

ON THE VARIATION AND ECOLOGY OF PTERYGONEURUM SUBSESSILE
AND P. KOZLOVII (POTTIACEAE, BRYOPHYTA)

ОБ ИЗМЕНЧИВОСТИ И ЭКОЛОГИИ PTERYGONEURUM SUBSESSILE
И P. KOZLOVII (POTTIACEAE, BRYOPHYTA)

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Abstract

Pterygoneurum kozlovii, a rare species worldwide, is found in Altaisky Territory, Kazakhstan and Central Yakutia, mainly in halophytic habitats. Study of morphology and anatomy of *P. subsepsile* and *P. kozlovii* reveals certain intergradation between typical morphotypes of these two species. Quantitative characteristics of plants and their illustrations are given, demonstrating complex situation in this group.

Резюме

Pterygoneurum kozlovii, повсеместно редкий вид, выявлен во многих местонахождениях в Алтайском крае, Казахстане и Центральной Якутии, преимущественно в засоленных местобитаниях. Морфологическое и анатомическое изучение образцов показало наличие промежуточных морфотипов между типичными *P. subsepsile* и *P. kozlovii*. Результаты измерений и иллюстрации показывают более сложные взаимоотношения в группе *P. subsepsile* – *P. kozlovii*.

INTRODUCTION

In the course of identification of *Pterygoneurum* collections from the Altaisky Territory (south of West Siberia), the problem of differentiation of *Pterygoneurum subsepsile* (Brid.) Jur. and *P. kozlovii* Laz. appeared. Typical morphotypes of these two species of *Pterygoneurum* with immersed capsules are quite distinct: *P. subsepsile* is stegocarpous moss; its tufts are grayish and hoary due to very long hyaline hairs points; *P. kozlovii* is cleistocarpous, its leaves have short hyaline hairs points, tufts are yellowish-green (Ignatov & Ignatova, 2003). However a number of intermediate plants, which are difficult to interpret were found as well.

Pterygoneurum subsepsile is a rather common species of xeric regions, widely distributed in central and southern Europe; in northeastern, eastern, central and southwestern Asia; in northern Africa; in North, Central and South America. In European Russia it is common in south-eastern provinces, sporadic in Central Chernozemje and in South Urals; in Siberia it occurs mainly in its southern part – in xeric areas of Altai Mts., West Sayan Mts.,

near Baikal Lake; in steppes of Altaisky Territory, Minusinsk and Tuva depressions, Chulym-Yenisei depression and Dauria; also it occurs in Central Yakutia and further to the north it is recorded in subarctic regions in the middle course of Indigirka River and on Putorana Plateau.

Pterygoneurum kozlovii is a rare species; known in the world only in a few localities (Fig. 1). It was described from Ukraine (Lazarenko, 1946), where it occurs in Zaporozh'e (Lazarenko, 1955) and Odessa (Bachurina, 1960) Provinces. Similar cleistocarpous *Pterygoneurum* species was described from Czechoslovakia (Vanek, 1952) as *P. smardaeanum* Vanek; later it was synonymized with *P. kozlovii* (Abramova & al., 1973). Then *P. kozlovii* was recorded for Romania (Wallfisch, 2001), Mongolia (Abramova & Tsegmed, 1989; Tsegmed, 2001), China (Tan, Zhao & Hu, 1995), Canada, inland areas of British Columbia (McIntosh, 1989). In Russia it is known from Saratov (Cherepanova, 1971) and Rostov (Babenko & Fedyaeva, 2001) Provinces and from continental Siberia in north Yakutia, Indigirka River (Afonina & al., 1979). [cont. p. 172]

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Table 1. Occurrence of *Pterygoneurum*-specimens in plant communities (described below):

Type of plant community	I	I	I	I	I	I	I	II	II	II	III	IV	V	VI
Releve field number	at04	at08	at09	at10	at11	at13	at14	at02	at07	at00	at12	at05	y00	k19
Collecting point	7	4	4	4	3	2	2	8	5	1	3	6	9-Y	10-K
'typical <i>P. subsessile</i> '	+	.	+	+	.	+	+	+
'atypical <i>P. subsessile</i> '	.	+	+	+	+	+	.	+	.	.	+	.	.	.
'debatable <i>P. kozlovii</i> '	+	.	+	.	+	.	.	.
'typical <i>P. kozlovii</i> '	+	+	+	+	.	.	.	+	+	.
? from Kazakhstan	+
<i>Pterygoneurum ovatum</i>	+
<i>Phascum cuspidatum</i>	+	.
<i>Bryum argenteum</i>	.	+	.	.	+	+	+	+	+	.	+	+	.	.
<i>Ceratodon purpureus</i>	+	.	.	.	+	.	.
<i>Entostodon hungaricus</i>	+	+
<i>Funaria hygrometrica</i>	.	.	+
<i>Bryum</i> sp.	+	+	.	.	.	+	.	.

I-IV halophyte communities from Altaisky Territory (steppe zone):

I – communities of small perennial halophyte succulent semishrubs.

The communities are poor in species (6-15 high vascular species per releve); herb layer is rarefied (cover 30-60%). Perennial semishrubs *Artemisia nitrosa* Web. ex Stechm., *Halocnemum strobilaceum* (Pall.) Bieb., *Halimione verrucifera* (Bieb.) Aell., *Limonium suffruticosum* (L.) O.Kuntze prevail. *Puccinellia tenuissima* Litv. ex V. Krecz. usually abundant. Annual herbs *Limonium gmelinii* (Willd.) O.Kuntze, *Bassia setoides* (Pall.) Aschers., *Ofaiston monandrum* (Pall.) Moq., *Salicornia perennans* N. Semen., *Suaeda prostrata* Pall., *Petrosimonia litwinowii* Korsh. are common and often abundant. Habitat salinization in ecological scale of L. G. Ramenskij is 20-21 degree, humidification is 37-43 degree. In Braun-Blanquet classification the communities belong to the association *Artemisia nitrosae-Halimionietum verruciferae* Korolyuk 1999 (class *Salicornietea fruticosae* (Br.-Bl. et R.Tx. 1943) R.Tx et Oberd. 1958 em. Golub et V.Sikh. 1988; order *Halostachyetalia* Topa 1939 em Golub et Tchorbadze 1987; union *Climacoptero-Suaedion* Golub et Tchorbadze 1989). Such communities are the most common halophyte vegetation type in West Siberian steppe zone. They occupy large areas on saline plains, on terraces of saline lakes, and on ancient gullies that became saline. The communities are situated on up-raised and the least salted sites among solonchaks (Korolyuk, 1999); frequently they contact with monodominant halophyte communities along shores of saline lakes and in place of temporary lakes flooding seasonally during spring time. In the last communities mosses were not found.

II – solonetz steppes with abundance of *Artemisia* species.

