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COMMENTS ON *SYNTRICHIA CANINERVIS* AND *S. PSEUDOHANDELII* IN RUSSIA

О *SYNTRICHIA CANINERVIS* И *S. PSEUDOHANDELII* В РОССИИ

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Abstract

Two species of *Syntrichia*—*S. caninervis* and *S. pseudohandelii*—with bistratose leaf lamina and pedicellate, branched papillae on dorsal side of costae occur in Russia. *Syntrichia caninervis* is sporadically distributed in European Russia in areas with limestone bedrocks, being especially frequent in its xeric south-eastern regions. In Asian Russia, it is much rarer, known from few localities in Altai, Buryatia, Taimyr, and Yakutia. Intraspecific variation of *S. caninervis* includes a development of rhizoidal gemmae, which is more frequent than it was thought previously, being especially regular in damaged plants. We found no differences in nrITS and cp *rpl*16 and *atp*B–*rbc*L between plants bearing and lacking gemmae, as well as between plants having almost completely bistratose leaf lamina and those having predominantly or even totally unistratose leaves. *Syntrichia pseudohandelii* occurs on Russia only in south-eastern European Russia and East Caucasus, being very rare in these areas. Molecular phylogenetic analysis of nrITS resolved *S. caninervis* in a clade sister to the *S. ruralis* complex while in the latter *S. pseudohandelii* clade is sister to all other species of this complex. The analysis of plastid *atp*B–*rbc*L also supports the species identity of *S. pseudohandelii* and its position within *S. ruralis* complex. Morphologically *S. pseudohandelii* combines features of *S. ruralis* s.l. and *S. caninervis,* and it is a well delimited species*,* despite more variable as it was previously thought.

Резюме

В России встречаются два вида *Syntrichia* с двуслойной пластинкой листа и высокими разветвленными папиллами на дорсальной стороне жилки – *S. caninervis* и *S. pseudohandelii*. *Syntrichia caninervis* имеет спорадическое распространение в европейской России, в районах выходов известняков, встречаясь особенно часто в засушливых регионах юго-востока; в азиатской части России этот вид значительно более редок, он известен из нескольких местонахождений на Алтае, в Бурятии, на Таймыре и в Якутии. Здесь мы обсуждаем внутривидовую вариабельность *S. caninervis* на примере образцов из России. Выявлено, что у *S. caninervis* выводковые тела на ризоидах встречаются чаще, чем считалось ранее; особенно часто они образуются на поврежденных растениях. Нами не было найдено отличий в ядерном ITS между растениями с выводковыми телами и без них, а также между растениями с почти полностью двуслойной пластинкой листа и растениями с полностью или преимущественно однослойной пластинкой, имеющей единичные двуслойные участки. *Syntrichia pseudohandelii* приводилась для юго-востока европейской России и российской части Кавказа, однако она очень редка в этих регионах. Молекулярно-филогенетический анализ последовательностей ядерного ITS показал, что *S. caninervis* образует кладу, сестринскую комплексу *S. ruralis,* в котором клада *S. pseudohandelii* находится в базальном положении по отношению ко всем остальным видам этого комплекса. Анализ пластидного маркера *atp*B–*rbc*L также поддерживает видовую самомтоятельность *S. pseudohandelii* и его положение внутри комплекса *S. ruralis*. В *S. pseudohandelii* сочетаются морфологические признаки *S. ruralis* s.l. и *S. caninervis,* и она является самостоятельным, хорошо отграниченным видом*,* хотя и несколько более вариабельным, чем считалось ранее.

KEYWORDS: mosses, Pottiaceae, nrITS, *atp*B–*rbc*L, *rpl*16, hybridization

INTRODUCTION

Syntrichia Brid. is a moderately large genus with 87 (Jauregui-Lazo *et al.*, 2022) or 101 (Brinda & Atwood, 2026) accepted species. In regional floras of Holarctic, its species diversity is not very high: 17 species in North America North of Mexico (Mishler, 2007), 16 in Russia (Ignatova & Afonina, 2025), 22 in Europe (Hodgetts *et al.*, 2020), and only 6 species in China (Li *et al*., 2001).

