Arctoa (2025) 34: *31–43*
doi: 10.15298/arctoa.34.03

ON THE GENUS *PTERYGONEURUM* (POTTIACEAE, BRYOPHYTA) IN RUSSIA

О РОДЕ *PTERYGONEURUM* (POTTIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

A partial taxonomic study of the genus *Pterygoneurum* with the focus on the Russian plants previously referred to *P. lamellatum* is conducted. In addition to morphological study, it includes a molecular phylogenetis analysis of the plastid *rps*4 and *trn*MV sequence data, which found in the genus three supported clades. The first one includes *P. ovatum* and Central European plants of *P. lamellatum*, the second is formed by European endemics *P. papillosum* and *P. sampaianum*, and the third includes *P. subsessile*, cleistocarpous *P. kozlovii* and *P. sibiricum*, and Russian plants referred to *P. lamellatum,* from two regions: the North Asia and the SE European Russia, the Caspian Lowland, which have distinct morphology. We suggest resurrecting the name *P. arcticum* for the 'North Asian *P. lamellatum*', which differs from the European *P. lamellatum* by the low lamellae that lack lateral outgrowths, and costa excurrent into a short awn. The second group of the 'Russian *P. lamellatum*', from the Caspian Lowland, is described as a new species, *P. volgense.* It has some characters common with a European *P. lamellatum*, i.e., recurved to revolute leaf margins, excurrent costae, exserted cylindric capsules with opercula possessing spiral cell rows, an occasional presence of peristome remnants, and a moderately large spores, but differs from it in having forked papillae on both leaf surfaces. Such morphology makes it distinct, though the studied phylogenetic markers in this group are low variable, not separating *P. kozlovii*, *P. volgense,* and one of the lineages of *P. subsessile*. A putative hybridogeneous speciation in *Pterygoneurum* is discussed, since some monophyletic groups in this genus include plants with a contrastingly different morphology, having at the same time a similar distribution.

Резюме

Проведена частичная таксономическая ревизия рода *Pterygoneurum,* с особым вниманием к российским образцам, относимым к *P. lamellatum*. В дополнение к изучению морфологических признаков, были получены последовательности пластидных маркеров *rps*4 и *trn*MV; их анализ показал, что образцы этого рода образуют три хорошо поддержанные клады. Первая клада включает *P. ovatum* и образцы *P. lamellatum* из Центральной Европы; вторая клада образована европейскими эндемиками *P. papillosum* и *P. sampaianum*; третья клада включает *P. subsessile*, два вида с клейстокарпными коробочками – *P. kozlovii* и *P. sibiricum*, и российские образцы, относимые к *P. lamellatum,* из двух регионов: азиатской Арктики и юго-восточных регионов европейской России, расположенных в Прикаспийской низменности, которые также различаются морфологически. Предложено восстановить название *P. arcticum* Steere для растений из арктических и субарктических регионов азиатской России, относимых к *'P. lamellatum*'; этот вид отличается от европейского *P. lamellatum* низкими вентральными пластиночками на жилке, у которых нет боковых выростов, и жилкой, выбегающей в виде короткого острия. Вторая группа образцов из России, относившихся к '*P. lamellatum*', с Прикаспийской низменности, описана как новый для науки вид *P. volgense.* Этот вид сходен с европейским *P. lamelatum* отогнутыми или отвороченными краями листьев, выбегающей жилкой, поднятой над перихецием цилиндрической коробочкой, крышечкой с клетками в спиральных рядах, иногда с фрагментарно развитым перистомом, который остается на внутренней поверхности крышечки, и умеренно крупными спорами, но отличается от него наличием разветвленных папилл на обеих сторонах листа. Этот вид хорошо отграничен морфологически, однако по изученным молекулярным маркерам он не отличается от *P. kozlovii* и одной из двух линий *P. subsessile*. Обсуждается возможное гибридогенное происхождение видов в *Pterygoneurum*, на что указывает тот факт, что некоторые монофилетические группы включают растения, контрастно отличающиеся морфологически, но имеющие сходное распространение.

KEYWORDS: taxonomy, xerophiles, *trn*MV, *rps*4, hybridization.

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INTRODUCTION

The genus *Pterygoneurum* Jur. includes 15 species (Brinda & Atwood, 2025) widely distributed in xeric habitats, bearing lamellae on the ventral surface of costae. According to the current treatments, this genus is represented by five to six species in Europe (Guerra *et al*., 1995; Lüth, 2019, Hoddgets *et al*., 2020; Hugonnot, *et al*., 2024) and four species in North America (Zander, 2007). The treatment of the genus for the territory of the USSR (Savicz-Lyubitskaya & Smirnova, 1970) accepted five species of the genus: *P. subsessile* (Brid.) Jur., *P. ovatum* (Hedw.) Dix., *P. lamellatum* (Lindb.) Jur., *P. kozlovii* Lazar., and *P. medium* (Salm.) Broth. Only three former species were recorded for the Russian Federation, since *P. kozlovii* was known that time only in Ukraine, and *P. medium* was reported only for the Middle Asian Republics. These authors also included *P. arcticum* Steere in their treatment as a species probably occurring in the Russian Arctic, as it was described from the neighboring Arctic Alaska (Steere, 1959).

Few years later, the genus was critically revised by Abramova *et al.* (1973), who reported *P. kozlovii* from Russia, Saratov Province, and provided its detailed description and illustrations. Their treatment addressed also to numerous specimens of *Pterygoneurum* collected in the Taimyr Peninsula by L. Blagodatskikh, who referred them to *P. arcticum*. However, a detailed study of the species variability based on these specimens and on Steere' comments on the species morphology led the authors to the conclusion that their plants belong to *P. lamellatum*, taking into account both gametophyte and sporophyte (presence of peristome remnants) traits. So, they referred specimens from Taimyr to *P. lamellatum* and challenged the taxonomic status of *P. arcticum*. Later, Steere (1978) accepted their arguments and referred *P. arcticum* into synonymy of *P. lamellatum*. Therefore, in the check-list of mosses of the former USSR (Ignatov & Afonina, 1992), four species of the genus were mentioned, while *P. medium* was considered as a synonym of *P. ovatum*. The same four species were included in the Handbook of mosses of Middle European Russia (Ignatov & Ignatova, 2003) and Check-list of mosses of East Europe and North Asia (Ignatov *et al*., 2006).

Ignatov & Ignatova (2003) recorded *P. lamellatum* from SE European Russia by the specimen from the Astrakhan Province, Caspian Lowland. This 'Caspian *P. lamellatum*' had an operculum with oblique cell rows and leaves with recurved to revolute margins, which is characteristic for 'typical *P. lamellatum*'; however, it had dense, forked papillae on both surfaces of leaf lamina and lamellae, and leaves with moderately long hyaline hair-points, whereas North Siberian plants, as they where described and illustrated by Abramova *et al*. (1973), had leaf laminae and lamellae with sparse, simple, low papillae, and their leaves had almost plane margins and short, concolorous awns.

Following the key provided for the European *Pterygoneurum* (Oesau, 2003), the 'Caspian *P. lamellatum*' could have been identified as *P. papillosum* Oesau, a species described from Germany (from a single locality) and later reported also from Great Britain, as an endangered species (Hodgetts & Lockhart, 2020). The latter species has bifurcate papillae on dorsal leaf side, but occasional presence of papillae on its ventral surface was also noticed, increasing a possible identity of the Caspian plants with *P. papillosum*; however, the latter species has a short operculum abruptly constricted to a long, narrow beak, which is different from high conic, gradually tapered operculum in *P. lamellatum*, including plants from Russia referred to this species. The scantiness of the material from Astrakhan Province precluded solving the problem of its identity that time.

