* and *P. transbaicalica* as separate species, indicated stems of *P. stepposa* as rough under the inflorescence with small obtuse crown cells, while for *P. transbaicalica* they were sharply rough. L.P. Sergievskaya (1968) and Liu Liang (2003) noted smooth stems for *P. stepposa*, and rough stems for *P. transbaicalica*, L.P. Sergievskaya to point the sharply rough ones. J.R. Edmondson (1980) also noted that *P. stepposa* had smooth stems and distinguished it from other European species close to *P. versicolor* genus on this basis. N.N. Tzvelev, who, within the framework of the polytypic concept, considered *P. transbaicalica* as a synonym for *P. versicolor* subsp. *P. stepposa* noted (Tzvelev, 1976) that the stems under the panicle and the sheaths in this subspecies were strongly rough because of rather large pricles, and by this character distinguished it from slightly rough or almost smooth subsp. *relaxa* (Ovcz.) Tzvel. and subsp. *ochotensis* (Trin.) Tzvel.

Thus, the review of the literature shows that the character of the stem surface under the panicle is of great importance in the systematics of xeromorphic bluegrass of the section *Stenopoa*. Nevertheless, the subjectivity of the assessment of the roughness degree determined by touch and conflicting information in the literature require a more detailed study. The sensation of roughness is objectively determined by the quantity and quality of the sculptural elements of the epidermis – crown cells, pricles and bristles. The aim of this work was to assess the variability of the sculptural features of the epidermis, which determine the degree of roughness of the stems and sheaths in xeromorphic bluegrass of the *Stenopoa* section, and the possibility of using these characters in taxonomy. N.N. Tzvelev (1976) and N.S. Probatova (Tzvelev, Probatova, 2019) also paid attention to the direction of the pricles under the nodes, and this feature also seems promising for research. The group of xeromorphic bluegrass of the section is very numerous, but European species will be considered separately since their main core is located within Asia.

The species under consideration belong to three aggregates – aggr. *P. versicolor*, its species are distributed in semiarid habitats from former Czechoslovakia and Yugoslavia (Edmondson, 1980) to Kamchatka (Tzvelev and Probatova, 2019); Central Asian aggr. *P. crymaphila*, which combines species that presumably resulted from the hybridization of representatives of the aggregates *P. versicolor* and *P .glauca*; as well as East Asian aggr. *P. mongolica*, including *P. skvortzovii*, *P. mongolica*, and *P. alta*. The distribution of the last two species need serious clarification, for this reason they are not included in the analysis until these data are available.

Species of the *P. versicolor* aggregate presumably appear to be the derivatives of the mesomorphic *P. palustris*, differentiated over a wide area of Eurasia through geological processes that promoted isolation and hybridization. Almost all of them are vicarious and occupy their special ecological and ecological-climatic niches. The most common species of the *P. versicolor* aggregate are *P. stepposa*, *P. relaxa*, *P. ochotensis*, *P. botryoides*, *P. argunensis*, *P. orinosa* Keng, *P. varia* Keng ex Liu. According to the degree of xeromorphism, these species represent the following evolutionary series: *P. relaxa*, *P. stepposa*, *P. ochotensis*, *P. botryoides*, *P. argunensis*, *P. varia* and *P. orinosa*. At the same time, *P. relaxa* is closely related to *P. nemoralis*, possibly through *P. urgutina*, which is now synonymized by most botanists with *P. relaxa* (Tzvelev, 1976). *Poa ochotensis* seems to be resulted from hybridization of *P. versicolor* s.l. and *P. sphondylodes*.

## Material and methods

The materials for the study were the collections of AA, ALTB, BSD, DD, E, K, LE, MAG, MHA, MO, MW, NS, NSK, O, PE, TK, TASH, US, UUH, VLAD, as well as collections kindly presented by Dr. R. Soreng (USA), Prof. G. Miehe, Dr. B. Dickoré and Dr. N. Tkach (Germany), E. B. Pospelova and I. N. Pospelov (Russia). In addition, we used our own collections made in the Russian Federation, Middle Asia, in the Chinese Xinjiang Uygur Autonomous Region in 2009, 2010, 2013, province

Sichuan in 2014 and 2015 and the Indian Himachal Pradesh and Uttarakhand in the summer of 2022.

The anatomical study of the surface of the stem and sheaths of the lower leaves was carried out using a light microscope and a Philips SEM 515 scanning electron microscope (SEM) (Holland). Population studies were carried out on a light microscope MBS 10 LOMO (Russia) at maximum magnification (8 x 7).

To study with an electron microscope, sections of the stem with an area of about 25 $mm^2$ were cut out at a distance of 1–2 cm from the panicle and glued with double tape on a metal table. To study the epidermis of leaf sheaths, sections of about 25 $mm^2$ were cut out in the lower part of the stem, above the node. To reduce the influence of the charge, the preparations were treated with silver by thermal spraying in a vacuum. The samples were examined in a high vacuum mode, the surface was scanned at an accelerating voltage of 25 kV. Determination of the structure of the stem epidermis was carried out at a magnification of 110, 300, and 600 times.

To describe the results we used the terminology suggested to describe the grasses epidermis by Metcalfe (1960), T.S. Nikolaevskaya and L.R. Petrova (1989), Ellis (1979).

To identify interspecific variability of the surface of stems and sheaths characters and the frequencies of their states, from 23 to 2 populations, depending of the range size and the rarity of species, were studied; to study intraspecific variability, from 15 (25) to 10 plants were taken from each of the populations. The epidermis of the following stem areas was studied: the stem under the panicle and under the lower nodes, leaf sheaths above the lower nodes. The presence and types of trichomes (crown cells, pricles and bristles) and their relative degree of density were taken into account. The orientation of the pricles or bristles was taken into account separately.

## Results

As it was shown by preliminary studies, the sculptural formations of xeromorphic *Stenopoa* do does not differ from mesomorphic ones in general (reference to part I) and are also represented by a variety crown cells, pricles or bristles. It should be noted that there is no sharp difference between pricles and bristles. Although formally the pricles are distinguished by their shorter length and relatively wide base, observations have shown that there are numerous intermediate forms between them (Fig. 1F) and short stiff hairs. To assess the roughness, the entire range of its variability, found in the xeromorphic bluegrass of the section, was divided into 5 stages, representing a series of increasing roughness and reflecting both qualitative and quantitative changes: a – surface with individual crown cells (rarely completely smooth ); b – surface with numerous crown cells; c – in addition to crown cells, random and rare pricles or bristles appear; d – pricles or bristles of medium density, usually arranged in rows; e – dense pricles or bristles, surface sharply rough to the touch (Figs 2–4). At the same time, it is noticeable that pricles or bristles are almost always accompanied by more or less pronounced crown cells, but the presence of

crown cells does not always imply the presence of pricles (bristles). Pricles (bristles) are a qualitatively new type of trichomes, and their appearance can be considered an evolutionary event. An important qualitative feature is also the orientation of the pricles or bristles. In the course of research among xeromorphic bluegrass of the section, 4 states of this character were revealed: a – trichomes are directed upwards; b – trichomes are directed downwards; c – trichomes are directed up and down; d – trichomes are directed perpendicular to the surface of the stem.