Herb layer is poor in species and rarefied, cover is 50-60%. *Puccinella tenuissima* Litv. ex V. Krecz. prevails, gramineous plants *Elytrigia repens* (L.) Nevski, *Psathyrostachys juncea* (Fisch.) Nevski and *Artemisia nitrosa*

Web., *A. austriaca* Jacq., *A. rupestris* L., *A. scoparia* Waldst. et Kit. are abundant. Halophytes *Limonium gmelinii*, *Kochia prostrata* (L.) Schrad. and others present. Habitat salinization is about 15-17 degree, humidification vary from 44 to 52 degree. In Braun-Blanquet classification the communities belong to union *Artemisia nitrosae* Korolyuk in Korolyuk et Kipriyanova 1998 (class *Festuco-Puccinellietea* Soo ex Vicherek 1973, order *Festuco valesiacae-Limonietalia gmelinii* Mirkin in Golub et V. Solomakha 1988). In southern West Siberia such communities participate in vegetation mosaic of saline territories. They occur on crust and shallow solonetz (Korolyuk, 1993; Korolyuk, Kipriyanova, 1998; Golub, Karpov, Sorokin, Nikolajchuk, 2005).

III – bunchgrass solonetz steppe.

The appearance of the community is created by tall tussocks of *Stipa capillata* L. and *Achnatherum splendens* (Trin.) Nevski; in lower layer *Festuca valesiaca* Gaudin, *Cleistogenes squarrosa* (Trin.) Keng, *Artemisia frigida* Willd. prevail; halophytes *Puccinella tenuissima*, *Limonium gmelinii* and others are not numerous. Habitat salinization is about 15 degree, humidification is about 48 degree. In Braun-Blanquet classification the communities as previous belong to order *Festuco valesiacae-Limonietalia gmelinii* (class *Festuco-Puccinellietea*).

IV – solonetz community with prevailing Poaceae and *Artemisia* species.

Tussock gramineous species *Psathyrostachys hyalantha* (Rupr.) Tzvel., *Leymus ramosus* (Trin.) Tzvel., *Stipa lessingiana* Trin. et Rupr., *Festuca valesiaca* prevail. *Artemisia* species – *Artemisia gracilescens* Krasch. et Iljin, *A. austriaca*, *A. frigida* and xerophytes semishrubs *Atriplex cana* C.A.Mey., *Camphorosma lessingii* Litv. are abundant (Korolyuk, Pristiaznyuk, Platonova, 2000). Habitat salinization is about 14-15 degree, humidification is about 40-43 degree. In Braun-Blanquet classification the community belongs to union *Stipion korshinskii* Toman 1969 (class *Festuco-Brometea* Br.-Bl. et Tx. 1943, order *Helictotricho-Stipetalia* Toman 1969).

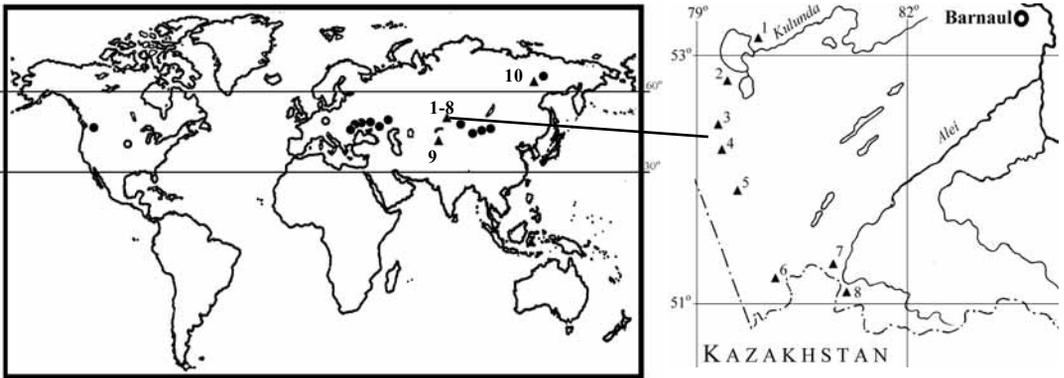


Fig. 1. Distribution of *Pterygoneurum* taxa. Filled circles – literature records of *P. kozlovii* Laz.; open circle in Europe – *P. smardecum* Vanek; open circle in North America – *P. sessile* var. *kieneri* Habeeb. Triangles – author's data, listed below:

Localities	Lat-Long	Alt, m	Releve number; date	Number in Fig. 2 – collector number
<i>Altaisky Territory</i>				
1 Blagoveshchenka Distr., Kulunda Lake	53°05'N 79°50'E	110	at00; 9.VI.1995	4 – op01109
2 Blagoveshchenka Distr., Bauzansor Lake	52°46'N 79°28'E	96	at13-14; 21.IX.2003	5 – op00813 8 – op01104 14,15,16 – op00814
3 Kljuchi Distr., Krivaja Puchina Lake	52°26'N 79°22'E	124	at11-12; 20.IX.2003	7,17 – op01108 12 – op01103
4 Kljuchi Distr., Petukhi	52°13'N 79°28'E	127	at8-10; 19.IX.2003	9,23 – op00445 10 – op01101 13,19 – op01107 22 – op01102
5 Mihajlovskoje Distr., between Nikolajevka and Nazarovka	51°59'N 79°28'E	141	at07; 18.IX.2003	6 – op01105 18 – op01106
6 Uglovskoje Distr., Bolshoj Tassor Lake	51°14'N 80°22'E	220	at105; 16.IX.2003	3 – op01110
7 Rubzovsk Distr., Veselojarsk	51°15'N 81°04'E	227	at04; 15.IX.2003	21 – op00804
8 Lokot Distr., Novenkoje	51°01'N 81°15'E	249	at02; 14.IX.2003	11 – op00802 20 – op00803
<i>Yakutia</i>				
9 Yakutsk area, Vladimirovka	61°45'N 129°32'E	127	y00; 27.VI.2006	1 24
<i>Kazakhstan</i>				
10 Alma-Ata Region, Chu-Ili Mts	43°55'N 75°21'E	820	k19; 19.V.2005	2 25

V – Central Yakutia, steppe on steep slope to Lena River valley.

The herbage is rich and dense. From Poaceae-species *Koeleria cristata* (L.) Pers., *Festuca lenensis* Drob., *Poa stepposa* (Kryl.) Rohev., *Stipa krylovii* Roshev are abundant. Forbs are diverse: *Diantus versicolor* Fisch. ex Link, *Veronica incana* L., *Lychnis sibirica* L., *Galium verum* L., *Pulsatilla flavescens* (Zucc.) Juz., *Potentilla bifurca* L. and others. In Braun-Blanquet classification the community belongs to class *Cleistogeneteta squarrosae* Mirk. et al. 1986.

VI – Kazakhstan, low Chu-Ili Mts., petrophytic desert in solonchak surroundings.

Few halophyte and petrophytic perennial plants – *Salsola arbusculiformis* Drob., *Anabasis salsa* (C.A. Mey.) Benth. ex Volkens, *Nanophyton erinaceum* (Pall.) Bge., *Camphorosma* sp., *Artemisia juncea* Kar. et Kir., *A. sublessingiana* Krasch. ex Poljak. are presented by solitary specimens. Aspect is created by ephemeroïd *Poa bulbosa* L.; tiny annual ephemers are numerous - *Eremopyrum buona-partis* (Spreng.) Nevski., *Ziziphora tenuior* L. and others.