In temperate and cold regions of Northern Hemisphere, the most widespread are terrestrial species of the *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr and related species, in some regions being an important component of

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certain types of xerophytic vegetation (Mishler, 1987; Jauregui-Lazo *et al*., 2022). Since the 19th century, taxonomic literature on this group was full of disagreements regarding the status of some species, which were accepted by some authors for areas studied by them, while other authors in different regions treated them as subspecies or varieties. The recent morpho-molecular revision of the *Syntrichia ruralis* complex in Scandinavia (Hedenäs *et al*., 2019) provided an overview of approaches to such disputable species and demonstrated that the molecular evidences support for most of them a narrow species delimitation, albeit some inconsistences in sequence data may indicate an occasional hybridization events.

The complex of terrestrial *Syntrichia* species that are characterized by bistratose leaf laminae, hereafter *Syntrichia caninervis* complex, was another point of disagreements. Kramer (1980) recognized in this complex, that time still classified in *Tortula*, four species: *T. caninervis* (Mitt.) Broth., *T. handelii* Schiffn., *T. pseudohandelii* J. Froehl., and *T. rigescens* Broth. & Geh., the two former species also having infraspecific taxa.

Shortly after that, the *Syntrichia caninervis* group was in a focus of special study by Gallego *et al*. (2002), who accepted in it three species: *S. handelii* (Schiffn.) Bachurina, *S. rigescens* (Broth. & Geh.) Ochyra, and *S. caninervis* Mitt. with four varieties: var. *abranchesii* (Luisier) R.H.Zander, var. *caninervis*, var. *gypsophila* (J.J.Amann ex G.Roth) Ochyra, and var. *pseudodesertorum* (Vondr.) M.T. Gallego. The latter variety included as a synonym *S. pseudohandelii* (J. Froechl.) S. Agnew & Vondr., opposing to the opinion of Agnew & Vondracek (1975) and Kramer (1980) who treated *S. pseudohandelii* as a separate species.

Gallego *et al*. (2002) claimed that intermediates between typical *S. caninervis* and *S. pseudohandelii* occur, so they are not separate species, while Kramer (1980) considered the latter as a species of its own, not a hybrid, and in the subsequent 'second edition' of his monograph stated that he could always separate *S. pseudohandelii* from *S. caninervis* and did not see any transitional morphotypes between them (Kramer, 2023, p. 99).

Recent studies of the genus based on integrative approach that involved both rich molecular and morphological investigations accepted *S. pseudohandelii* as a separate species. However, its position in the phylogenetic reconstructions varied.

The analysis of Hedenäs *et al*. (2019) included 174 samples of *Syntrichia*; it was addressed mostly to the Scandinavian plants of the *Syntrichia ruralis* complex, but several samples of other species from different regions were also added. Among them were *S. caninervis* (3 samples), *S. handelii* (2), *S. pseudohandelii* (1), and *S. rigescens* (2). The NeighborNet split network for nuclear ITS1 and two plastid loci, *atp*B–*rbc*L and *rpl*16 found that *S. handelii* and *S. pseudohandelii* are closely related to the Scandinavian *S. ruralis* species complex. At the same time, *S. caninervis* appeared somewhat separate from *S. ruralis* and closely related species. *Syntrichia caninervis, S. handelii* and *S. pseudohandelii*, however, were not discussed in detail as they do not occur in Scandinavia.

Jauregui-Lazo *et al.* (2022) analysis which included 82 species using GoFlag 408 probe set resulted in the alignment of 72 263 molecular characters from an average of 354 loci. This comprehensive analysis found *Syntrichia ruralis* complex and *S. caninervis* complex closely related, but nevertheless in separate clades, and *S. handelii* was found within the former clade, while *S. pseudohandelii* within the latter one.

Both these studies, however, included only solitary samples of *S. caninervis* and *S. pseudohandelii*, thus the specific status of the latter species could not be either supported or rejected. Before these studies, six samples of *Syntrichia caninervis* were sequenced in the course of the revision of *Syntrichia submontata / S. sinensis* complex (Afonina *et al*., 2014). That analysis, based on ITS2 sequences only, surprisingly found *S. canivervis* var. *astrakhanica* Ignatov, Ignatova & Suragina and 'typical' *S. caninervis* from Dagestan and Mongolia in two unrelated clades. *Syntrichia caninervis* var. *astrakhanica* has been segregated from *S. canivervis* var. *canivervis* by the presence of copious rhizoidal gemmae, which were never reported for this species earlier (Suragina *et al*., 2002). It was first discovered in a xeric region of Cis-Caspian lowland, but later found in other regions of Russia (Afonina *et al*., 2014), including some not especially xeric areas, and this variety was subsequently reported for Estonia (Leis & Kannukene, 2007) and France (Skrzypczak, 2006).