Recent additional collections of '*P. lamellatum*' from different areas of Taimyr and Chukotka (hereafter 'North Asian *P. lamellatum*') and of '*P. lamellatum*'from Volgograd and Atrakhan Provinces and Kalmykia (hereafter 'Caspian *P. lamellatum*') supported their morphological distinctions mentioned above. Both morphotypes of 'Russian *P. lamellatum*' are similar to European *P. lamellatum* in high conic operculum with spiral cell rows and occasional presence of a rudimentary peristome (cf. Guerra *et al*., 1995; Lüth, 2019; Hugonnot *et al.*, 2024), but they differ from it in lacking lateral outgrowths of ventral lamellae and in possessing only (1)2(3) lamellae instead of 2–3(–4).

The pioneer molecular phylogenetic study of *Pterygoneurum* by Hugonnot *et al*. (2024) based on the plastid data revealed no difference among *P. ovatum*, *P. crossidioides* W. Frey, Herrnst. & Kürschner, and *P. lamellatum*. Since 'Russian *P. lamellatum*' posesses some morphological differences, here we address its identity with the molecular data. Additionally, in this study we tested the molecular and morphological variation in *P. subsessile* and *P. kozlovii*, and also the identity of *P. sibiricum* Otnyukova, which has been recently segregated from *P. kozlovii* (Otnyukova, 2020). Finally, we tested one collection of tiny *P. ovatum*-like plants with large spores, 38–48 μm, from the North Siberia, the Anabar Plateau, totally lacking hyaline hair points and therefore being suspected to represent *P. sampaianum* (Guim.) Guim.

MATERIALS AND METHODS

Molecular phylogenetic studies

Phylogenetic part of the study was based on the plastid markers *trn*MV, and *rps*4-*trn*S. This selection follows that in the study of European species of the *Pterygoneurum* (Hugonnot *et al*., 2024), so we complement their data available in GenBank with sequences obtained from 19 newly studied Russian specimens of *Pterygoneurum*. They cover representatives of all-five species previously recognized in Russia: *P. kozlovii* (2 specimens); *P. lamellatum* (5, with two representing 'North Asian'

and three representing 'Caspian' morphotype); *P. ovatum* (5); *P. sibiricum* (4), and *P. subsessile* (3). Two accessions of *Stegonia latifolia* (including one originally studied) and two accessions of *Tortula* were included as outgroups, and two accessions of *Crossidium squamiferum* were added for rooting the tree; so, the dataset included 36 specimens and 1373 positions. Vouchers and GenBank accession numbers of de nove studied specimens are provided in Appendix. The PCR was conducted according to the protocol described by Kučera *et al*. (2013). Also we attempted to obtain nr ITS sequences for several our specimens according to the protocol described by Gardiner *et al*. (2005), but the obtained sequences appeared to be heterogeneous, suggesting presence of different paralogues of ribosomal RNA operon in their genomes, so only plastid data was used for the phylogenetic purposes.

Sequences were aligned manually using BioEdit (Hall, 1999). Indel data were scored using the simple indel coding (SIC) approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1. (Müller, 2005) and added to the datasets prepared to Bayesian inferences. Bayesian analysis in MrBayes 3.2.7. (Ronquist *et al*., 2012) were set for 2.5 million generations and sampling frequency one tree each 500 generations, average standard deviations of split frequencies were checked to have decreased below 0.01 after first 250 thousand generations. The chain temperature was set at 0.02 in all analyses and GTR model with sampling throughout the model space (setting nst = mixed) was used. Convergence of the analyses was assessed via ESS values, checked using Tracer v.1.7.2. (Rambaut *et al*., 2018) to be higher than 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. ML trees were computed in iQ-tree (Trifinopoulos *et al*., 2016) via the web server http://iqtree.cibiv.univie.ac.at/ with 1000 generations of ultrafast bootstrap, GTR+G+I model of nucleotide substitutions and otherwise standard settings.

Morphological studies

Microscopic observations and photography were done using stereomicroscope Nikon SMZ-25 and compound light microscope Olympus CX-43 with an Infinity 1-2 digital camera. Stacked micrographs using several optical sections were composed using the software package HeliconFocus 4.50 (Kozub *et al.*, 2008).

Results

The genus *Pterygoneurum* was resolved monophyletic in the trees inferred from BA and ML analyses (Fig. 1) with nearly maximal support (PP=1, BS=99). All samples of *P. ovatum*, including morphologically aberrant one from North Siberia (TF65), and European accessions of *P. lamellatum* form a highly supported clade (PP=1, BS=94) sister to a weakly supported clade, which includes two subclades. The first of these subclades includes *P. papillosum* and *P. sampaianum* with a moderately high support (PP=1, BS=91). The second subclade includes accessions of *P. subsessile, P. kozlovii, P. sibiricum*, and Russian specimens of '*P. lamellatum*'; it is weakly supported (PP=1, BS=77). It starts with a polytomy, where two accessions of *P. sibiricum* occupy a basal position, which is followed by two not supported clades corresponding to (1) *P. subsessile* p.p. (specimens from Europe and East Sayan) and (2) remaining accessions. Within the latter, two accessions of 'North Asian *P. lamellatum*' form a highly supported clade (PP=1, BS=94) sister to the not supported clade with two remaining accessions of *P. sibiricum* and moderately supported (PP=1, BS=92) polytomic clade, where all accessions of *P. kozlovii*, 'Caspian *P. lamellatum*', and *P. subsessile* p.p. (specimens from Volgograd Province and Altai) are found. In the ML tree, the order of clades differs, but all the supported clades have the same composition.

Summing up, the output from the phylogenetic part of the study may be presented as follow:

(1) *P. sampaianum*-like plants from North Siberia are not monophyletic with European *P. sampaianum*;

(2) North Asian '*P. lamellatum*' and Caspian '*P. lamellatum*' have different affinities and no one of the two is close to European specimens of this species included in the analysis. Plants from North Asia differ from all other taxa involved in the analysis, while those from Caspian Lowland appeared inseparable by the studied plastid DNA sequences from *P. kozlovii*;

(3) Two morphologically distinct species, *P. subsessile* and *P. sibiricum*, are not separable by the studied plastid data, and the later appears paraphyletic, while the former is polyphyletic;

(4) *P. kozlovii* represents an advanced haplotype as compared to *P. sibiricum* and can be separated from the latter;

(5) Plastid based phylogeny supports a morphology-based delimitation of several European taxa, while the topology of the Eastern (Asian) clade agrees with geography rather than with morphology-based species concepts.