Descriptions of *P. kozlovii* in different publications (based on different specimens) are somewhat inconsistent. For example, ventral lamellae are described as short, 2-5 cells high (Abramova & al., 1973) or tall – 6-11 cells high (Ignatov & Ignatova, 2003, Fig. 214, p.305). Laminal cells are described as papillose on both sides (Abramova & al., 1973), as weakly papillose on dorsal side (Ignatov & Ignatova, 2003) and as smooth (Zander, 2003). In description of Abramova & al. (1973, p. 311): ‘capsule is not dehiscent; operculum is delimited from capsule by only 2-4 rows of smaller cells’ (further in the article the cells named ‘marking cells’). However Zander (l. c.) stated, in contrary, that the distinguishing feature of *P. kozlovii* is the absence of such cells, as opposed to *P. subsessile* var. *kieneri* Habeeb (see also Habeeb, 1949). The latter variety has ‘capsule facultatively cleistocarpous: annulus differentiated but operculum remains attached and spores are releasing through the ruptured capsule walls. This taxon is *P. subsessile* with possibly hybrid sporophytes. Two forms with identical gametophytes were present in the type collection, one with typical sporophyte, the other with that of the variety. The operculum is not dehiscent and the capsule bursts irregularly. The sporophyte apparently falls as a unit, breaking off at the base of the seta’ (Zander, 2003).

My collections of *Pterygoneurum* with immersed capsules were found to be morphologically heterogeneous. Besides typical *P. subsessile* and *P. kozlovii*, there were intermediate plants. In the present study we tried to define more clearly the distinguishing characters between these species and interpret these transitional morphotypes.

MATERIAL AND METHOD

Morphological studies are based mainly on collections of 2003 for geobotanical relevés of halophyte plant communities in Altaisky Territory (southern West Siberia, Fig. 1). The territory is situated within the steppe zone and vast areas in its western part are saline; different variants of saline soils and halophyte communities replace each other according to weak differences in relief position and, correspondingly, according to differences in amount of migrated water and soluble salts. The material was collected within one week, so the plants were approximately at the same stage

of development. In summer 2006 some *Pterygoneurum* samples were collected near Yakutsk on steppe slope. In addition *Pterygoneurum* samples of 2005 from steppe and desert communities of Kazakhstan were studied. All samples are in Bryophyte Herbarium of Central Siberian Botanical Garden, Novosibirsk (curator O. Yu. Pisarenko).

Most collections from non-halophytic habitats were found to be fairly homogeneous and fit well to *Pterygoneurum subsessile*. However a preliminary look at a number of collections, especially from saline habitats, suggests the presence of two species. In the latter case two groups of plants were taken off the tuft (in one case four superficially distinct plants), one being most ‘typical *subsessile*’ (plants greyish, leaves with long hyaline hair-point, stegocarpous), whereas another being maximally ‘typical *kozlovii*’ (plants greenish, leaves with short hyaline hair-points, cleistocarpous). Each of these groups were analyzed for qualitative characters, while all measurements were made from slides of one best developed plant that fits the following requirements: (1) presence of calyptra and mature capsule of ‘normal’ shape (in stegocarpous plants at the stage of beginning of operculum separating, and in cleistocarpous plants – with just scarce breakage of capsule walls); (2) plants not much buried in the soil, thus possessing at least 5 large leaves totally above soil level; (3) all hyaline hair-points not broken. Measurements were done using 5 leaves, starting from lower leaf with well-developed hyaline hair-point up to perichaetial one. Cross-sections were done from these leaves after their measurements. Lamellae height was counted in the widest part of a leaf (Fig. 2 displays minimal and maximal height of lamellae at this place). Cells were measured in the area shown in Fig. 6. Among the characters studied were also *spore size*; *beak length* and *seta length above vaginula* (measured in slides of sporophytes in water); *exothecial cell size* in the mid-capsule; *size of cells at capsule mouth and operculum margin* for stegocarpous plants and *size of marking cells*, if present, for cleistocarpous plants (in cell measurements the smallest and the biggest values were recorded). Also for every plant calyptra shape, number of lamellae, their shape, laminal cell papillosity and awn serrulation were estimated.