Studies of the epidermal sculpture of the stem under panicle, under the lower nodes and sheathes above the nodes within populations have shown that, despite the prevailing opinion that the stems of xeromorphic *Stenopoa* species are usually rough with pricles, there were found some individuals, and often entire populations, were the pricles were absent at all, different species to demonstrate the different ratios between crown cells and pricles, different density of these trichomes as well. Various types of trichomes, their density and orientation, revealed as a result of the research, are shown in Figs 2–4.

*Poa relaxa* is one of the three most common species of *P. versicolor* aggregate, growing mainly in the mountains of Central Asia. Their morphological features, in particular, the shape and structure of the panicle and spikelets may indicate its hybrid nature and getting some genes from the genpool of *P. glauca* aggregate. Nevertheless, morphologically it is much closer to *P. stepposa* and on this basis attributed to the *P. versicolor* aggregate. According to its ecological and morphological features, this species is one of the most mesomorphic among the species of the *P. versicolor* aggregate.

According to the literature data (Rozhevits, 1934; Gamayunova, 1956; Tzvelev, 1968, 1974; Liu, 2003), the stem of this species is rough, at least under the panicle, while R.Yu. Rozhevits notes sharply rough stems under the panicle, A.P. Gamayunova also indicates rough sheaths, and P.N. Ovchinnikov and A.P. Chukavina (1957) suggested almost smooth stems.

To reveal the variability of the sculptural features of the epidermis and their frequencies in *P. relaxa* populations, the ratios of the states of these characters were calculated (Fig. 5). All populations, involved in analisys morphologically corresponded to *P. relaxa*.

Studies of the characters of epidermal sculpture in different parts of the *P. relaxa* range showed a wide scatter in the occurrence of both the type of trychomes (crown cells and pricles) and the frequencies of displaying of these character states (Fig. 5). The graphs show that, the same types of trichomes and the degree of their density were constant only in two populations. These are population 5 from the Chinese Tien Shan, where both stems and leaf sheaths were densely covered with pricles in all the studied parts, and population 15 from East Kazakhstan, where, on the contrary, all the studied parts had no pricles at all. Our preliminary studies confirmed the observations of P.N. Ovchinnikov and A.P. Chukavina (1957) that this species sometimes has stems that are almost smooth to the touch, which is explained by the predominance of crown cells on the surface of the epidermis and rare, often com-

plete absence of pricles. This is visualized on the graph as a predominance of pink (crown cells) and light blue color (rare pricles). At the same time, 12 (63%) of the 19 examined populations revealed the individuals that had both crown cells and pricles in the epidermis. Three populations out of these twelve had these combinations in the epidermis of all three parts of the shoot studied. At the same time, different variability was observed in different parts. Thus, under the panicle, both types of trichomes were found in 47% of the populations, under the nodes, only in 21% of the populations, and, finally, in leaf sheaths above the lower nodes, in 58% of the studied populations, trichomes were represented by both crown cells and pricles. In other words, the stems under the nodes are distinguished by the greatest monomorphism in the studied species. Among the sculptural elements monomorphic in structure of individual parts of the plant populations, most of the trichomes were represented by pricles or bristles. They are represented by six populations (3, 5, 6, 12, 16, and 17). The epidermal sculpture of mere crown cells was found in only one population. Studies have shown that although this population should be attributed to *P. relaxa* according to formal morphological features, it approaches to *P. nemoralis*, grows nearby and possibly has a hybrid origin or belongs to a special ecotype.

The graphs of frequency of trichomes in terms of their directionality, generally showed a predominance of blue, which marks upwardly directed trichomes (Fig. 5 II). At the same time, no other states are observed under the panicle. Under the nodes in the vast majority of populations (except for 1 and 9), the dominance of this state (upwardly directed) kept, and in nine populations (47%) it was constant. In addition, downwardly directed pricles were observed in seven populations, while in populations 1 and 9 this state predominated. In populations 8, 9, and 11, pricles directed up and down were also observed. Perpendicularly directed trichomes (bristles) were found only in the epidermis of leaf sheaths. They were observed in eleven populations (53%), and in populations 5, 11 and 19 their presence was constant. In eight populations, the bristles directed upwards were found above the nodes, while in populations 4, 7, 13, and 16, the bristles directed upwards were found in all parts of all studied specimens. In six populations, specimens with leaf sheath bristles directed downwards were found, while in population 8 all bristles were directed upwards. Bristles directed both downwards and upwards were also found in six populations (Fig. 5 II).

Geographical analysis of the material did not reveal regional anatomical and morphological peculiarities. Thus, in the Pamir populations (7–11), one can note both a variability of characters (both crown cells and pricles are found), and a different degree of their density. The same can be said about populations 3–5 from the Chinese Xinjiang Uygur Autonomous Region: among them some have the stem epidermis of all the studied individuals densely covered with pricles, and some ones are without the pricles at all. But the greatest diversity is observed both among and within populations from Kazakhstan (13, 15–19). There are populations, where all (population 15) or almost all (population 13) do not have pricles at all. At the same time, some of the populations of this area consisted of rather rigid individuals, the epidermis of which always included pricles (16, 17).