Until recently, *Syntrichia caninervis* was considered the only species of the genus with bistratose leaf lamina occurring in Russia (Savicz-Lyubitskaya & Smirnova, 1970; Ignatov *et al.*, 2006). The second species, *S. pseudohandelii,* was recorded from Russia by Kramer (2023), based on two herbarium collections from the eastern Caucasus, Dagestan Republic, and south-east European Russia, Astrakhan Province. These records were the first for Europe; this species was missing in the last European checklist (Hodgetts *et al*., 2020), but included in the "Moss flora of Russia" (Ignatova & Afonina, 2025).

The main aim of the present study was a better understanding the *Syntrichia caninervis* complex in Russia. Particularly, we attempted to support the species status of *S. pseudohandelii* with the help of more sequences obtained from samples from Russia and to elucidate its distinctions from other species. Another aim implied a molecular delimitation of *Syntrichia caninervis* var. *astrakhanica* and *S. canivervis* var. *gypsophila* from *S. canivervis* var. *canivervis*.

Materials and Methods

Dataset

The previous studies of *Syntricha ruralis* complex reached a phylogenetic and/or molecular barcoding solution by using ITS1+*atp*B–*rbc*L+*rpl*16 (Hedenäs *et al*.,

2019), or with only ITS2 (Afonina *et al.*, 2014). Currently we obtained new sequences of ITS1-2 for 3 specimens of *S. pseudohandelii* and 9 of *S. caninervis*.

Dataset ITS#1 includes ITS data for 74 accessions, where 23 samples have both ITS1+ ITS2, 41 ITS1 only and 10 ITS2 only. Outgroup of distantly related species, according to Jauregui-Lazo *et al.* (2022), includes *Syntrichia filaris* (Müll. Hal.) R.H. Zander*, S. magellanica* (Mont.) R.H. Zander*, S. sinensis* (Broth.) Ochyra*, S. obtusissima* (Müll. Hal.) R.H. Zander*,* and *S. princeps* (De Not.) Mitt. The group of *Syntrichia caninervis*+*S. pseudohandelii* is represented by 23 samples.

Dataset ITS#2 of 102 accessions (21 accessions of ITS1+ ITS2, 60 of ITS1 only, and 21 of ITS2 only) was built to expand representation of *S. ruralis* and *S. ruraliformis* lineages from Hedenäs *et al*. (2019) in order to exclude possible affinity of *S. pseudohandelii* with some rare genotypes of *S. ruralis* not included in the Dataset 1. This dataset did not include distantly related species; it was rooted on one of the most peculiar ITS1 of *S. ruralis* (found as most deviating in preliminary analysis). The group of *Syntrichia caninervis*+*S. pseudohandelii* was represented by 23 samples.

Plastid datasets of *atp*B–*rbc*L (76 accessions) and rpl16 (62 accessions) included an outgroup of distantly related species, such as *Syntrichia sinensis, S. laevipila* Brid.*,* and *S. princeps*. It contained mainly samples of various lineages of *S. ruralis* complex from the study of Hedenäs *et al*. (2019), with 19 additional samples of *Syntrichia caninervis*+*S. pseudohandelii* (altogether 23 samples of this group).

Sequences were aligned using MAFFT v. 7.520 (Katoh *et al*., 2019) with E-INS-I strategy, 1000 iterative cycles, and otherwise default settings.

The laboratory and sequencing protocols were essentially the same as in our previous moss studies for ITS1-2 (Gardiner *et al.,* 2005), for *atp*B–*rbc*L as in Chiang *et al.* (1998), and for *rpl*16 as in Jordan *et al*. (1996) and Hedenäs (2008).

Molecular phylogenetic analysis

Phylogenetic analyses were implemented under Bayesian inference (BI) performed using MrBayes v.3.2.6 (Ronquist *et al*., 2012), with the HKY model, four parallel runs each consisting of six Markov chains, the chain temperature was set at 0.02, 5,000,000 generations. These resulted in all ESS higher than 2000, PSRF 1.000.