Discussion

'Caspian P. lamellatum'

Our molecular data confirmed that two Russian morphotypes earlier referred to *Pterygoneurum lamellatum* differ from each other and both are not the same as European *P. lamellatum*. This species was described by Lindberg (1864) as *Tortula lamellata* Lindb. as follow: "*autoica, subgregarie crescens; folia apice serrulata et dorso summo papillosa, margine revolute, nervo et gonidia et laminas gerente; seta longa; capsula subcylindrica; saepe leniter curvata; peristomum rudimentarum; areolatio opercula dextrorsum torta*". The sporophyte traits in the protologue agree in addition to Central European plants also with 'Caspian *P. lamellatum*', and 'North Asian *P. lamellatum*'. The same is true for the recurved leaf margins (though less pronounced in 'North Asian *P.*

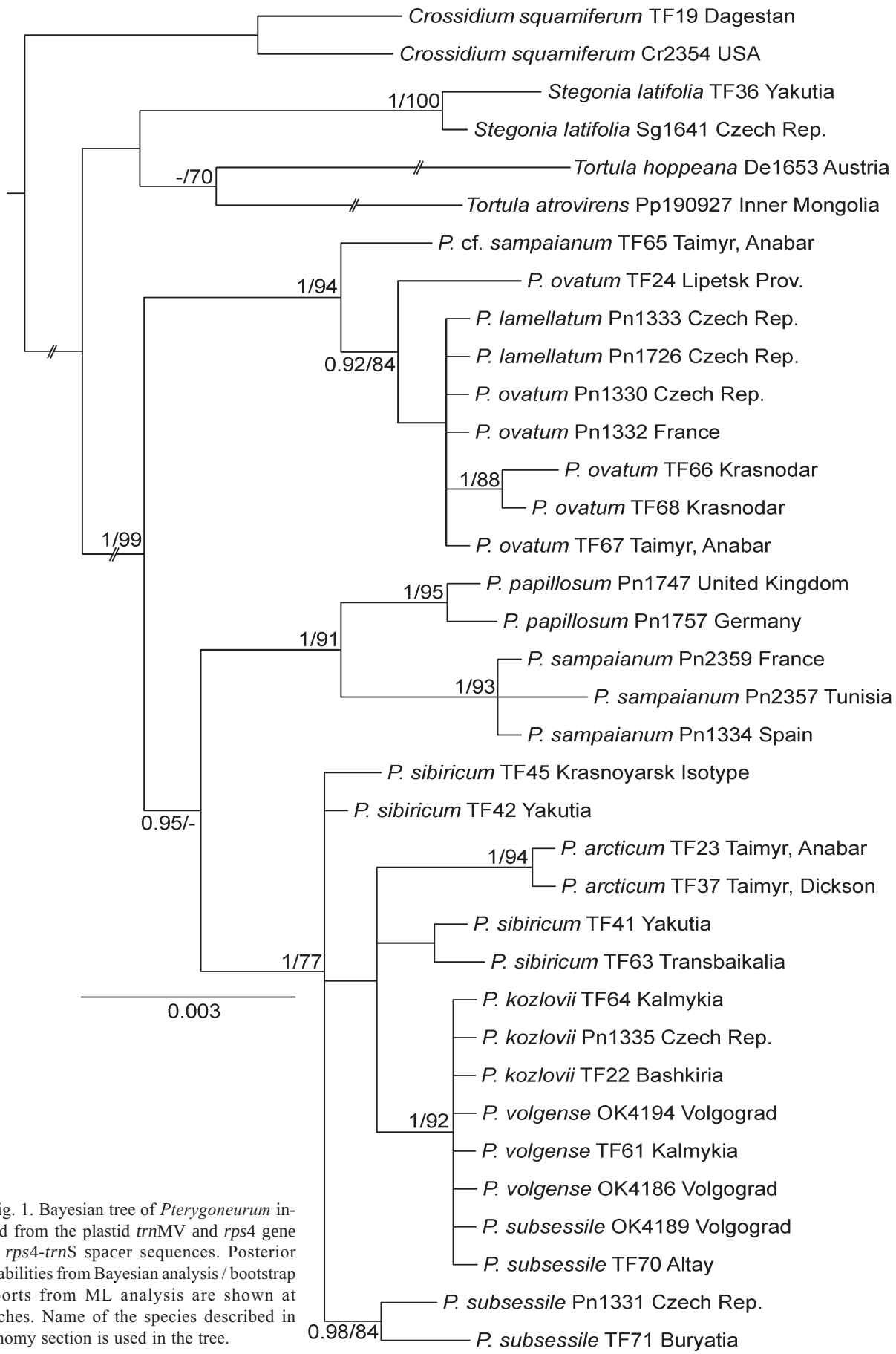


Fig. 1. Bayesian tree of *Pterygoneurum* inferred from the plastid *trn*MV and *rps*4 gene with *rps*4-*trn*S spacer sequences. Posterior probabilities from Bayesian analysis / bootstrap supports from ML analysis are shown at branches. Name of the species described in taxonomy section is used in the tree.

lamellatum'), whereas lamina papillose only on dorsal side is not a trait in the so-called Russian plants. The descriptions of *P. lamellatum* in European literature are somewhat controversial: despite all authors are consistent in the cell counterclockwise twisting in the operculum, many illustrations show no dorsal papillae on leaf laminae or at best a few low ones. Leaf margins are originally described as revolute (Lindberg, 1864), but in some treatments they are shown as slightly recurved (Cano &Guerra, 2006; Lüth, 2019), while in 'Caspian *P. lamellatum*' leaf margins are recurved to strongly revolute agreeing with Lindberg' description. Smith (2004) mentioned that the only reliable distinction of *P. lamellatum* from *P. ovatum* is the spiral cell rows in operculum, while the leaves are similar to *P. ovatum*, which margins he described as ±plane. Guerra *et al*. (1995) undertook a search in herbaria for the original material of *P. lamellatum*, but failed to find any specimen appropriate for the lectotype selection. Therefore, we use the name *P. lamellatum* following its current usage in West European literature (Cano &Guerra, 2006; Lüth, 2019; https://www.swissbryophytes.ch/index.php/de/bilder? taxon_id=nism-2060).

European authors never show dense papillosity on both dorsal and ventral leaf side as in 'Caspian *P. lamellatum*. Thus, taking into account also its molecular distinction from Europaean *P. lamellatum* we consider that it merits taxonomic recognition. The most similar to the 'Caspian *P. lamellatum*' are probably the plants from the steppes of Alaska and British Columbia, first reported by McIntosh (1989) as *Pottia wilsonii* and discussed by Murray (1992) and Zander (2007). These plants were circumscribed as having a broadly recurved leaf margins and multiple papillae on both sides of the leaf lamina above mid-leaf. Murray (1992) suggested its affinity to either *Crossidium* or *Pterygoneurum*, while Zander (2007) noted that this plant is most similar to *P. lamellatum*. Both Murray (1992) and Zander (2007) suggested that this is likely a new species, which, however, has so far not been described (Buck & Goffinet, 2024). Are these North American plants identical to the 'Caspian *P. lamellaltum*' is a question for further studies.

'North Asian P. lamellatum'

The molecular phylogenentic studies show that morphologically distinct 'North Asian *P. lamellatum*' forms a well supported clade, has a distinct distribution and therefore deserves recognition at the species level, since its identity with no one of the two remaining lineages earlier referred to *P. lamellatum* is proved. Having examined the variability of this taxon in North Asia and compared it with the description and illustrations of *P. arcticum* and critical comments of Abramova *et al*. (1973), we see no better solution than resurrecting this name to be applied to the Beringian taxon sampled here based on the specimens from Taimyr and Chukotka. They agree with the original description and illustrations of *P. arcticum* (Steere, 1959) in all the essential traits, including occasional presence of large inflated papillose cells on the ventral surface of costa and total lack of the lateral outgrowths of ventral lamellae.

In Anabar Plateau, 'North Siberian *P. lamellatum*' occasionally occurs sympatrically with *P. ovatum* on xeric rocky slopes, but its most typical habitat is deposits of saline marine clay, where it grows with *Aloina brevirostris, Calcidicranella obtusifolia, Hennediella heimii, Pohlia atropurpurea, Stegonia latifolia,* and *Tortula* spp. In lack of hyaline hair points, entire upper leaf margins formed by quadrate to short rectangular cells, absence of lateral outgrowths on lamellae, and longer capsules with rudimentary peristome teeth, it differs from *P. ovatum*.