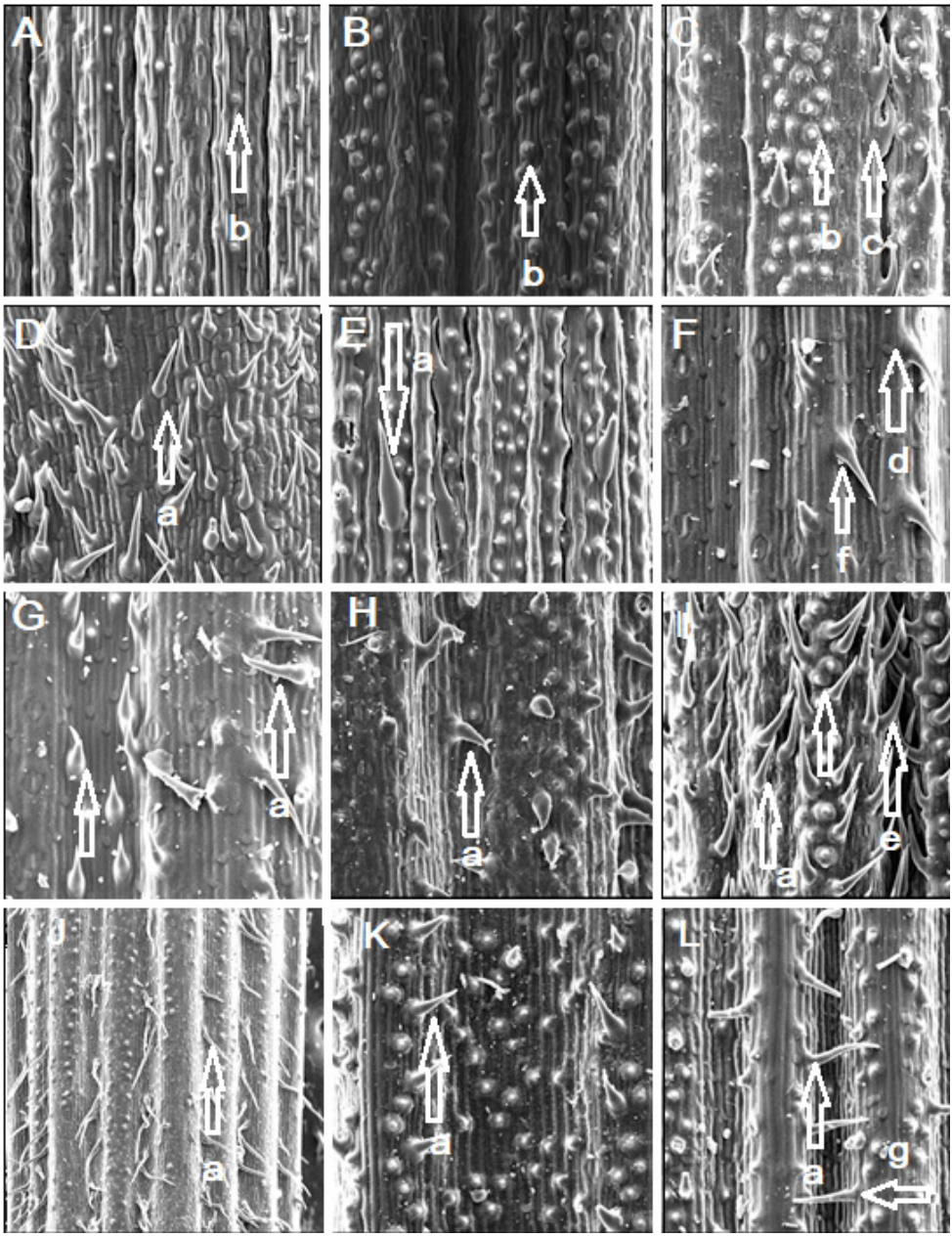


**Figure 1.** Different types of epidermal trichomes of stems and leaf sheaths of xeromorphic bluegrass of the section *Stenopoa*. A–C – stem under panicle; D–F – stem under a node; G–L – sheath above the node. A–I, K, L (× 300). J (× 110); a – bristles; b – crown cells; c – pricles; d – structures, intermediate between pricles and bristles; e – trichomes are directed upwards; f – trichomes are directed downwards; g –trichomes are directed perpendicular to the surface of the stem.

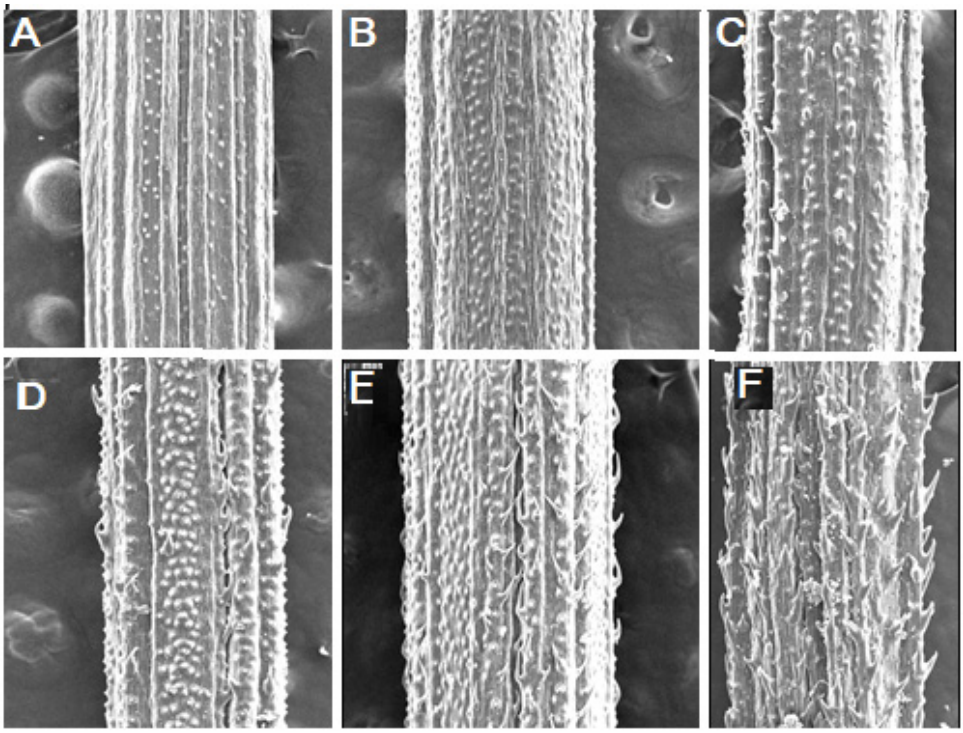


**Figure 2.** Sculptural elements of the stem epidermis under the panicle (× 110). Character states: A – individual crown cells (rarely almost completely smooth ); B – numerous crown cells; C – in addition to crown cells, random and rare pricles appear; D – pricles of medium density, usually arranged in rows; E, F– dense pricles.

An analysis of the geographical distribution of various states of the trichome orientation characters did not reveal obvious patterns: all epidermal trichomes were upwardly directed in populations from the Chinese Tien Shan, and from Tajikistan, and from East Kazakhstan, and from the Kazakh Tien Shan; all bristles of the the leaf sheaths epidermis above the nodes were directed perpendicularly in populations from the Chinese Tien Shan, Tajikistan, and Kazakhstan.