Morphological study

All sequenced specimens were studied using common morphological methods of light microscopy. Additionally, herbarium collections of *Syntrichia caninervis* and *S. pseudohandelii* from MHA, MW and selected specimens from LE were revisited. The photographs were taken under Olympus CX43 light microscope with the Infinity 1–2 camera. Z-stacks of several images were generated using HeliconFocus 4.50 (Kozub *et al*., 2008), and stereomicroscope Nikon SMZ-25, with Z-stacking with NIS-element.

RESULTS

Molecular phylogenetic analysis

Dataset ITS #1

The analysis with the outgroup of species obviously outside *S. ruralis* complex (Fig. 1) resolves the studied *Syntrichia* species in two clades; one of them includes all 17 studied samples of *S. caninervis* (P=1, BS=100), while another clade, almost unsupported (P=0.76, BS<70), includes the remaining samples and forms a grade where most on internal clades lack a marked support. Only few internal clades composed of few samples of the same species are supported, namely: *S. calcicola*, 5 samples (P=0.91, BS=100); *S. rigescens*, 2 samples (P=0.99, BS=100); *S. norvegica* F. Weber, 3 samples (P=0.96, BS=100)[but note that some specimens of this species are outside of this clade].

The earliest divergent clade (P=1, BS=86) in the larger clade includes six samples. One of them, from Kazakhstan, was taken from GenBank, where it was deposited as *'S. caninervis'*; another sample, from Turkey, also from GenBank deposited as *S. pseudohandelii,* is from the dataset of Hedenäs *et al*. (2019); two samples, from Dagestan and Mongolia, were reported by Afonina *et al.* (2014) as *S. caninervis*; and two samples, from Volgograd and Astrakhan Provinces, were newly selected for DNA study. Four latterspecimens studied by us are illustrated in Figs. 4 and 5.

Despite we did not see Kazakh specimen deposited in GenBank as *S. caninervis*, and Turkish specimen referred to *S. pseudohandelii* in GenBank, we presume, with a certain reservation, that all six samples belong to *S. pseudohandelii,* and will call this clade hereafter '*S. pseudohandelii*-clade'.

This clade is subdivided into two subclades: the better supported one (P=0.98, BS=97) includes specimens from Kazakhstan, Mongolia and eastern Caucasus (Dagestan Republic). The second subclade (P=0.76, BS=93) includes samples from Cis-Caspian European Russia (Astrakhan and Volgograd Provinces) and from Turkey. In both these clades there are terminal subclades of two samples from geographically closer regions than the the third sample (Fig. 1).

Dataset ITS #2

The tree inferred from the Dataset 2 (Supplementary materials Fig. SM1) does not include an outgroup of more distant species, and its main part has only short branches. Within the *Syntrichia ruralis*-complex sensu Hedenäs *et al.* (2023), only the clade of *S. calcicola* includes many species and has a maximal support. The internal clades are supported only if they are formed of few samples of one species.

Syntrichia caninervis forms a maximally supported clade in a terminal position of the poorly resolved grade of most accessions. It is on an exceptionally long branch; there is also a clade on a short branch that includes two subclades: (1) of *S. pseudohandelii* and (2) of two accessions of *S. montana* Nees. The internal structure of '*S.*