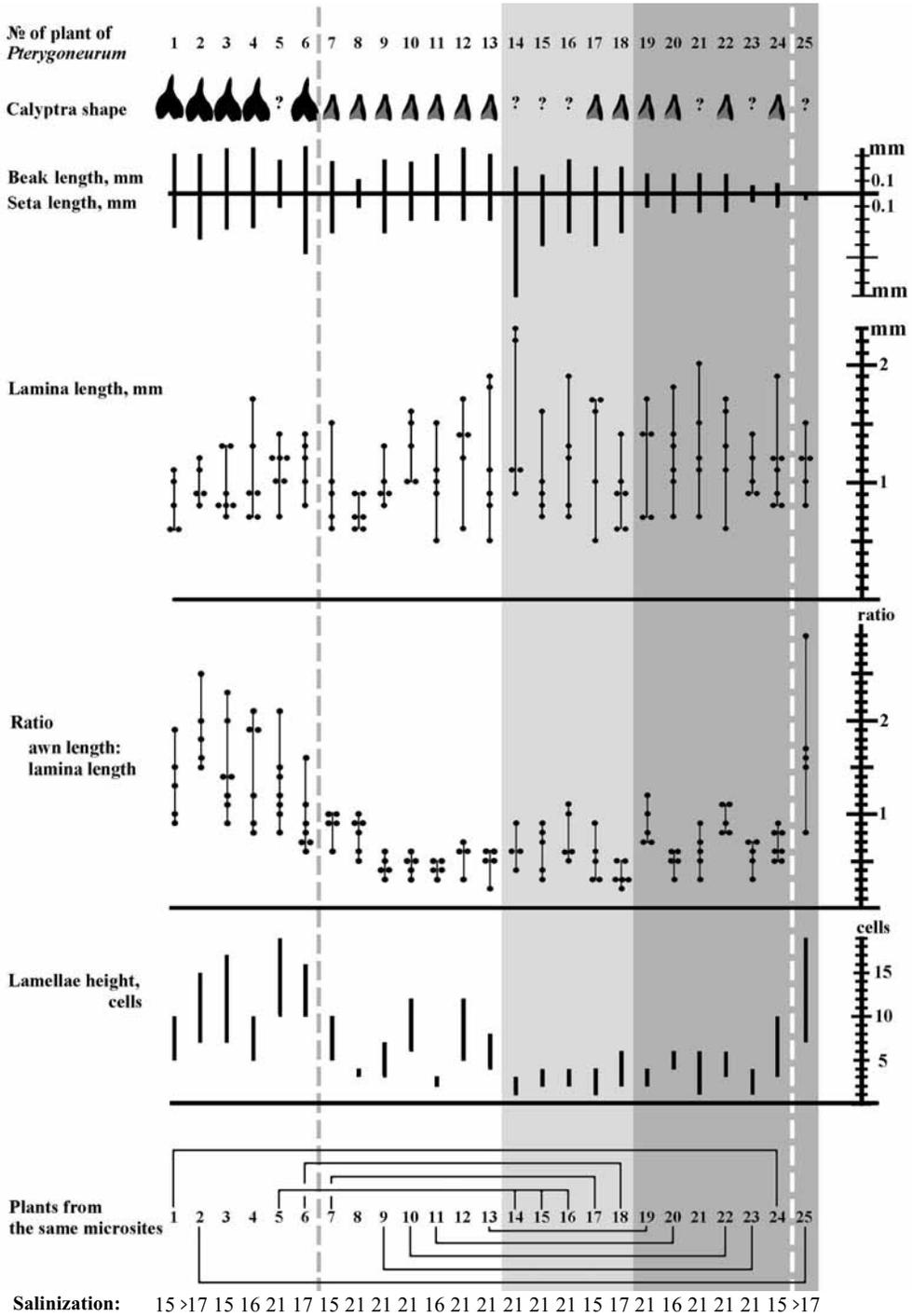


Fig. 2. Bar graphs of variations of some morphological parameters in different plants of *Pterygoneurum subsessile* (Brid.) Jur. and *P. kozlovii* Laz., description in text. White background is for stegocarpous plants, grey background is for cleistocarpous plants (light-grey for plants with marking cells in caplula; deep-grey for plants without marking cells). (1, 24 – from Yakutia; 2, 25 – from Kazakhstan; the localities are under table 1. 3–23 – from Altaysky Territory. Herbarium numbers of the samples and localities are in explanation of Fig. 1). Plants from the same microsities are connected by brackets.

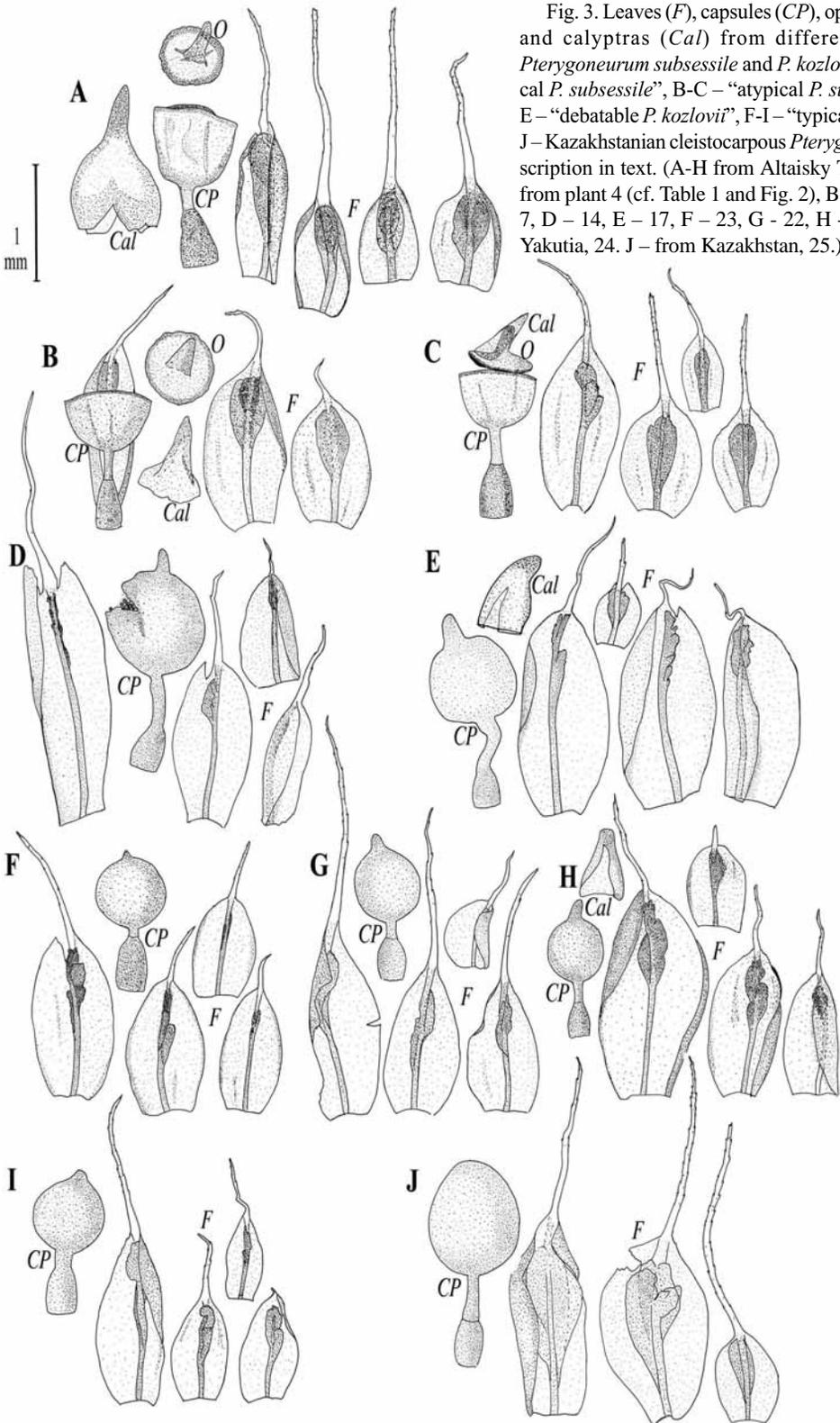


Fig. 3. Leaves (*F*), capsules (*CP*), operculums (*O*) and calypters (*Cal*) from different plants of *Pterygoneurum subsessile* and *P. kozlovii*. A – “typical *P. subsessile*”, B–C – “atypical *P. subsessile*”, D–E – “debatable *P. kozlovii*”, F–I – “typical *P. kozlovii*”; J – Kazakhstanian cleistocarpous *Pterygoneurum*; description in text. (A–H from Altaysky Territory: A – from plant 4 (cf. Table 1 and Fig. 2), B – from 9, C – 7, D – 14, E – 17, F – 23, G – 22, H – 20. I – from Yakutia, 24. J – from Kazakhstan, 25.)

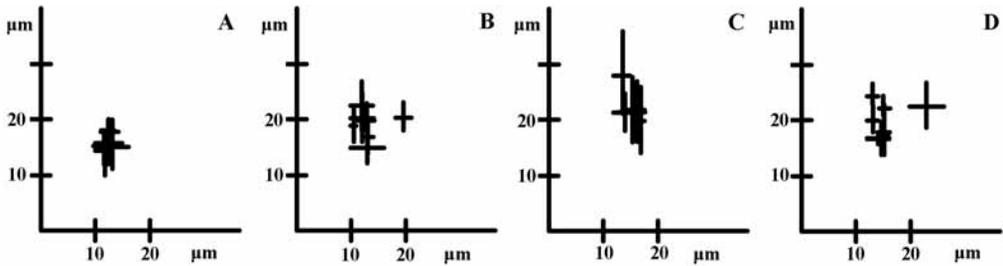


Fig. 4. Variations of mid-leaf cells of *Pterygoneurum subsessile* (Brid.) Jur. and *P. kozlovii* Laz.; X – cell width, Y – cell length. A – “typical *P. subsessile*”, B – “atypical *P. subsessile*”, C – “debatable *P. kozlovii*”, D – “typical *P. kozlovii*”.