The conducted studies of *P. relaxa* showed that, despite the predominance of specimens with pricles, which made the plant a greater rough (blue color in the diagram), the epidermis without pricles (pink), is quite widespread. This confirms the observations of P.N. Ovchinnikov and A.P. Chukavina (1957) that this species can have both rough and almost smooth stems.

*Poa stepposa* is the central species of the *P. versicolor* aggregate, distributed in Siberia, Eastern Europe, and the Russian Far East, inhabiting both the plains and rising to the mid-mountain belt. According to its ecological and morphological features, this species occupies an intermediate position between the more mesomorphic *P. relaxa* and the more xeromorphic *P. botryoides*.

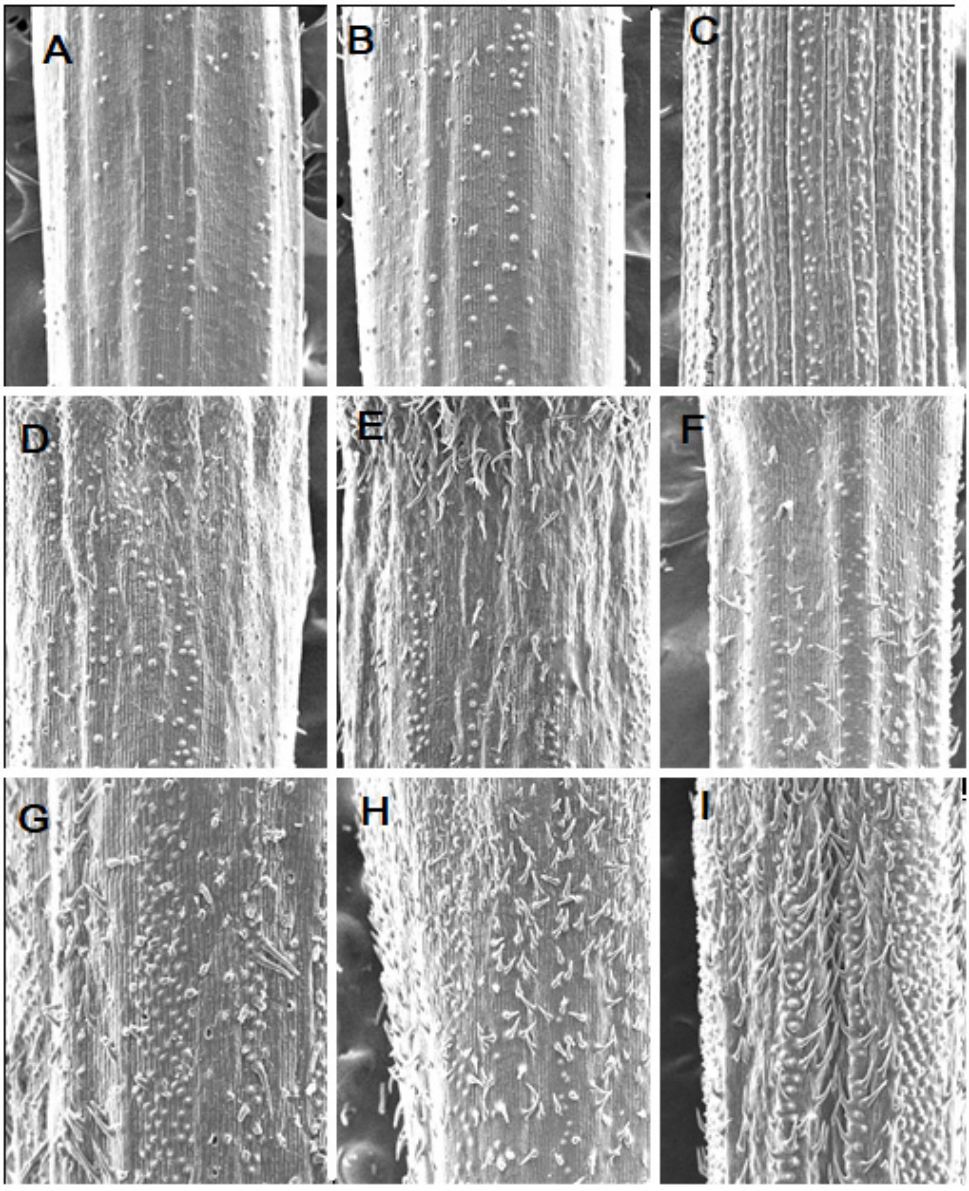


**Figure 3.** Sculptural elements of the stem epidermis under the nodes (× 110). Character states: A, B – individual crown cells (rarely almost completely smooth ); C – numerous crown cells; D – in addition to crown cells, random and rare pricles appear; E– G – pricles of medium density, usually arranged in rows; H, I – dense pricles.