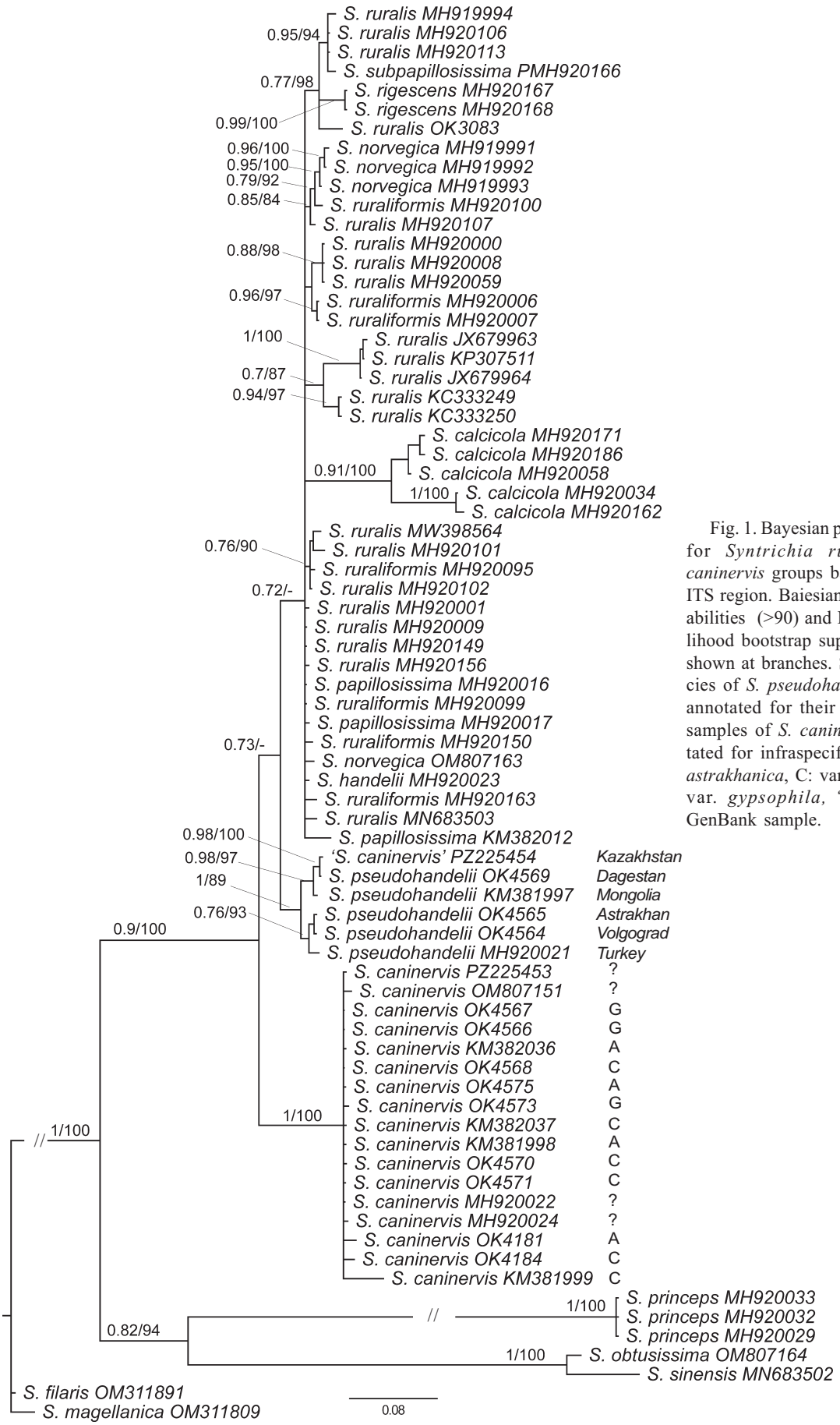

Fig. 1. Bayesian phylogenetic tree for *Syntrichia ruralis* and *S. caninervis* groups based on nuclear ITS region. Baiesian posterior probabilities (>90) and Maximum Likelihood bootstrap supports (>70) are shown at branches. Samples of species of *S. pseudohandelii*-clade are annotated for their origin. Studied samples of *S. caninervis* are annotated for infraspecific taxa: A: var. *astrakhanica*, C: var. *caninervis*, G: var. *gypsophila,* ?: not studied GenBank sample.