Habitat salinization and humidification were determined according to ecological scales of L. G. Ramenskij (Methodical ..., 1974; Korolyuk, 2000) that are more detailed in comparison with Ellenberg's scales (their correlation is given by Samoilov, 1973). In Ramenskij's scale of the soil prolificacy and salinity has 1-30 degrees, from oligotrophic soils (degree 1-3) to extreme solonchak soils (degree 29-30). Investigated sites (see legend of Table 1) have ‘rich soils’ (degree 14-16: pH 7.0-7.5, no salts poisonous for plants), ‘weakly saline soils’ (degree 17-19: pH 7.5-8.3, minute amount of sulphates and chlorides), and ‘average saline soils’ (degree 20-21: pH 7.5-8.3, in aqueous extract 0.1-0.3% SO_4^{2-} and 0.05-0.1% Cl^-).

RESULTS

The collected data were not enough for statistic analysis, mainly due to limited number of cleistocarpous plants. Moreover, the cleistocarpous populations appear to be more heterogeneous than it was expected. So the studied samples were classified into five groups according to their morphological characters (Figs. 2-5).

1) ‘typical *P. subsessile*’ (Fig. 2, columns 1-6; Fig. 3 A; Fig. 5 A; Fig. 6 A). Tufts grayish and hoary. Leaves 0.6-1.3 x 0.4-0.8 mm (perichaetial leaves bigger, up to 1.7 x 0.8 mm), with long serrulate hyaline awn. Awn 0.6-1.8(-2.1) mm long, usually longer than lamina, the ratio awn:lamina length (0.8-)1-2(-2.3). Median laminal cells quadrate to shortly rectangular, 9-16 x 11-20 µm; smooth to weakly mamilliose or papillose on dorsal side. Ventral lamellae (2-)4, from 5-7 to 10-15(-19) cells high. Lamella cells smooth to mamilliose. Calyptra mitrate. Seta above vaginula 0.1-0.4 mm long. Operculum separating, with beak up to 0.3 mm long. Operculum marginal cells in 2-3 rows small, quadrate to shortly rectangular,

from 9-16 x 9-16 to 16-23 x 21-27 µm; above cells bigger, 27-40 x 36-70 µm. Urn cells in 2-3 rows below mouth small, 9-16x18-27 µm, rather abruptly delimited from exothecial cells (23-36x50-90µm in mid-urn).

The plants from Altaisky Territory (Fig. 2, columns 3-6) and Yakutia (Fig. 2, column 1) and Kazakhstan (Fig. 2, column 2) are similar and are in agreement with the species descriptions (Savicz-Lubitskaya & Smirnova, 1970; Ignatov & Ignatova, 2003). The same appearance has a specimen from Novosibirsk Province (Salair Range, Pisarenko, 9.VII.1993).

2) ‘atypical *P. subsessile*’ (Fig. 2, columns 7-13; Fig. 3, B-C; Fig. 5 B-D; Fig. 6 B). Tufts yellowish-green, not hoary. Leaves 0.6-1.5 x 0.3-1 mm (perichaetial leaves up to 1.8 x 1.1 mm), with relatively short and weakly serrulate hyaline awn. Awn 0.3-0.9(-1.1) mm long, usually shorter than lamina; the ratio awn:lamina length (0.2-)0.3-1. Median laminal cells quadrate to shortly rectangular, 9-16 x (12-)14-25(-27) µm; smooth to mamilliose or papillose on dorsal side (one sample has rather bigger cells – 18-21 x 18-23 µm). Ventral lamellae 2 to 4, 2-12 cell high; lamellae number, shape and size often variable in leaves of one plant; in lower leaves lamellae usually short. Lamellae cells smooth to mamilliose. Calyptra cucullate. Seta above vaginula 0.1-0.3 mm long. Operculum separating, with beak 0.1-0.3 mm long. Operculum often have uneven, ‘jagged’ margin; marginal cells in 2-3 rows small, quadrate to shortly rectangular, from 8-16 x 9-18 to 16-27 x 18-27(-37) µm; above cells larger, 18-32 x 33-63 µm. Urn cells in 2-3 rows below mouth small, 9-14(-19) x 9-25 µm; abruptly delimited from exothecial cells [23-36 x (36-)54-70(-100) µm in mid-urn].