A putative hybridization in the Pterygoneurum

The facts of the hybridization event in small Pottiaceae mosses from the xeric habitats strarted accumulating since the beginning of 20th century. The possibility of this has been proved experimentally (Wettstein, 1924, 1940). Lazarenko (1955) suggested the hybridogenous origin of *P. lamellatum* from one of *Pterygoneurum* species and one of a peristomate *Tortula* or *Aloina* species basing on its peristomate capsules and spores relatively small for the genus. The identical plastid markers provide a further evidence for the affinity of European *P. lamellatum* s.str. and *P. ovatum*, and both these species have lateral outgrowths on the lamellae, which further support the hypothesis of Lazarenko.

Known distribution of 'Caspian *P. lamellatum*' is restricted to the southern East Europe, i.e. is somewhat similar to that of *P. kozlovii* s. str. (i.e. excluding *P. sibiricum*), despite of their clear morphological distinction both in gametophyte and sporophyte traits.

An admission of the hybridization between species of *Pterygoneurum* with other taxa partly explains the rarity of *Pterygoneurum* species excepting *P. ovatum* and *P. subsessile*. Various unusual morphotypes of *Pterygoneurum* were earlier suspected in having a hybrid origin (Lazarenko, 1955; Guerra *et al.*, 1994). Although Novotný & Sutorý (2019) excluded hybridization as a possible mechanism of *P. kozlovii* origin, they considered this taxon broader than it is currently circumscribed, thus already Jadranin *et al*. (2023) mentioned hybridization as an important topic to be studied in the course of assessing the identity of *P. kozlovii* and *P. sibiricum*. This remains to be completed employing nuclear data; our attempts of obtaining nrITS sequences were not successful due to heterogeneous sequences, apparently originating from the recent hybridization events. High morphological variability blurring species boundaries of *P. kozlovii*, *P. sibiricum*, and *P. subsessile* (Pisarenko, 2006) also may have originated from hybridization.

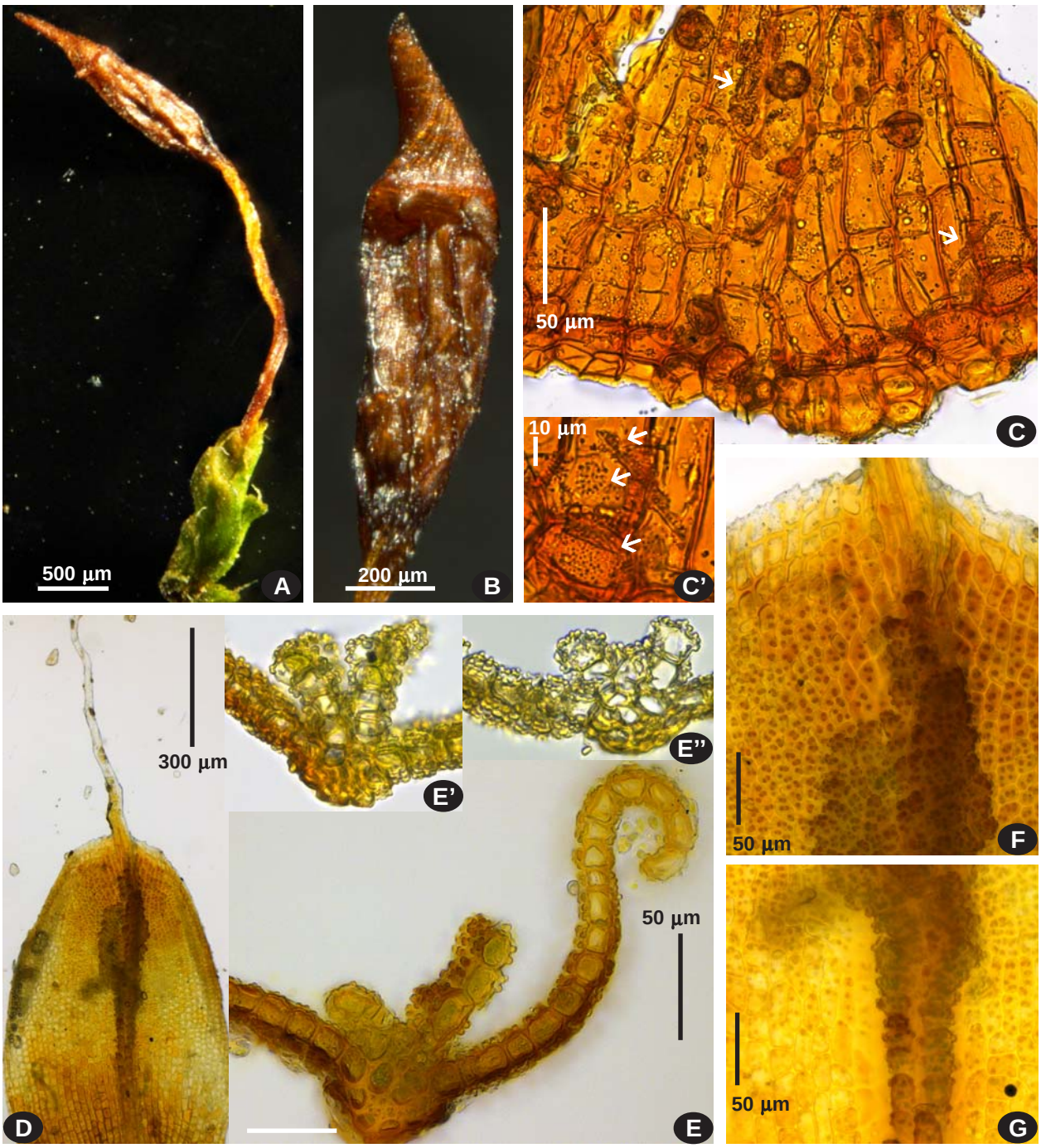


Fig. 2. *Pterygoneurum volgense* (from holotype). A: habit, dry; B: capsule, showing operculum with twisted cell rows; C: a reduced peristome fragments (arrowed); D: leaf, ventral view; E: leaf transverse sections; F–G: ventral lamellae and laminal cells in distal 'F' and median 'G' leaf parts.

TAXONOMY

Pterygoneurum volgense Ignatov & Fedosov sp. nov., Figs. 2, 3.

Diagnosis: The species is similar to *Pterygoneurum lamellatum* (Lindb.) Jur. in having leaves with recurved margins, papillose laminal cells and lamellae, operculae with cells in oblique rows, and rudimentary peristome falling off with opercula, but differs from it in having dense, forked papillae on both leaf surfaces and lamellae, and lacking lateral outgrowths on lamellae.

Type: Russia, Volgograd Province, Pallasovka District, Elton Nature Park, 49°12'58"N – 45°40'19"E, 0 m a.s.l., steep slope on the right bank of Chernavka Creek (north of Elton Lake), on soil among *Spiraea*, 2.V.2023 (loc. 13). Coll. *M. Ignatov, E. Ignatova, N. Stepanova & S. Suragina #23-141* (Holotype MHA9063026). DNA: isolates OK4186 & OK4194.

Etymology: The species name refers to the Volga River: the species is described from its lower course, not far from the Caspian Sea.