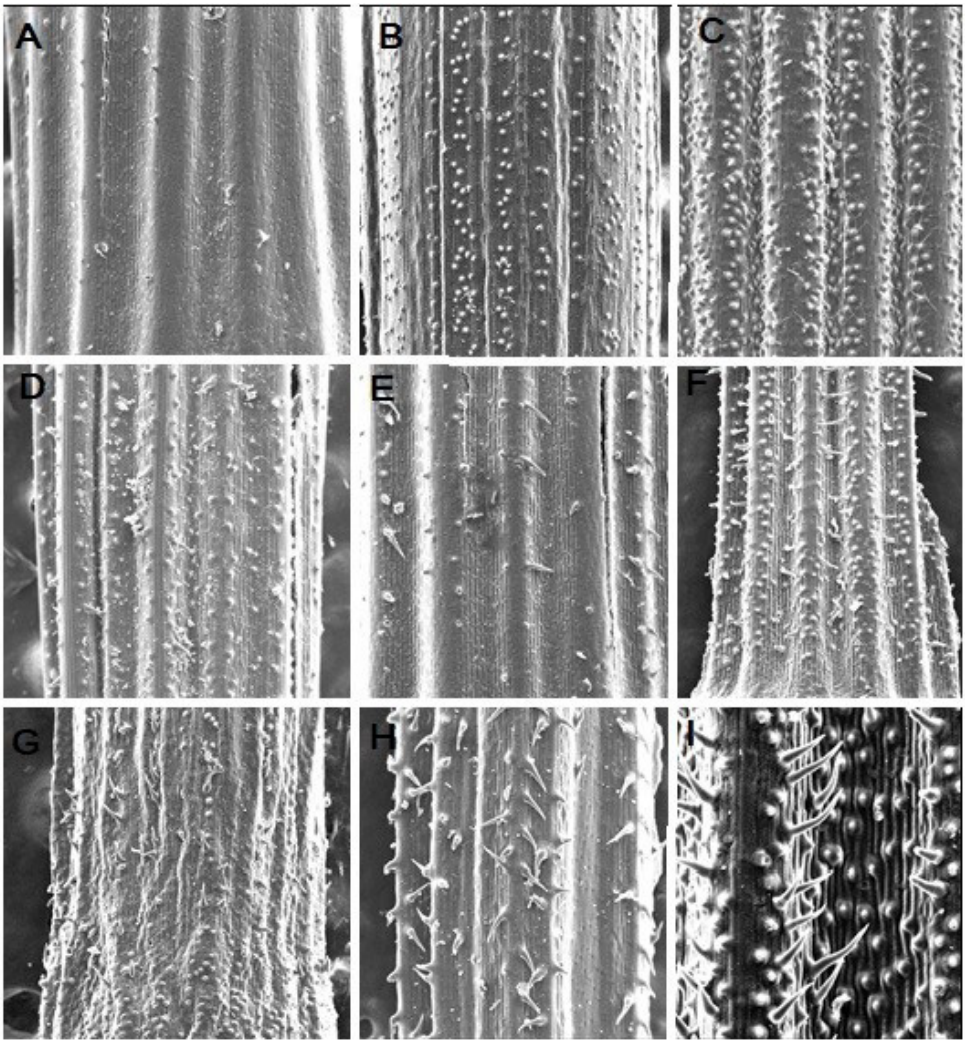


**Figure 4.** Sculptural elements of the leaf sheaths epidermis above the nodes. A–H (× 100). I (× 300). Character states: A – individual crown cells (rarely almost completely smooth ); B, C – numerous crown cells; D, E – in addition to crown cells, random and rare pricles appear; F, G – pricles of medium density, usually arranged in rows; H, I – dense pricles.

Literature data on the smoothness/roughness of this species stem surface are contradictory: L.P. Sergievskaya (1961, 1969), Yu.N. Prokudin (1977), Edmondson (1980) and Liu Liang (2003) indicate a smooth stem. The strongly rough stem of *P. stepposa* is pointed out by R.Yu. Rozhevitz (1934), N.N. Tzvelev (1976), G.A. Peshkova (1979) and N.S. Probatova (1985); V.V. Reverdatto (1964) notes that under the panicle the stem is rough because of small obtuse tubercles, and A.P. Gamayunova (1956) suggested both sharp-rough and smooth stems.

To identify the anatomical features of the epidermis and the frequencies of character states in populations, 23 populations of *P. stepposa* were studied. These studies also made it possible to reveal fairly wide interpopulation and intrapopulation variability in the structure of the epidermis of this species. Both the types of sculptural elements of the epidermis (crown cells and pricles) and the frequencies of the states of these characters varied (Fig. 6 I). At the same time, in none of the studied populations, any one type and severity (density) of trichomes was stably kept, as was observed twice within *P. relaxa*.

At the same time, it can be seen that the proportion of individuals bearing pricles (they are marked in blue on the graph) is higher in *P. stepposa* than in *P. relaxa*; an increase in the proportion of individuals with dense pricles is also noticeable (dark blue color on the graph). Only in one population – 7 from Altai mountains demonstrates the predominance of crown cells over pricles in the structure of the epidermis in all parts of the stem; in addition, in two populations, 12 and 23, crown cells predominated over bristles over nodes. At the same time, in two populations – 1 and 2 – both types of trichomes were presented in equal proportions. The predominance of pricles in all studied parts of the plant was observed in 12 populations (52%), and the pricles only were found in five (22%) populations.

Thus, the opinion about the rougher stems of this species compared to *P. relaxa* was confirmed, as well as the observation of A.P Gamayunova (1956) that in *P. stepposa*, in addition to the rough stem, it can also be found almost smooth one, although quite rarely. The greatest variation in both character states and their frequencies was observed in populations 12 and 16 (both from Buryatia).

An analysis of the specimens on the basis of the orientation of the sculptural elements showed even greater predominance of upward directed trichomes than in the previous species. Significantly more often, in 19 populations (83%), perpendicularly directed bristles were encountered, and in seven populations this character state was noted in all specimens. At the same time, like within *P. relaxa* populations, these bristles were observed only in the epidermis of leaf sheaths. Pricles or hairs turned down were quite rare, while those turned both up and down were much more common, both above and below the nodes. In populations 10, 12, 14, and 16, they even predominated (Fig. 6 II). It should be noted that, despite the undoubted predominance of upward directed pricles under the nodes, the populations with downward directed pricles, which are characteristic for European *P. versicolor* and *P. erythropoda*, were observed among *P. stepposa* as well (populations 12, 16, 21, 22).

Geographical analysis also did not reveal the special regional anatomical and morphological features. Thus, in Khakassia and in the south of the Krasnoyarsk district, there were populations of moderately rough individuals with a large proportion of crown cells and rare pricles (populations 2, 3, 4), and with a predominance of pricles, albeit not very dense (population 11), and, finally, the population 18 included the plants, rather densely covered with pricles. The same diversity is demonstrated by the territories of Buryatia and the Chita region, including the Baikal populations, and the steppe regions of Western Siberia (21, 22, 23). The largest scat-

ter was observed within the populations of Altai Mountain (including its Chinese territory). On one hand, in population 7, there were individuals only with crown cells under the panicle and above the nodes, and crown cells also predominated under the nodes, although sparse or medium-dense pricles were observed as well; on the other hand, in population 8, pricles were found in all the studied individuals and in all the studied parts of the plant. We were unable to detect the geographical patterns in the distribution of trichomes of different directions as well.