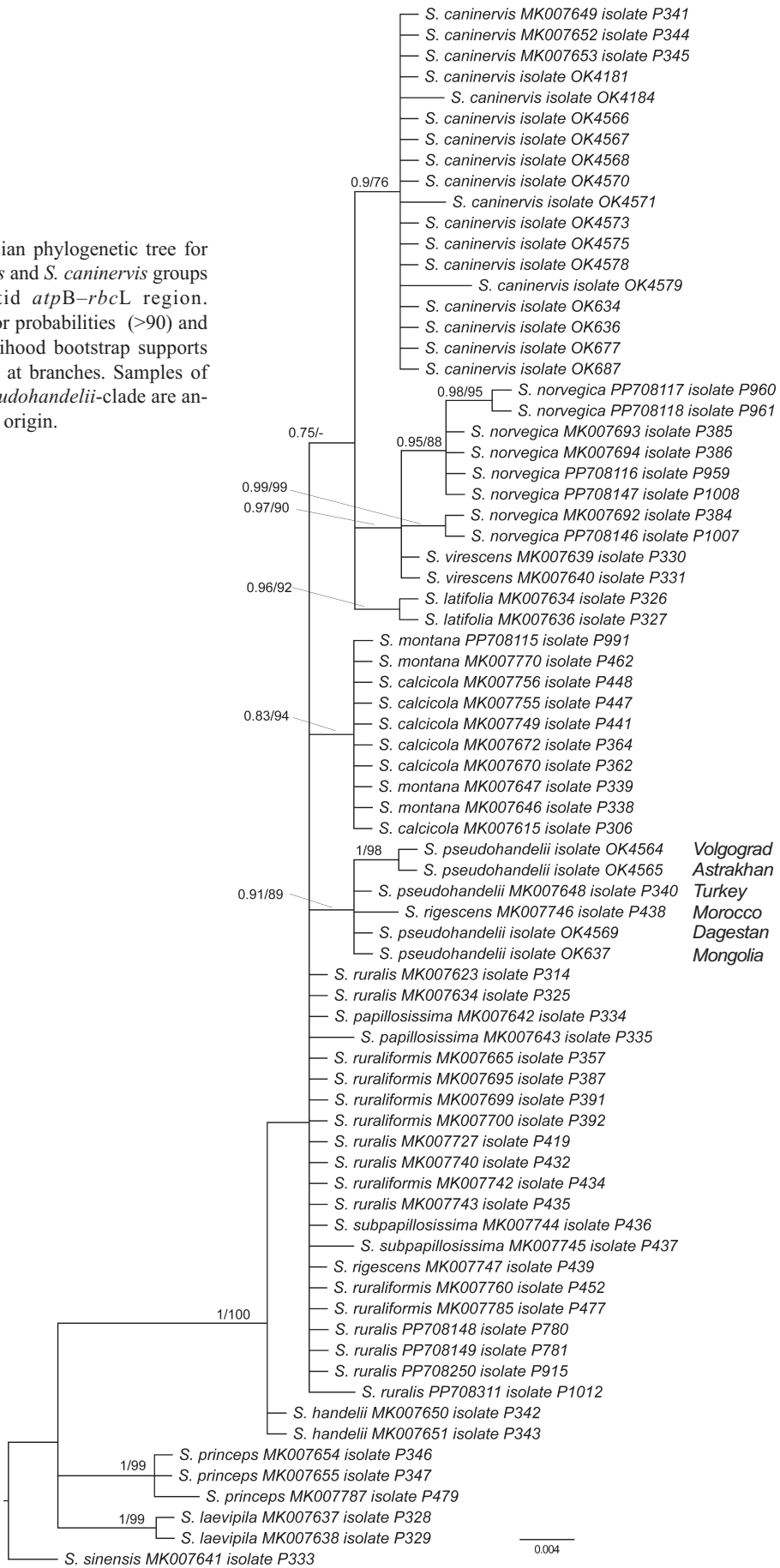

Fig. 2. Bayesian phylogenetic tree for *Syntrichia ruralis* and *S. caninervis* groups based on plastid *atp*B–*rbc*L region. Baiesian posterior probabilities (>90) and Maximum Likelihood bootstrap supports (>70) are shown at branches. Samples of species of *S. pseudohandelii*-clade are annotated for their origin.