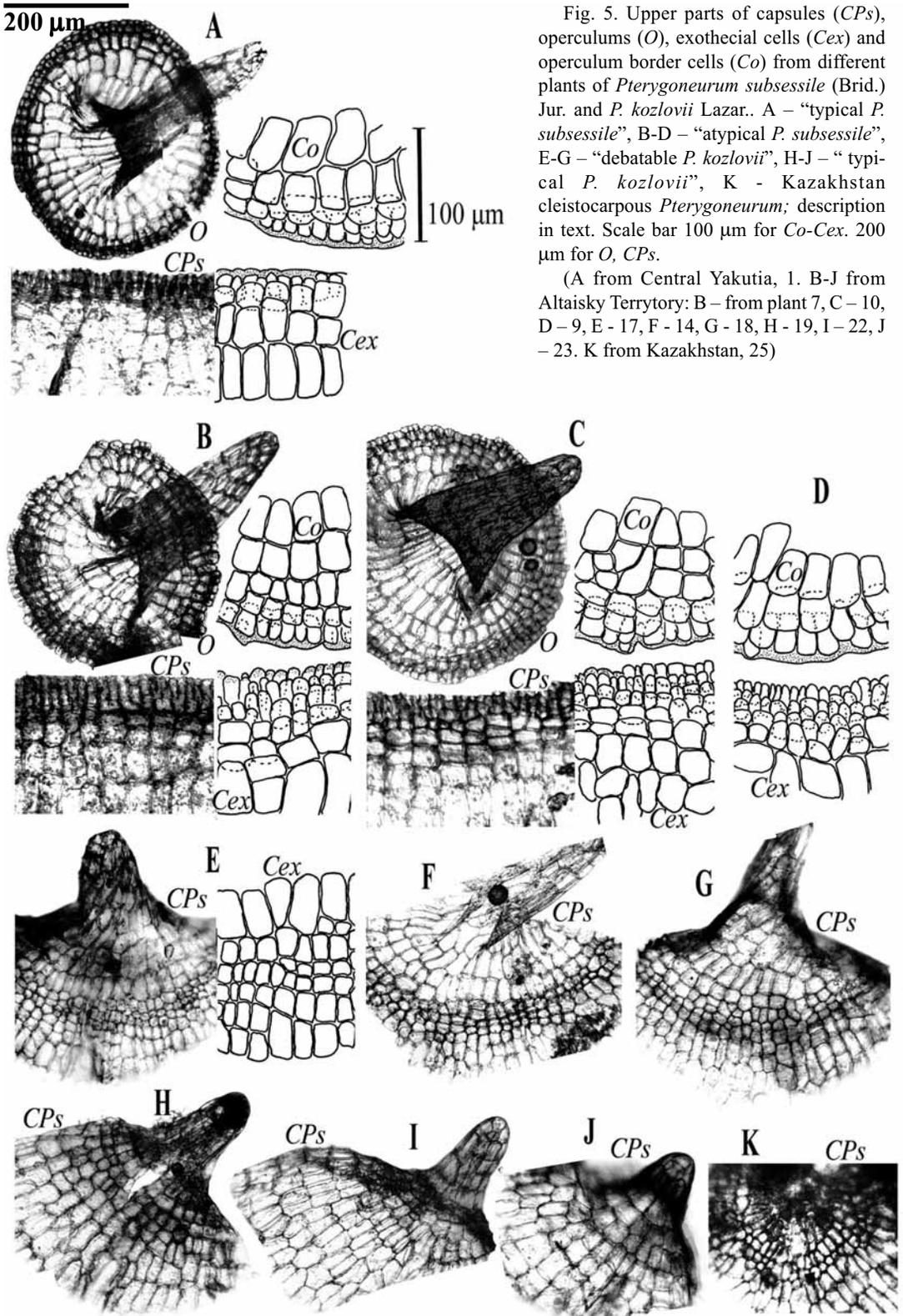


Fig. 5. Upper parts of capsules (CPs), operculums (O), exothecial cells (Cex) and operculum border cells (Co) from different plants of *Pterygoneurum subsessile* (Brid.) Jur. and *P. kozlovii* Lazar.. A – “typical *P. subsessile*”, B-D – “atypical *P. subsessile*”, E-G – “debatable *P. kozlovii*”, H-J – “typical *P. kozlovii*”, K - Kazakhstan cleistocarpous *Pterygoneurum*; description in text. Scale bar 100 μm for Co-Cex. 200 μm for O, CPs.

(A from Central Yakutia, 1. B-J from Altaysky Territory: B – from plant 7, C – 10, D – 9, E – 17, F – 14, G – 18, H – 19, I – 22, J – 23. K from Kazakhstan, 25)

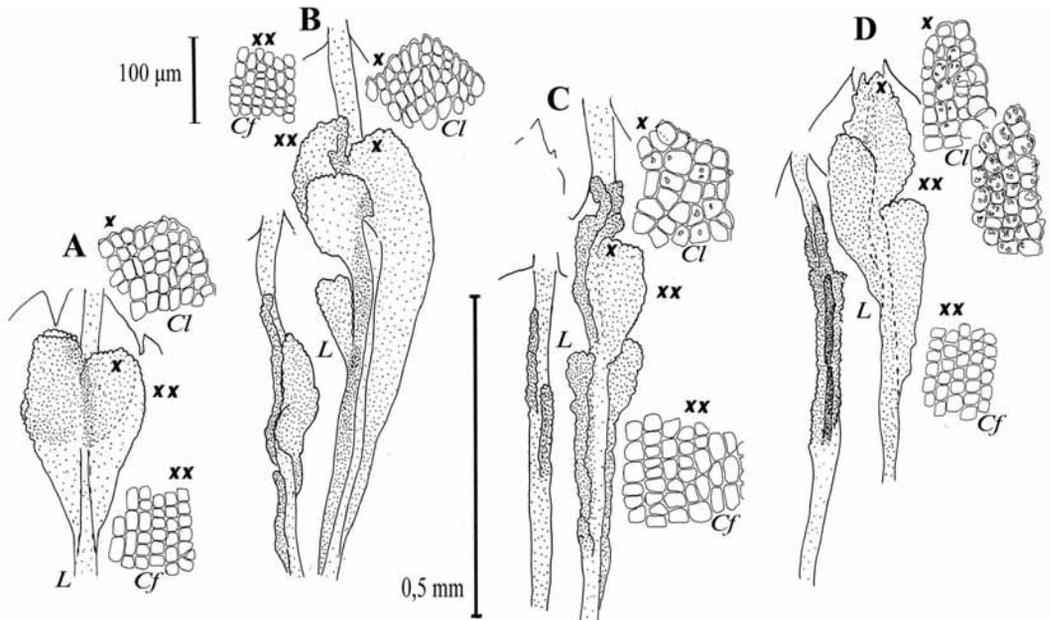


Fig. 6. Costa with lamellae (L), areolation of lamellae (Cl) and lamina cells of mid-leaf (Cf) from different plants of *Pterygoneurum subsessile* (Brid.) Jur. and *P. kozlovii* Laz. A - "typical *P. subsessile*", B - "atypical *P. subsessile*", C-D - "typical *P. kozlovii*", description in text. Scale bars: 0,5mm - for L; 100 μ m - for Cl and Cf. (A&D - from Central Yakutia; A - from plant 1, D - 24. B&C - from Altaisky Territory, from plants 9 and 23).

So, these stegocarpous plants differ from the typical *P. subsessile* in cucullate calyptra, greenish color of plants, relatively short and weakly serrulate awn and by in general less developed lamellae. By gametophytic characters and calyptra they are more similar to *P. kozlovii*. All these 'atypical *P. subsessile*' are from Altaisky Territory.

3) 'debatable *P. kozlovii*' (Fig. 2, columns 14-18; Fig. 3, D-E; Fig. 5 D-G). Tufts yellowish-green, not hoary. Leaves (0.5-0.6-1.7 x 0.4-1 mm (perichaetial leaves up to 2.3 x 1.1 mm), with relatively short and weakly serrulate hyaline awn. Awn (0.1-0.3-1.1(-1.3) mm long, usually shorter than lamina; the ratio awn:lamina length (0.2-0.3-0.9(-1.1)). Median laminal cells quadrate to shortly rectangular, 12-18 x 14-27(-36) μ m; smooth to weakly mamilliose or papillose on dorsal side. Ventral lamellae 2; in upper and perichaetial leaves 4-6 cell high, in median leaves 1-3 cell high, on lower leaves lamellae often lacking at all. Lamellae cells smooth to mamilliose. Calyptra cucullate. Seta above vaginula 0.3-0.4(-0.8) mm long. Capsule with beak about 0.2 mm, without separating operculum, but with with 2-4 rows of 'marking cells' in position of annulus; 'marking cells' small, 9-14x12-23 μ m,

abruptly or gradually transiting to large exothecial cells (18-27 x 45-70 μ m in mid-urn).

So, in gametophytic characters and calyptra these plants are close to 'atypical *P. subsessile*' specimens, but they are cleistocarpous. All samples are from Altaisky Territory. The samples are in agreement with the descriptions of *P. kozlovii* from Saratov Region (Abramova & al., 1973); but according to Zander (2003) they belong to *Pterygoneurum subsessile* var. *kieneri*.