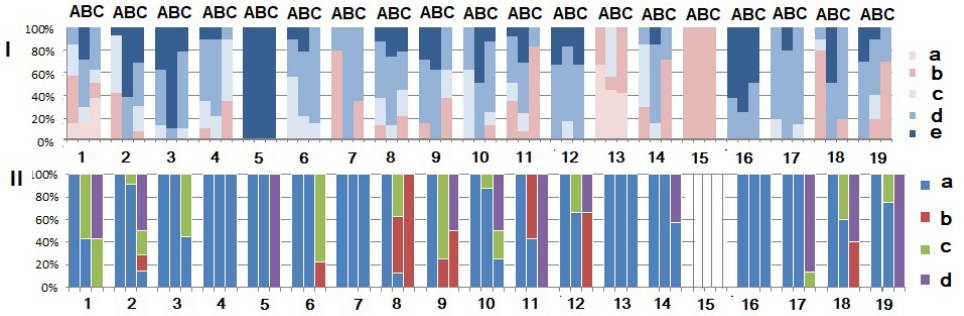


**Figure 5.** Anatomical structure of the stem and leaf (lower leaf sheaths) epidermis of *Poa relaxa*. A – stem under panicle; B – stem under the node (in the lower part); C – sheaths of lower leaves. Locations of the studied populations: 1 – Uzbekistan (Turkestan Ridge), 2 – Uzbekistan (Pskem Ridge), 3–5 – China, Xinjiang (Tien Shan), 6 – South Kazakhstan (Baraldai Ridge), 7 – Tajikistan (South-Eastern Pamir), 8, 9 – Tajikistan (Western Pamir), 10, 11 – Tajikistan (Eastern Pamir), 12 – Tajikistan, 13 – East Kazakhstan, 14 , 15 – Kazakhstan (Altai), 16 – Kazakhstan (Northern Tien Shan), 17–19 – East Kazakhstan. I Morphological types of trychomes: a – surface with rare crown cells (rarely completely smooth); b – numerous crown cells; c – rare pricles or bristles appear; d – pricles or bristles of medium density, often arranged in rows; e – pricles or bristles dense. Crown cells are pink, pricles are blue. II Direction of trychomes; a –upwards; b –downwards; c – directed up and down; d –directed perpendicular to the surface of the stem.

*Poa botryoides* is species of the *P. versicolor* aggregate. It is a bit more xeromorphic than *P. stepposa*, and replaces it in the drier communities of the Southern Siberian mountains, also growing both on the plains and rising to the mid-mountain belt (Sergievskaya, 1961). All researchers suggested the rough stems of this species (Rozhevits, 1934; Sergievskaya, 1961, 1969; Reverdatto, 1964; Probatova, 1985; Liu, 2003). Thus, the prevailing of the pricles and their density may be suspected within the most populations, and found in the most individuals within populations.

To test this assumption, 14 populations of *P. botryoides* were studied. The graphs obtained from result of data processing (Fig. 7 I) showed that both interpopulation and intrapopulation variability within this specialized species proved to be very high. Contrary to expectations, many plants within the populations of this species had only crown cells in some positions (shown in pink on the graph), and their number was higher than recorded among the generally more mesomorphic *P. stepposa*.

However, the proportion of populations, all members of which bear pricles, is 29%, which is 7% higher than the same proportion in *P. stepposa*. At the same time, there are a high proportion of plants with dense pricles (colored in dark blue) at least in one position. Thus, a large proportion of pink color on the graphs, indicating the absence of pricles, speaks contrary to established ideas, and shows that among *P. botryoides* there are not only separate individuals with almost smooth stem without pricles, but also entire populations, in which such individuals predominate.

The histograms reflecting the distribution of states of the trichome orientation characters reflect the lower intrapopulation variability of *P. botryoides* in comparison with two species considered earlier. In seven out of fourteen populations, no variability in the orientation of trichomes is observed on different parts of the stem, the pricles and bristles facing upwards to be predominating (Fig. 7 II). As in other species, there are pricles under the panicle facing exclusively upwards, and bristles located perpendicular to the surface of the stem are found only on leaf sheaths above the nodes. Such bristles occur with varying frequency above the nodes in eight populations (57%). However, only in two populations (5 and 11) this feature is constant. The predominant trichomes in this part of the stem also remain upwardly directed pricles, however, some are downwardly directed (populations 4 and 9) and both upward and downwardly directed (populations 2, 9) also occur. Under the nodes, the stem epidermis also includes mainly pricles directed upwards, but downward-facing ones, like in European *P. erythropoda* and *P. versicolor* (populations 2, 9, 14), and directed in different sides (2, 4, 9, 11) are also found.

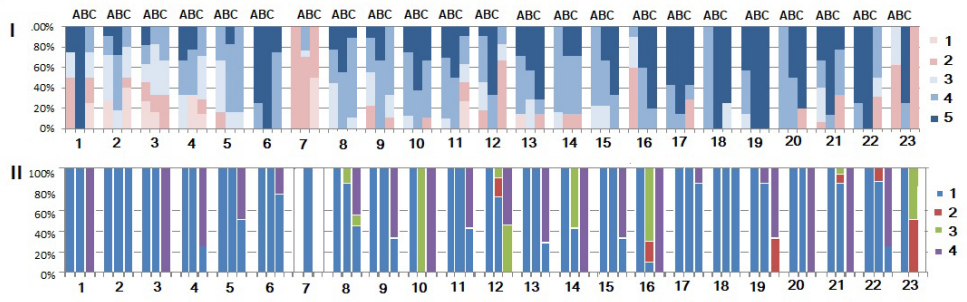


**Figure 6.** Anatomical structure of the stem and leaf (lower leaf sheaths) epidermis of *Poa stepposa*. A – stem under panicle; B – stem under the node (in the lower part); C – sheaths of lower leaves. Locations of the studied populations: 1 – Taimyr; 2, 3 – Khakasia; 4 – south of the Krasnoyarsk district; 5 – Altai mountains; 6 – West Buryatia, 7 – Altai mountains; 8–10 – Chinese Altai; 11 – Khakasia; 12 – Buryatia, 13 – Baikal, 14 – Altai mountains; 15 – East Kazakhstan; 16 – Buryatia; 17 – Baikal; 18 – south of the Krasnoyarsk district; 19, 20 – Chita region; 21, 22 – Altai region; 23 – Omsk region;. I Morphological types of trychomes: a – surface with rare crown cells (rarely completely smooth); b – numerous crown cells; c – rare pricles or bristles appear; d – pricles or bristles of medium density, often arranged in rows; e – pricles or bristles dense. Crown cells are pink, pricles are blue. II Direction of trychomes; a – upwards; b – downwards; c – directed up and down; d – directed perpendicular to the surface of the stem.

Geographically, no special features of the morphotypes distribution were observed. Thus, populations with a predominance of crown cells in the stem epidermis and weakly expressed, rare pricles are found both in the Irkutsk region, and in Magadan and Khakasia. Nevertheless, the populations where dense pricles predominate in most individuals (1, 2, 7) occurs, as a rule, in Eastern Siberia. But as a whole, there is no general regularity in the distribution of patterns of sculpture of the epidermis.

Attempts to establish the geographical patterns of placement of trichomes with different orientations also did not give the desired result: populations that were monomorphic in terms of the orientation of trichomes were found in Khakassia, Buryatia, Chita, Magadan, and Irkutsk regions (Fig. 7 II). At the same time, the greatest polymorphism in the sculpture epidermis above the nodes was observed in population 4 (Buryatia), and under the nodes, in population 2 (Chita region).