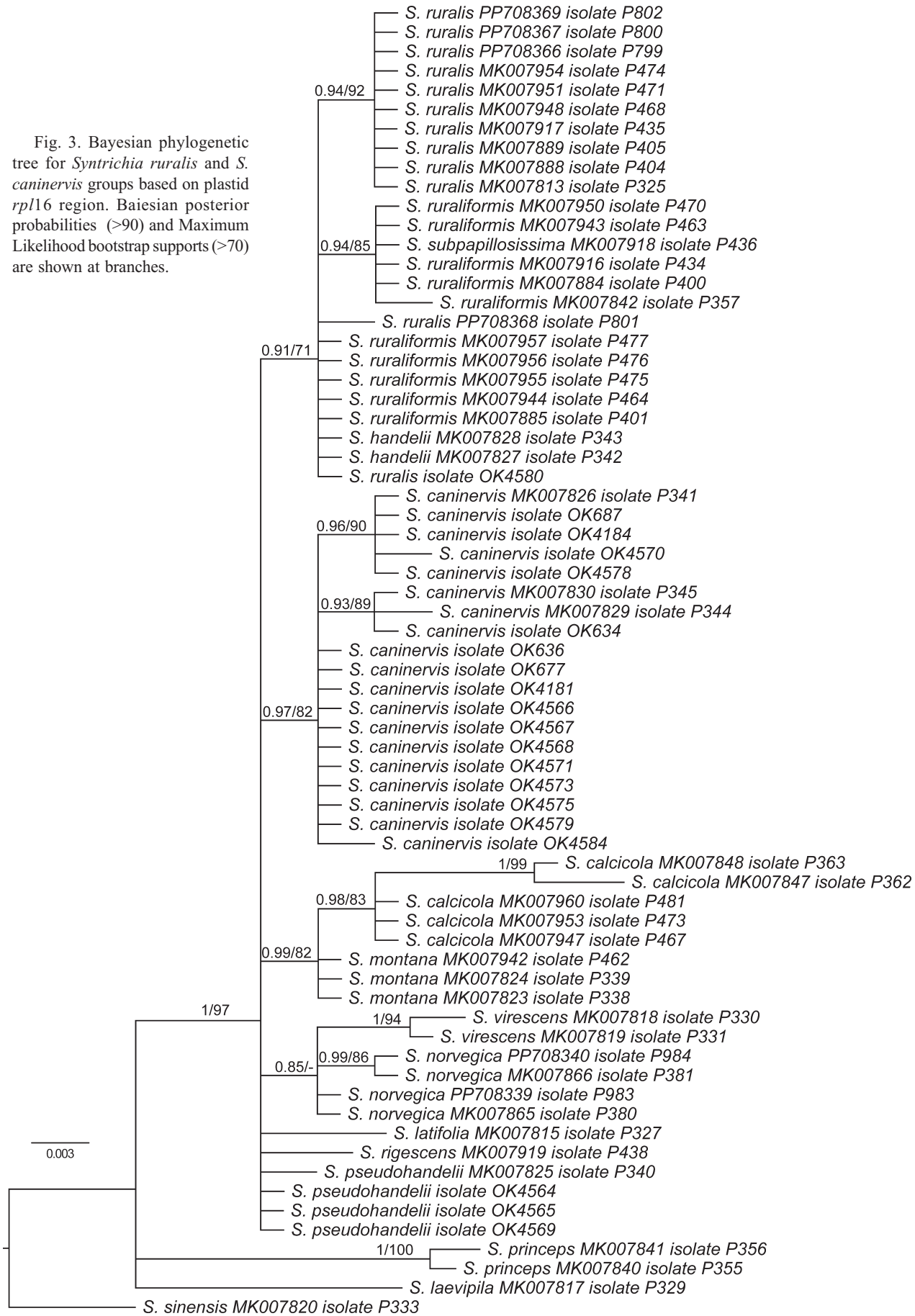

Fig. 3. Bayesian phylogenetic tree for *Syntrichia ruralis* and *S. caninervis* groups based on plastid *rpl*16 region. Baiesian posterior probabilities (>90) and Maximum Likelihood bootstrap supports (>70) are shown at branches.

pseudohandelii-clade', i.e. two groups of three specimens each, remains the same.

Datasets *atp*B_*rbc*L and *rpl*16

Both trees inferred from plastid sequences with an outgroup of distant taxa show less resolution than ITS trees. The *S. caninervis* clade is the best supported, though the support itself is rather low: P=0.90 and BS=76 in in *atp*B–*rbc*L tree, and P=0.97 and BS=82 in *rpl*16 tree. *Syntrichia pseudohandelii* appears in an unresolved polytomy in *rpl*16 tree, but in *atp*B–*rbc*L tree all studied specimens referred to *S. pseudohandelii* were found in a clade with one specimen of *S. rigescens* from Morocco, with moderate support (P=0.91, BS=89), which, however, is at the level of other mono- or oligospecific clades.