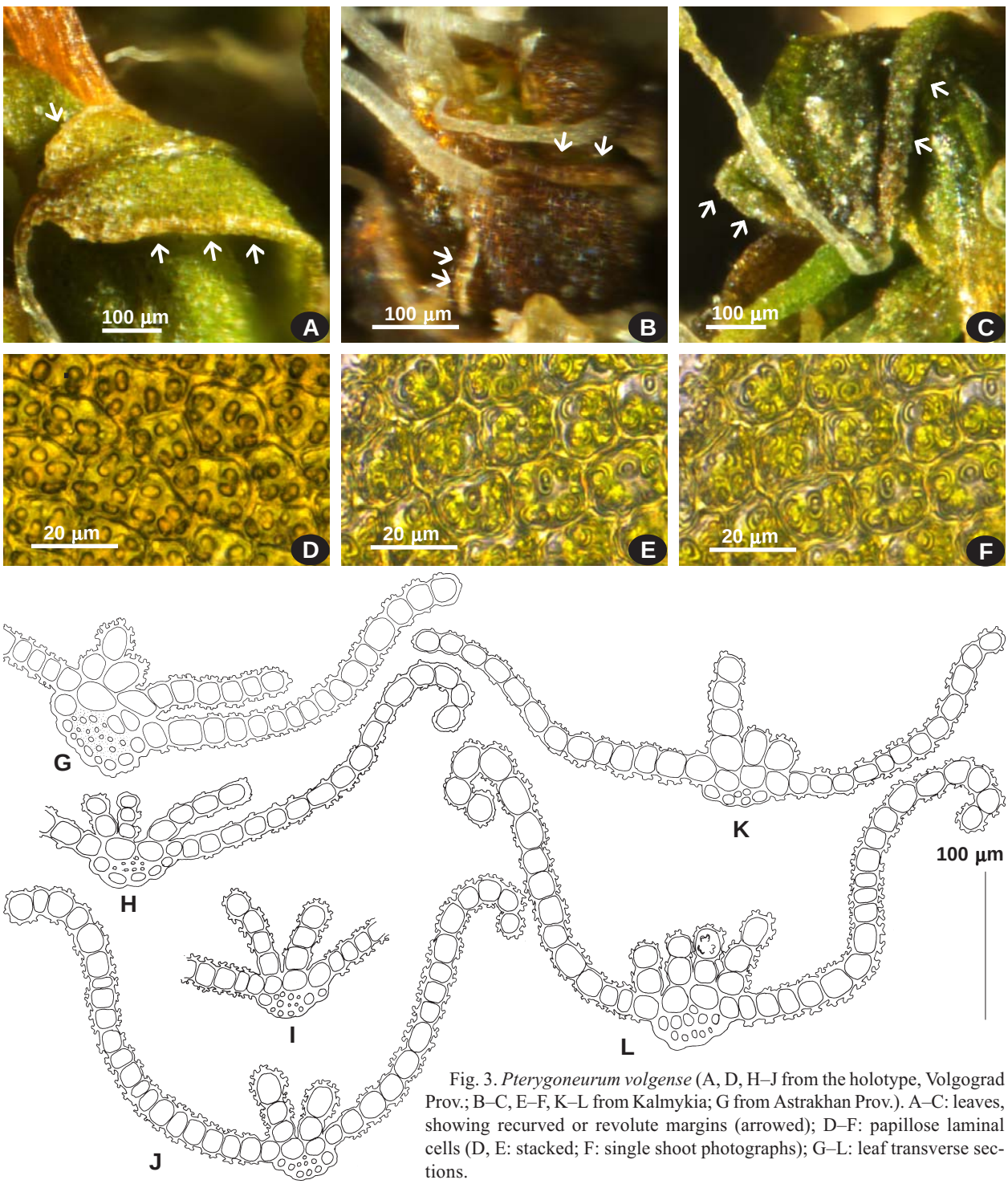


Fig. 3. *Pterygoneurum volgense* (A, D, H–J from the holotype, Volgograd Prov.; B–C, E–F, K–L from Kalmykia; G from Astrakhan Prov.). A–C: leaves, showing recurved or revolute margins (arrowed); D–F: papillose laminal cells (D, E: stacked; F: single shoot photographs); G–L: leaf transverse sections.

Description: *Plants* small, in dense or loose tufts, greyish-green to brownish-black. *Stems* from hardly reaching 1 mm to 3 mm long, simple, without central strand, with cortex composed of homogeneous, thin-walled cells. *Leaves* 0.5–1.4×0.4–0.6 mm, broadly ovate or lingulate, concave, acute, with hyaline hair-points 0.5–1.1 mm long, smooth or nearly so, curved to flexuose; *margins* entire to serrulate above, recurved nearly from the base, in upper leaf portion recurved or broadly revolute, rarely narrowly recurved; *costa* single, strong, with dorsal stereid band, in upper leaf portion with dorsal epidermis, with large, inflated, thin-walled cells on ventral surface, smooth in basal leaf portion, covered by numerous branched or looking as C-shaped papillae distally, in distal 1/5–1/3 with 1–2(–3) simple lamellae to 6 cells high; *upper and median laminal cells* rounded-quadrate, short rectangular to transverse-rectangular, (12–)15–21(–25)×15–19 µm, moderately thick-walled, with 3–8 branched papillae, looking as C-shaped from above; basal leaf cells short rectangular, 20–32×18–25 µm, thin-

walled, smooth. *Autoicous*. *Perichaetial leaves* to 1.6 mm long, with almost plane margins and lower ventral lamellae. *Setae* ca. 5 mm. *Capsules* exserted, cylindric, ca. 1.2 mm long. *Opercula* differentiated, conic-rostrate with cells in oblique rows. *Peristome* rudimentary, observed through translucent opercula and usually falling with them. *Spores* 19–24(–27) µm. Calyptrae cucullate.

Variation: Collections referred to the new species are heterogeneous, likely because of the habitat conditions, and probably also because of the age of plants. The Volgograd plants were collected in a meso-xeric conditions: at base of steep slope to a narrow valley of small creek, under *Spiraea hypericifolia* shrubs, associated with the moss species characteristic for dry steppes of this region: *Encalypta vulgaris, Pterygoneurum ovatum, P. subsessile, Pseudocrossidium hornschuchianum, Microbryum curvicollum, Acaulon triquetrum, Entosthodon hungaricus*, and *E. pulchellus*. Plants of *P. volgense* formed loose tufts, mostly possessing sporophytes (Fig. 2). In their leaves, hair-points are short or as long as the lamina; margins are slightly recurved to almost revolute (Fig. 3A, H, J); papillae are bifurcate on a relatively narrow stalk, scattered (Figs. 2F, G, 3D).