4) 'typical *P. kozlovii*' (Fig. 2, columns 19-24; Fig. 3 F-I; Fig. 5 H-J; Fig. 6 C-D). Tufts yellowish-green, not hoary. Leaves (0.6-0.7-1.6 x 0.3-0.8 mm (perichaetial leaves up to 2.0 x 1.1 mm) with weakly serrulate hyaline awn. Awn length from 0.2 to 1.7 mm long, usually shorter than lamina; the ratio awn:lamina length 0.3-1.0(-1.2). Median laminal cells quadrate to shortly rectangular, 12-16 x (14-)16-27 μ m; smooth to strongly mamilliose or papillose on dorsal side (one sample has rather bigger cells - 19-26 x 19-27 μ m). Ventral lamellae 2, low and often implicit, often present only in perichaetial leaves, up to 6 cell high (up to 10 cell high in Yakutian plants); lamellae cells smooth to strongly papillose. Calyptra cucullate.

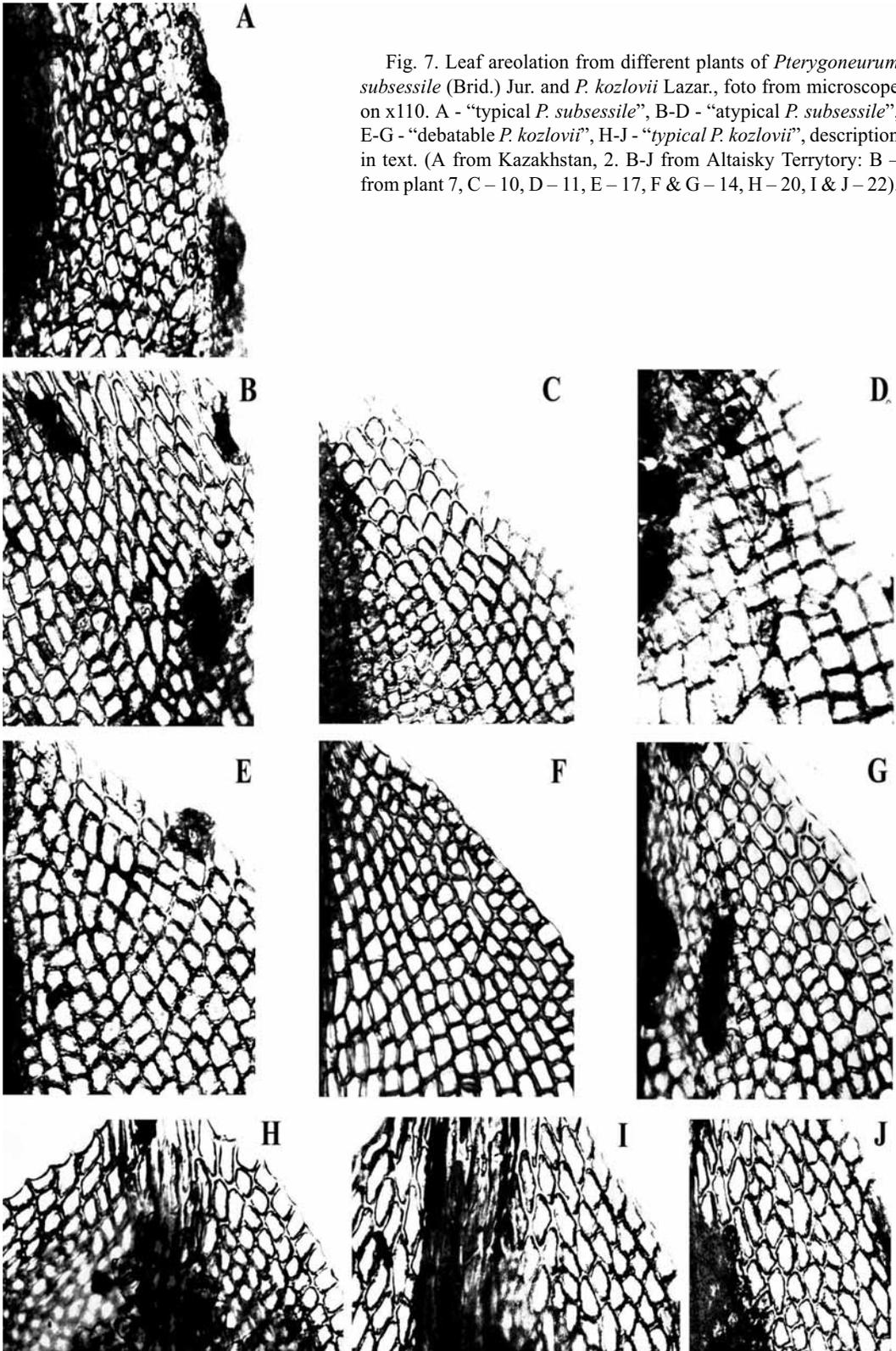


Fig. 7. Leaf areolation from different plants of *Pterygoneurum subsessile* (Brid.) Jur. and *P. kozlovii* Lazar., foto from microscope on x110. A - "typical *P. subsessile*", B-D - "atypical *P. subsessile*", E-G - "debatable *P. kozlovii*", H-J - "typical *P. kozlovii*", description in text. (A from Kazakhstan, 2. B-J from Altaisky Territory: B - from plant 7, C - 10, D - 11, E - 17, F & G - 14, H - 20, I & J - 22).

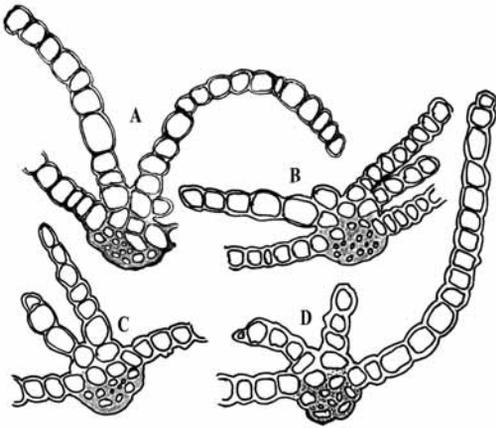


Fig. 8. Leaf transverse sections from of *Pterygoneurum subsessile* (Brid.) Jur. and *P. kozlovii* Laz. A-B – “typical *P. subsessile*”, C-D – “typical *P. kozlovii*”. (A, C, D from Altaisky Territory: A – from plant 5; C – 21, D – 23. B from Central Yakutia, 1).

Seta above vaginula 0.06–0.15 mm long. Capsule with beak about 0.06–0.2 mm, without separating operculum and any ‘marking cells’ in annulus position. Exothecial cells 18–32(–45) x 54–90 μm in mid-urn. Upper exothecial cell variable in shape in different plants: either cells gradually shortened towards beak (Fig. 5 J), or several rows of small cells at beak base abruptly delimited, but the beak itself being formed by elongate cells (Fig. 5 H).

The plants from Yakutia (Fig. 2, column 24) differ from plants of Altaisky Territory only by somewhat taller lamellae and more strongly papillose cells.