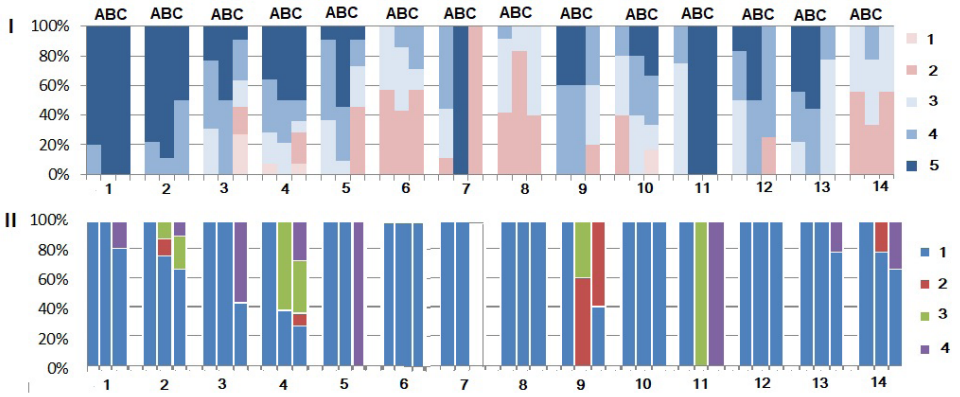


**Figure 7.** Anatomical structure of the stem and leaf (lower leaf sheaths) epidermis of *Poa botryoides*. A – stem under panicle; B – stem under the node (in the lower part); C – sheaths of lower leaves. Locations of the studied populations: 1 – Buryatia; 2 – Chita region; 3 – Khakasia; 4 – Buryatia; 5 – Baikal; 6 – Irkutsk region; 7 – Buryatia; 8 – Magadan region; 9 – south of the Krasnoyarsk district; 10, 11 – Chita region; 12 – Khakasia; 13 – south of the Krasnoyarsk district; 14 – Khakasia. I Morphological types of trychomes: a – surface with rare crown cells (rarely completely smooth); b – numerous crown cells; c – rare pricles or bristles appear; d – pricles or bristles of medium density, often arranged in rows; e – pricles or bristles dense. Crown cells are pink, pricles are blue. II Direction of trychomes; a – upwards; b – downwards; c – directed up and down; d – directed perpendicular to the surface of the stem.

*Poa argunensis* and *P. reverdattoi* are two South Siberian mountain-steppe species of the *P. versicolor* aggregate. Both of these morphologically close species also have a contradictory opinion on its surface. It is suggested to be smooth under the panicle (Tzvelev and Probatova, 2019) or rough (Rozhevitz, 1934; Reverdatto, 1964; Sergievskaya, 1961; Liu, 2003), but R.Yu. Rozhevitz notes that in the latter species, the sheaths are sharply rough, whereas L.P. Sergievskaya wrote that in both species

the stems are only slightly rough under the panicle. Protology and author's descriptions of both species (Rozhevitz, 1934, 1936) and comparison of type specimens show that it is *P. reverdattoi* that is more xeromorphic and rigid. However, a study of the epidermis in seven populations of *P. argunensis* and six populations of *P. reverdattoi* (Fig. 8 I) revealed a noticeable predominance of individuals with dense pricles (dark blue color on the graph) within *P. argunensis*. Moreover, in three out of seven (43%) ones the pricles were found in all three parts of the plant, and in population 2 this character state was generally constant. In contrast, in *P. reverdattoi*, the specimens with crown cells only (pink color) or with sparse pricles (light blue color) predominated. At the same time, populations with the most rough stems (1, 2, 3, 6, 7, 8) were confined to the eastern part of the range.

*Poa ochotensis*, a Far Eastern mountain-steppe species, also belongs to the P. *versicolor* aggregate and, presumably, arouse as a result of the hybridization of *P. stepposa* x *P. sphondylodes*. Due to its rather narrow range, the species has been little studied; however, R.Yu. Rozhevitz (1934) and N.S. Probatova (1985) noted rough stems, and N.N. Tzvelev, who considered *P. ochotensis* as a subspecies of the polytypic *P. versicolor*, suggested its stems under the panicle and leaf sheaths less rough than those of *P. stepposa*, often to be almost smooth.

A study of three populations from the Russian Far East (Fig. 8 I) confirmed the poor development of *P. ochotensis* epidermal trichomes. In all studied populations, trichomes were represented by crown cells and sparse pricles. Only in one population several individuals show dense pricles under the node.

A study of the variability of trichome directions among *P. argunensis*, *P. reverdattoi* and *P. ochotensis* revealed much less pronounced interpopulation and intrapopulation variability within *P. reverdattoi* (Fig. 8 II). Only few individuals within the populations of this species deviated from the general type. As in all studied species, the stem epidermis under the panicle was represented by pricles directed exclusively upwards, but the epidermis under the nodes already contains the pricles directed downwards (population 1 of *P. argunensis* and population 9 of *P. reverdattoi*). At the same time, populations 1 and 6 of *P. argunensis* also contain pricles pointed in different directions, which is not observed within *P. reverdattoi*. The structure of the leaf epidermis of *P. argunensis* is also more diverse: for example, in four populations of this species, often with high frequencies, multidirectional trichomes are found, while within *P. reverdattoi* they are observed only in one population and in a very limited number of individuals.

*Poa ochotensis* also does not differ in the constancy of the studied characters, especially in relation to the leaf epidermis, however, among all the studied samples, there was not a single one where the trichomes were directed both up and down (Fig. 8 II).

*Poa skvortzovii*, a Far Eastern mountain-steppe species, belongs to the Far Eastern aggregate *P. alta*, which presumably includes xeromorphic derivatives of *P. nemoralis*. There is no information in the literature about the surface of the stem of this species, but all examined authentic materials had more or less rough stems. The

study of three populations of *P. skvortzovii* from the territory of the Russian Far East revealed poor expressed trichomes represented, as in the previous species, by crown cells and sparse pricles (Fig. 9 I).

Like *P. ochotensis*, *P. skvortzovii* is not distinguished by a particular variety of trichome orientation: in all cases when the stem epidermis contains pricles, they are directed upwards. In this regard, the structure of the epidermis of leaf sheaths is somewhat more diverse: in addition to bristles, which can be directed both upwards and downwards, this species also has bristles directed perpendicular to the surface of the stem.