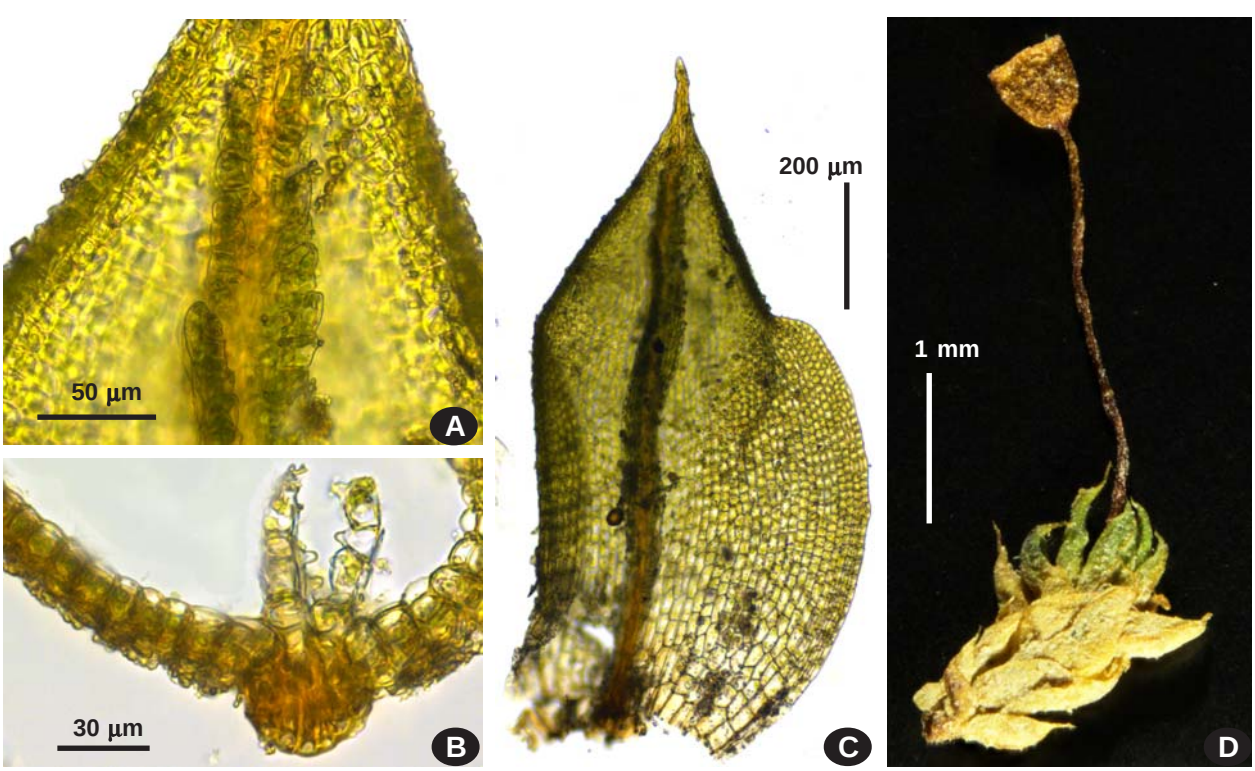
The Kalmykian plants were collected in more xeric conditions, with the only associated species being *P. subsessile*. Plants formed a more compact tufts, lacked sporophytes, but had unfertilized archegonia, probably indicating that they started development shortly before being collected. Leaves have long hyaline hair-points that exceed the lamina length and are strongly flexuose. Leaf margins are ranging from slightly recurved (Fig. 3K) to distinctly so (Fig. 3B) and to revolute (Fig. 3C, L). Papillae are simple or forked, the latter are most common in leaf transverse sections (Fig. 3K, L). However, they are mostly low, and in frontal leaf views are of various shape (bifid, solid, and C-shaped) in Z-stacked photographs (Fig. 3E), while look mostly C-shaped or O-shaped in single-shoot photographs (Fig. 3F). The difference in papillae between Volgograd and Kalmykian plans is probably explained by a more xeric, harsh environments in Kalmykia.

Differentiation: By morphology, *Pterygoneurum volgense* is similar to *P. lamellatum* and *P. arcticum*: these three species have recurved to revolute leaf margins, ranging from rather indistinct to quite conspicuous; they are also similar in having long capsules with conic opercula with the counterclockwise spiral rows of cells, and occasional presence of rudimentary peristome, sometimes vestigal, formed of fragments attached to the inner surface of opercula or sometimes wanting.

Pterygoneurum volgense differs from *P. arcticum* and the Central European *P. lamellatum* s.str. in having cells with dense, branched papillae. In *P. arcticum*, papillae are observed on both leaf surfaces, but they are usually very low, simple, and scarce. In European *P. lamellatum* s.str., papillae are restricted to the dorsal leaf surface, and they are simple, sparse, and low.

The distinction of *P. volgense* from the undescribed North American species commented by Zander (2007) under *P. lamellatum*, remains unclear, but the occasional absence of lamellae in American plants (vs. always present

Fig. 4. *Pterygoneurum papillosum* (from isotype, Germany, Oesau #14455, MHA (dupl. from Oesau herbarium). A: leaf ventral lamellae and leaf margins; B: leaf transverse section; C leaf, ventral view; D: habit.



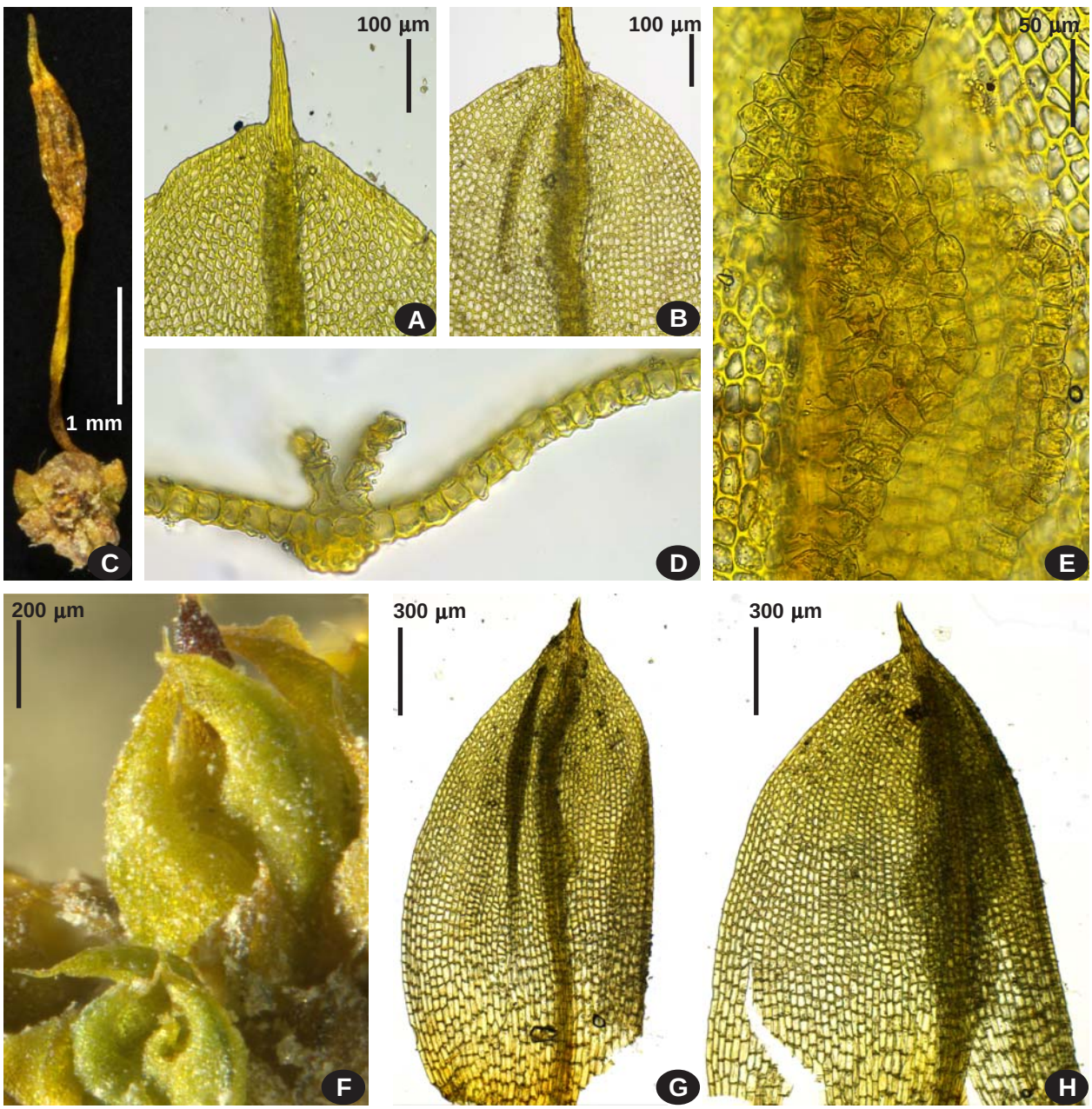


Fig. 5. *Pterygoneurum arcticum* (A–B, D–E, G–H from Taimyr, MW9061137; C, F from Chukotka, Afonina, 30.VII.1980, LE). A–B: leaf distal parts, ventral views, showing short concolorous awns and low ventral lamellae sometimes looking as rows of inflated papillose cells on costa, 'A', or they are 2–3 cells high, 'B'; C: habit of plant with cylindric capsule and high conic operculum; D: leaf transverse section; E: a relatively tall ventral lamella, 5–6 cells high, showing a somewhat undulate arrangement on costa; F: habit of plant with juvenile sporophyte; G–H: leaves.

in *P. volgense*), and their occurrence in so distant areas call for their additional comparison, ideally with molecular markers.