5) Two cleistocarpous *Pterygoneurum* plants were found in tuft of ‘typical *P. subsessile*’ in a specimen from Kazakhstan (Fig. 2, column 25; Fig. 3 J; Fig. 5 K). In gametophyte features the plants are almost identical to ‘typical *P. subsessile*’ from the same tuft: leaves are with sharply serrulate long awn; the ratio awn:lamina length is 1.5–2.9; lamina cells are 14–16 x 14–16 μm , strongly papillose; the lamellae are 2–4, tall, 7–19 cell high. The only difference in gametophyte from the ‘typical *P. subsessile*’ from the same tuft is that the plants have papillose lamellae cells. Seta above vaginula is 0.3 mm long. Cleistocarpous capsula has neither annulus of ‘marking cells’, nor beak; exothecial cells in mid-urn are 18–34 x 54–70 μm , gradually transiting into small quadrate cells (9–12 x 9–18 μm) on the top of the capsula.

In the spores, costa transverse sections and shape and size of lamina cells all the studied specimens were more or less similar. The spores are ((27–)30–36(–40) μm), brown and papillose. Costa in transverse section has 2 guide cells and only

dorsal stereid band (Fig. 8).

Lamina cells (Fig. 6–8) are smooth to mamilllose or papillose on dorsal side; the cells below apex are rhomboidal, towards the base gradually becoming heterogeneously quadrate and shortly rectangular, 9–16(–18)x(9–)11–27(–36) μm , at leaf base thin-walled and enlarged, to 18–30x36–72 μm . Regarding cell size the group of ‘typical *P. subsessile*’ is the most homogeneous (Fig. 4 A); other groups have larger variations. Two samples, from ‘atypical *P. subsessile*’ and ‘typical *P. kozlovii*’ are outstanding by laminal cells shape and size (Fig. 4B,D; Fig. 6C; Fig. 7D): all mid-leaf cells thin-walled and big, to 18–26 x 18–27 μm ; but in other characters these plants are in agreement with their groups.

Bar graphs (Fig. 2) show the absence of correlation between the character of operculum dehiscence and the gametophyte characters. There is an indistinct correlation between calyptra shape, awn length/lamina length ratio and lamellae height: plants with mitrate calyptra have relatively more long awn and in general more high lamellae. But in any group variation limits of awn/lamina length ratio and lamellae height overlap with variation limits of adjacent groups.

Variation in sporophyte and gametophyte characters is not always correlated: ‘typical *P. subsessile*’ and ‘atypical *P. subsessile*’ are similar in sporophyte, but differ in gametophyte and calyptra characters; ‘atypical *P. subsessile*’-‘debatable *P. kozlovii*’-‘typical *P. kozlovii*’ demonstrate great variation in sporophyte structure and a relative stability of the gametophytic characters.

It is possible to arrange specimens of *P. subsessile* – *P. kozlovii* complex as a series: ‘typical *P. subsessile*’ – ‘atypical *P. subsessile*’-‘debatable *P. kozlovii*’-‘typical *P. kozlovii*’. However, the cleistocarpous *Pterygoneurum* from Kazakhstan (specimen 25) is out of this series: it has long-awned leaves with high lamellae, but cleistocarpous capsula even without ‘marking cells’.

Plants of these four types occur in various combinations in the same habitats (Figs. 1–2, Tabl. 1). According to literature, *P. subsessile*

and *P. kozlovii* are different in their ecology (Smarda, 1952; Abramova & al., 1973; McIntosh, 1989): *P. subsessile* is common in a broad range of xeric habitats – on soil and sand in steppe and desert communities, on fine earth on dry rocky outcrops, often on limestones, while *P. kozlovii* also occurs in xeric areas, preferring more or less saline habitats. This is also true in Altaisky Territory: *P. subsessile* is not a rare species (Nozinkov, 2002), it occurs on soil in different steppes and along planted forest belts. At the same time ‘typical *P. kozlovii*’, ‘debatable *P. kozlovii*’ and ‘atypical *P. subsessile*’ were found only in solonetz and solonchak communities, with salinization degree 14-21. ‘Typical *P. subsessile*’ in saline habitat (salinization degree more than 17) was recorded only once. Numerous *Pterygoneurum*-samples from different desert communities of Kazakhstan (from transect Ust-Kamenogorsk – Lepsi – Topar – Alma-Ata) are mainly *Pterygoneurum ovatum* (Hedw.) Dix., rarely in mixture with *P. subsessile*. Cleistocarpous *Pterygoneurum* plants were found only in the sample from the described more or less saline habitat. But in Yakutia *P. kozlovii* was collected in non-saline habitat and in mixture with *P. subsessile*. Substrate of the samples from Altaisky Territory and Kazakhstan was calcareous, ‘boiling’ with HCl, it is not so with sample substratum from Yakutia. Preceding samples from Yakutia, Indigirka River (LE) were also collected in non-saline habitats: *Artemisia-Koeleria* steppe on steep slope (16.VI.1976, Afonina); dry *Artemisia-Koeleria-Helictotrichon* steppe with lichens on flat surface near a top (18.VI.1976, Afonina); *Helictotrichon-Poa* meadow steppe (1.VII.1976, Afonina).

DISCUSSION

Both typical morphotypes of *P. subsessile* and *P. kozlovii* and intermediates between them occur in Altaisky Territory. The ‘atypical *P. subsessile*’, ‘debatable *P. kozlovii*’ and typical *P. kozlovii* grow almost exclusively in more or less saline habitats, occurring usually side by side with each other in one tuft.

It seems that the situation found in Altaisky Territory is not unique: at least the mentioned above inconsistencies in descriptions of *P. kozlovii* from different regions can be interpreted in this

way. However the variation within the populations of *P. kozlovii* is not well described mainly due to the overall rarity of this small cleistocarpous moss.

Intermediate morphotypes found in Altaisky Territory are not the only possible ones; two more cases are known (and in both cases the plants were found in tufts with the ‘typical *P. subsessile*’):

(1) cleistocarpous plants with ‘marking cells’ and rigid long-awned leaves that were described as *Pterygoneurum subsessile* var. *kieneri* from Nebraska (Zander, 2003);

(2) cleistocarpous plants without ‘marking cells’ and rigid long-awn leaves (our sample from Kazakhstan, ‘plant 25’).

At the same time, Yakutian collections include only typical *P. subsessile* and typical *P. kozlovii* without any intermediates, they grow in non-saline habitats and sometimes in the same microsites.

Hypothesis about the hybrid origin of *P. kozlovii* from *Pterygoneurum* (*P. subsessile* or *P. ovatum*) and *Tortula acaulon* (= *Phascum cuspidatum*) was suggested repeatedly (Lazarenko, 1946; Corley & al., 1981), and the same explanation was proposed for *P. subsessile* var. *kieneri* (Guerra & al., 1994; Zander, 2003). However no direct evidence has been obtained for that so far.

According to the present data, the hypothesis of hybrid origin seems to be insufficient for explanation of all these cases, although it may take place as well. However the strong ecological plasticity can be explained also by the blocking of the last stages of the sporophyte ontogenesis by toxic concentrations of potassium chloride. Are all the cleistocarpous *Pterygoneurum* genetically identical or some of population comprise the aberrations of *P. subsessile*, and if so – did they originate once or few or many times? Present data do not answer these questions, but allow to put them for the further checking.

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