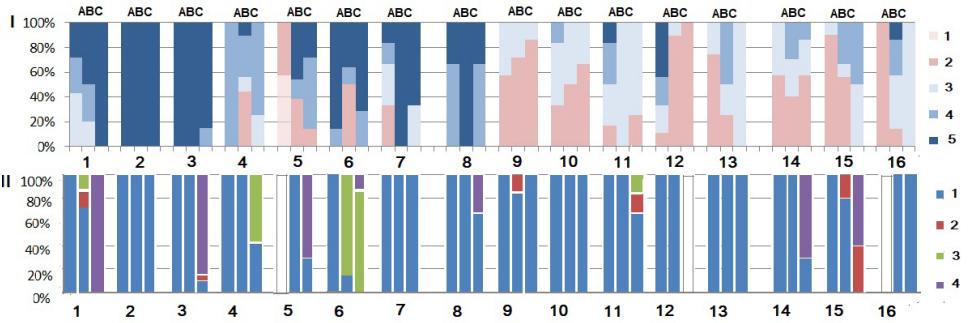


**Figure 8.** Anatomical structure of the stem and leaf (lower leaf sheaths) epidermis of *Poa argunensis* (1–7), *P. reverdattoi* (8–13), and *P. ochotensis* (14–16). A – stem under panicle; B – stem under the node (in the lower part); C – sheaths of lower leaves. Locations of the studied populations: 1 – Buryatia; 2 – Chita region; 3 – Buryatia; 4 – Khakassia; 5 6 – Lake Baikal; 7, 8 – Chita region; 9 – Altai mountains, 10, 11, 12 – south of the Krasnoyarsk district; 13 – Khakassia, 14–16 – Magadan region. I Morphological types of trychomes: a – surface with rare crown cells (rarely completely smooth); b – numerous crown cells; c – rare pricles or bristles appear; d – pricles or bristles of medium density, often arranged in rows; e – pricles or bristles dense. Crown cells are pink, pricles are blue. II Direction of trychomes; a – upwards; b – downwards; c – directed up and down; d – directed perpendicular to the surface of the stem.

*Poa orinosa* Keng, *P. incerta* Keng ex L.Liu, *P. elanata* Keng ex Tzvel. and *P. varia* Keng ex L.Liu are Chinese, or rather, Central Asian mountain-steppe representatives of the *P. versicolor* aggregate. All these species have rough stems (Liu, 2003), while *P. elanata* has smooth or slightly rough stems and sheaths (Tzvelev, 1968). Studies of the type and mass herbarium material for these species showed that all of them, with the exception of *P. varia*, which has especially strong and rough stems, were distinguished by a poor development of sculptural elements of the epidermis, represented by crown cells, or, with few exceptions, by sparse pricles.

Chinese species are less polymorphic than Siberian ones. Some polymorphism in the structure of the epidermis of leaf sheaths was observed in two species: downwardly directed epidermal bristles were observed only within one of the populations of *P. orinosa* and bristles directed perpendicular to the surface presented within one

of the populations of *P. incerta*. In both cases, the characters were constant, i.e., they were found in all the studied individuals of the population. All other species either had pricles directed upwards or did not have them at all.

The study of the variability of these characters within populations confirmed the impressions, induced by working with herbarium material. At the same time, within *P. elanata*, the trichomes of all the studied individuals were represented by crown cells only.

*Poa psilolepis* Keng. belongs to the *P. crymophila* aggregate, which combines species that presumably resulted from hybridization between representatives of the *P. glauca* and *P. versicolor* aggregates. L. Liang (2003) noted that this species has smooth stems, and studies have confirmed this: out of 6 studied populations, only two had several specimens with more or less dense pricles under the panicle and (or) above the nodes.

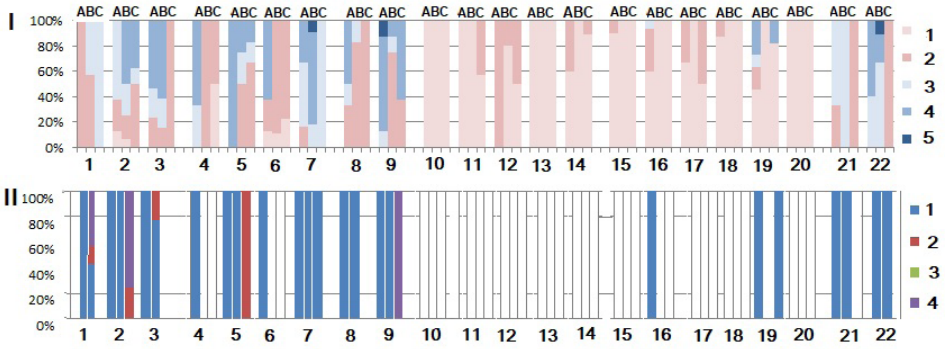


**Figure 9.** Anatomical structure of the stem and leaf (lower leaf sheaths) epidermis of *Poa skvortzovii*, (1–3), *P. orinosa* (4–7), *P. incerta* (8–9), *P. elanata* (10–14), *P psilolepis* (15–20), *P. varia* (21–22). A – stem under panicle; B – stem under the node (in the lower part); C – sheaths of lower leaves. Locations of the studied populations: 1 – Sakhalin; 2, 3 – Primorye; 4–6 – China, Sichuan, 7 – China, Tibet, 8, 9 – China, Sichuan, 10–22 – China, Tibet. I Morphological types of trychomes: a – surface with rare crown cells (rarely completely smooth); b – numerous crown cells; c – rarel pricles or bristles appear; d – pricles or bristles of medium density, often arranged in rows; e – pricles or bristles dense. Crown cells are pink, pricles are blue. II Direction of trychomes; a – upwards; b – downwards; c – directed up and down; d – directed perpendicular to the surface of the stem.

## Conclusion

The results of the anatomo-morphological analysis of population of xeromorphic bluegrass the Stenopoa section made it possible to establish only general trends in the structure of their epidermis. As a result of the study, no species-specific types of epidermal structure were revealed. In all the studied species, with the exception of the Central Asian hybridogenic species *P. psilolepis*, the epidermis of the stem

and leaf sheaths contained crown cells and pricles or bristles in varying proportions. Under the panicle only crown cells or pricles directed upwards were observed. The most species, exclusing the Central Asian ones showed high interpopulation and intrapopulation variability. The conducted preliminary studies do not yet allow drawing botanico-geographical conclusions, but, based on the obtained results, one cannot assume a special geographical confinement of populations with a predominance of one or another type of trichomes.

The conducted studies cast doubt on the possibility of widespread use of epidermal sculpture as a discriminator for xeromorphic Stenopoa species, including for distinguishing between the Siberian *P. stepposa* and the European *P. erythropoda*.

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