Recently described European *P. papillosum* Oesau possesses similar to *P. volgense* furcate papillae, but only on dorsal leaf surface (Fig. 4); in addition, its hair-points are shorter, capsules are short, cupulate (cylindric in *P. volgense*), and its spores are larger (30–38 µm vs. 19–24(–27) µm in *P. volgense*). Also, the upper edge of ventral lamellae in this species is sharply serrate, at least at places (Fig. 4A).

Distribution: *Pterygoneurum volgense* is known from few localities in xeric Caspian Lowland, in salted areas of Volgograd and Astrakhan Provinces, and Kalmykia Republic.

Other specimens examined: Republic of Kalmykia, Iki-Burul Settl. 45.817°N, 44.617°E, on soil, 23.V.2010, *G.Ya. Ukrainskaya Kl134* (LE). Astrakhan' Province, Bogdo-Baskunchak Nature Reserve, 48.266°N, 46.799°E, Bogdo Mt., Kristal'naya Cave, bottom of the karst depression, 5.V.2002, *S.A. Suragina* (MHA9046879).

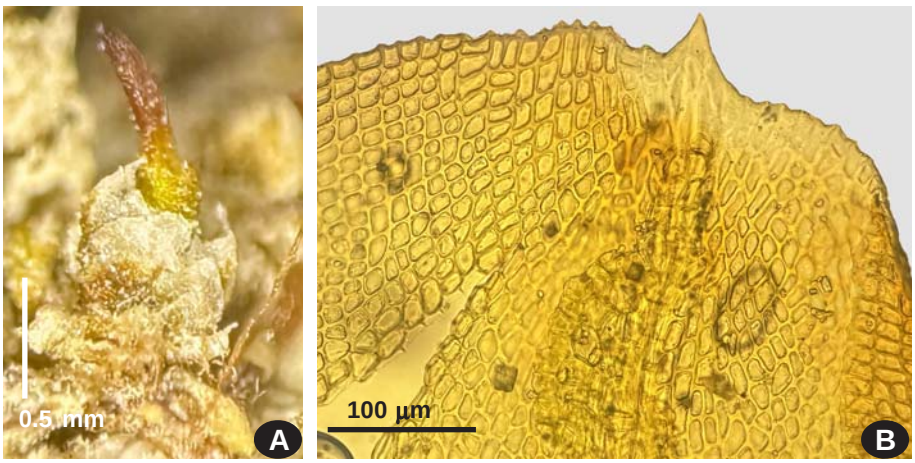


Fig. 6. *Pterygoneurum* cf. *ovatum* (*P. sampaianum*-like plant from Taimyr, MW9061193). A: habit of a plant with immature sporophyte; B: distal leaf portion showing percurrent costa.

Pterygoneurum arcticum Steere, Bryologist 62: 217, f. 1–18. 1959. Fig. 5.

This species was described in details and illustrated by Steere (1959) based on plants from Arctic Alaska (type of *P. arcticum*) and by Abramova *et al*. (1973) based on specimens from the Western Taimyr. Although these descriptions and illustrations differ in several details of papillae distribution, peristome development, and position of opercula, more detailed analysis of the species variability led Abramova *et al*. (1973) to the conclusion that actually they represent the same species. After the revision of herbarium collections in LE and MW, additional specimens from different areas of Taimyr, and also from Severnaya Zemlya Archipelago and from two localities on Chukotka were referred to this taxon. The later records fulfilled the gap between Siberian and North American partitions of the species distribution, suggesting its probable occurrence also in Arctic Yakutia. We presume that this species may have a continuous distribution along the Beringian Arctic shore, but might have been overlooked or misidentified due to having extremely small size (as experienced based on specimens from the Dikson area) and growing sunken in silt.

A light yellow-green color of awn and distal part of leaf is suggestive for the species identification (Fig. 5). Unlike most other species of the genus, the dark-brown or blackish pigmentation was not observed in it.

Specimens examined: RUSSIA: **Krasnoyarsk Territory**, Severnaya Zemlya Archipelago, Bol'shevik Island, ancient terrace in the middle course of Lagernaya River, 78°22'N, 103°31'E, 8.VII.2000, *Matveeva s.n.* (LE). Taimyr Distr., vicinity of Dickson village, Bol'shoy Arctichesky State Reserve, 2 km southwards Lemberova River Mouth, 73.403°N, 80.655°E, on eroded slope, 30.VII.2019, *Fedosov & Koltysheva* (MW9113999, MW9114127); Pyasina River middle course near Tareya settl., 73°17'N, 90°49'E, steep slope, *Dryas* & herb dominated tundra, on loamy ground, 28.VII.1968, *Blagodatskikh & Afonina s.n.* (LE); same locality: grass & herb dominated tundra, on loamy ground, 31.VII.1968, *Blagodatskikh & Afonina s.n*. (LE), S-faced slope, with *Tortula leucostoma* and *Bryum* sp., 31.VII.1968, *Blagodatskikh s.n.* (LE), herb & moss dominated tundra, 3.VIII.1969, *Blagodatskikh s.n*. (LE), dwarf-shrub & herb & moss dominated tundra, 23.VIII.1969, *Blagodatskikh s.n*. (LE), spotty tundra, on bare spots, 8.VII.1970, *Blagodatskikh s.n*. (LE), upper part of steep S-faced slope, *Dryas* & herb dominated tundra, 1.VIII.1970, *Blagodatskikh s.n*. (LE); Kotuyskoe Plateau, vicinity of Ereechka River mouth, variegate deposits outcrops, 71.150°N, 102.580°E, on salty soil, 21.VIII.2011, *Fedosov 11-1219* (MW9061139); same area: calcareous rock outcrops Kysyl-Khaya, 71.000°N, 102.696°E, rock ledge, on finesoil, 15.VIII.2007 *Fedosov 07-848* (MW9075003); North periphery of Anabar Plateau, rocky slope of hill with altitudinal mark 386 m to Fomich River ca. 15 km above its mouth, 72.06°N, 110.210°E, on finesoil, 13.VII.2008, *Fedosov 08-99* (MW9061137); same area: rock outcrops along Rossokha River 27 km upstream its mouth, 71.7509°N, 110.234°E, on finesoil, 27.VII.2008, *Fedosov 08-185* (MW9061138), rock outcrops along Popigai River 4 km downstream Popigai abandoned village, 71.9221°N, 110.735°E, on fine soil, 28.VII.2008, *Fedosov 08-165* (MW9061140). **Chukotsky Autonomous District**, vicinities of Valkumey settl., dry seashore with steppe vegetation, 10.VII.1983, *Afonina s.n.* (LE); NW spurs of Pekulney Range, vicinities of Baran'e Lake, 66°54'N, 176°15'E, rock outcrops along a creek, 31.VII.1980, *Afonina s.n.* (LE).

* * *

An unusual *Pterygoneurum* specimen from North Siberia (Russia, Krasnoyarsk Territory, Taimyr Autonomous Distr., rocky canyon of Kotuy River valley 1 km downstream Kotuykan River mouth, steep rocky slope, on calcareous fine soil, 11.VIII.2011, *Fedosov 11-1128*, MW9061193) (Fig. 6) represented by tiny *P. sampaianum*-like plants without hyaline hair points and with large, 38–48 µm spores was proved to belong to the sympatrically distributed *P. ovatum*, but appeared distinct in plastid sequences both from the European accessions of this species and from a single involved specimen of typical *P. ovatum* from the area, where *P. sampaianum*-like plants were collected. Although weak molecular justification of the aberrant morphology of this specimen might indicate the need for its taxonomical recognition, it is postponed until additional similar specimens could be studied. Morphologically, it may represent a lineage parallel to *P. arcticum* and *P. sampaianum*, adopted to a very short growth season due to cold or/and xeric environments. Deeper sampling of reduced epilose morphotypes of *P. ovatum*, as well as those with the very short setae sometimes considered as *P. medium,* and also those with an

abundant lateral lamellae outgrowths sometimes considered as *P. crossidioides,* is needed to complete the comprehensive revision of this group in the Holarctic region.

Key to identification of *Pterygoneurum* species in the Holarctic region

1. Setae longer than urn; capsules exserted 2
— Setae shorter than urn; capsules immersed 8
2. Leaf margins recurved to revolute; upper laminal cells with forked papillae on both surfaces ... *P. volgense*
— Leaf margins plain or slightly recurved; upper laminal cells smooth or with simple or forked papillae on dorsal surface 3
3. Leaves short awned; lamellae without lateral outgrowths 4
— Leaves with long hyaline hair point; lamellae often with lateral outgrowths 7
4. Capsules cylindric; opercula composed of cells in oblique rows; peristome remnants occasionally present; spores 20–26 µm ..... *P. arcticum*
— Capsules ovate to short cylindric; opercula composed of cells in straight rows; peristome remnants absent; spores (22–)30–58 µm 5
5. Distal laminal cells with forked papillae on dorsal side ..... *P. papillosum*
— Distal laminal cells smooth or with simple papillae on dorsal side 6
6. Capsules short cylindric; spores 38–48 µm; [North Siberia] ..... *P. ovatum p.p.*
— Capsules ovate; spores 35–58 µm; [Mediterranean region] ..... *P. sampaianum*
7. Opercula composed of cells in oblique rows .... *P. lamellatum*
— Opercula composed of cells in straight rows .... *P. ovatum*
8. Capsules stegocarpous ..... *P. subsessile*
— Capsules cleistocarpous 9
9. Distal laminal cells with simple or forked papillae on dorsal surface; ventral lamellae 4–10(–15) cells high, with forked or C-shaped papillae; paroicous . ..... *P. sibiricum*
— Distal laminal cells smooth or with simple papillae on dorsal surface; ventral lamellae 1–4 cells high, with simple papillae; perigonia well below perichaetia ..... *P. kozlovii*

Acknowledgements

We are grateful to Jan Kučera for the fruitful discussion of the results and the identity of *P. lamellatum* and to the curator of LE for kind permission to study herbarium material and use duplicates for DNA study. The work was supported by the Russian Science Foundation project 23-14-00043 (field studies, laboratory work and sequencing, phylogenetic analysis, and manuscript preparation). Herbarium collections in MW are supported by the MSU state assignment, and CCU "Herbarium MBG RAS" thanks Minobrnauka for support its facilities. Work of MI was conducted within the MBG RAS institutional project 122042700002-6.

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Received 22 January 2025 *Accepted 28 May 2025*

Appendix. Specimen voucher information of *de novo* studied specimens and GenBank accession numbers (boldfaced for the newly obtained sequences).

Species	Isolate	Country	Specimen voucher	*rps*4	*trn*MV
Crossidium squamiferum	Cr2354	Russia: Dagestan Republic	-	PQ587219	PQ587247
Crossidium squamigerum	TF19	Russia: Dagestan Republic	MW9030065	**PV755929**	**PV755901**
Pterygoneurum arcticum	TF23	Russia: Taimyr	MW9061137	**PV755934**	**PV755907**
Pterygoneurum arcticum	TF37	Russia: Taimyr	MW9061140	**PV755923**	**PV755908**
Pterygoneurum kozlovii	Pn1335	Czech Republic	-	PQ587220	PQ587248
Pterygoneurum kozlovii	TF64	Russia: Kalmykia Republic	Ukrainskaya Kl163(LE)	**PV755928**	**PV755913**
Pterygoneurum kozlovii	TF22	Russia: Bashkiria	MW9078555	**PV755936**	**PV755914**
Pterygoneurum lamellatum	Pn1333	Czech Republic	-	PQ587221	PQ587249
Pterygoneurum lamellatum	Pn1726	Czech Republic	-	PQ587222	PQ587250
Pterygoneurum ovatum	Pn1330	Czech Republic	-	PQ587223	PQ587251
Pterygoneurum ovatum	Pn1332	France	-	PQ587224	PQ587252
Pterygoneurum ovatum	TF65	Russia: Taimyr	MW9061193	**PV755930**	**PV755902**
Pterygoneurum ovatum	TF24	Russia: Lipetzk Province	MW9075163	**PV755922**	**PV755903**
Pterygoneurum ovatum	TF66	Russia: Krasnodar Territory	MW9092452	**PV755931**	**PV755904**
Pterygoneurum ovatum	TF68	Russia: Krasnodar Territory	MW9092313	**PV755932**	**PV755905**
Pterygoneurum ovatum	TF67	Russia: Taimyr	MW9061179	**PV755933**	**PV755906**
Pterygoneurum papillosum	Pn1747	United Kingdom	-	PQ587225	PQ587253
Pterygoneurum papillosum	Pn1757	Germany	-	PQ587226	PQ587254

Pterygoneurum sampaianum	Pn2359	France	-	PQ587228	PQ587255
Pterygoneurum sampaianum	Pn1334	Spain	-	PQ587229	PQ587256
Pterygoneurum sampaianum	Pn2357	Tunisia	-	PQ587230	PQ587257
Pterygoneurum sibiricum	TF42	Russia: Yakutia	MHA9046873	**PV755924**	**PV755909**
Pterygoneurum sibiricum	TF41	Russia: Yakutia	MHA9046874	**PV755925**	**PV755910**
Pterygoneurum sibiricum	TF45	Russia: Krasnoyarsk	MW9117597 (Isotype)	**PV755926**	**PV755911**
Pterygoneurum sibiricum	TF63	Russia: Transbaikalia	Afonina 5805 (LE)	**PV755935**	**PV755912**
Pterygoneurum sp.	OK4194	Russia: Volgograd Province	MHA9063027	**PV755937**	**PV755915**
Pterygoneurum sp.	TF61	Russia: Kalmykia	Ukrainskaya Kl134 (LE)	**PV755938**	**PV755916**
Pterygoneurum sp.	OK4186	Russia: Volgograd Province	MHA9063027	**PV755939**	**PV755917**
Pterygoneurum subsessile	Pn1331	Czech Republic	-	PQ587231	PQ587258
Pterygoneurum subsessile	OK4189	Russia: Volgograd Province	MHA9063026	**PV755940**	**PV755918**
Pterygoneurum subsessile	TF70	Russia: Altay	MW9061204	**PV755941**	**PV755919**
Pterygoneurum subsessile	TF71	Russia: Buryatia	MW9131464	**PV755942**	**PV755920**
Stegonia latifolia	Sg1641	Czech Republic	-	PQ587232	PQ587259
Stegonia latifolia	TF36	Russia: Yakutia	MW9021747	**PV755927**	**PV755921**
Tortula atrovirens	-	China	-	PP190927	PP190927
Tortula hoppeana	De1653	Austria	-	PQ587236	PQ587263