Morphological study

The results of morphological observations are presented in Figs. 4–5, where the differences between the studied specimens in leaf shape, size and costa structure are shown for sequenced specimens and some additional samples of *Syntrichia*, mainly *S. caninervis* and *S. pseudohandelii*. Their descriptions, as well as a comparison with the results of the molecular phylogenetic study are given in the Discussion section.

DISCUSSION

Syntichia pseudohandelii

Syntrichia pseudohandelii shares with *S. caninervis* partially bistratose leaf lamina, dorsal surface of costa in distal part covered with pedicellate, branched or stellate papillae, and costa in transverse section having stereids with wide lumens or substereids. This similarity caused numerous misidentifications of the former species, so that it was stored in herbaria under the latter name. Kramer (2023) suggested to separate *S. pseudohandelii* from *S. caninervis* mainly by leaf shape: narrow, ovate-lingulate to lingulate vs. often broad, ovate to ovate-lingulate (cf. Fig. 4). He also stated that *S. caninervis* var. *caninervis* has totally bistratose leaves, whereas *S. pseudohandelii* has leaves partially bistratose to various extent, thus resembling *S. caninervis* var. *gypsophila*. He considered *S. pseudohandelii* scarcely variable morphologically and easily recognizable.

Our observations are generally in agreement with morphological circumscription provided by Kramer (2023). Three of four specimens resolved in our molecular-phylogenetic analysis in *S. pseudohandelii*-clade have lingulate leaves resembling in shape rather *S. ruralis* than *S. caninervis* (Fig. 4: P1–P3); similar leaves has an additional specimen from Dagestan (P5), as well as specimens from Middle Asian countries and Mongolia (see specimens examined). In the circumscription of *S. pseudohandelii,* Kramer (2023) provided some quantitative characters, i.e. leaves 3–4 mm long. However, in our specimens leaves varied considerably in size: 4.0–4.2 mm long in specimen from Dagestan (P1 in Fig.4, isolate OK4569), 3.2–3.4 mm in specimen from Elton Lake area, Volgograd Province (P2 in Fig. 4, isolate OK4564), 2.4–3.1 mm in another specimen from Dagestan (P5 in Fig. 4) and only 2.0–2.2 mm in specimen from Bogdo Mt., Astrakhan Province (P3 in Fig. 4, isolate OK4565). Nevertheless, the difference in leaf shape between *S. pseudohandelii* and *S. caninervis* is sufficient for separating them: the leaves are ovate, with conspicuous constriction at ca. 0.8 the leaf length in *S. caninervis*, while in *S. pseudohandelii* leaves are lingulate, rounded or broadly acute at apex. The only exception is the Mongolian specimen (Fig. 4: P4), in which leaves have the constriction somewhat similar to *S. caninervis*, but their size approaches that of *S. ruralis*, being contrastingly different from *S. caninervis*. The position of this specimen within *S. pseudohandelii* is supported by both nr ITS (Fig. 1) and cp *atp*B–*rbc*L (Fig. 2).

All plants of *S. pseudohandelii* have partially bistratose leaf laminae and costae with high, branched papillae on dorsal surface (Fig. 5: P1–P3 and less expressed in P5). In costa structure, they are contrastingly different from *S. ruralis*. In the latter species, guide cells are comparatively small, hydroids absent, and stereids are uniform, very thick-walled, with small lumens (Fig. 5: R). In studied specimens of *S. pseudohandelii*, in larger plants, guide cells are very large, hydroids present, and substereids or stereids differ in size, sometimes becoming smaller towards the abaxial surface, they have less thickened walls and larger lumens than in *S. ruralis* (Fig. 5: P1–P2). In the smallest plant from Astrakhan Province, the costae are narrower and thinner, with smaller guide cells, but otherwise similar in having hydroids and substereids varying in size (Fig. 5: P3). Thus, in the costa structure, these specimens also fit *S. pseudohandelii* as it is described by Kramer (2023) and Gallego (2002).

Six specimens of *Syntrichia pseudohandelii* clade, as it defined above, were subdivided into two subclades, forming the subclade of specimens from Mongolia+ Kazakhstan+Dagestan and from Turkey+Astrakhan+ Volgograd Provinces (Fig. 1 and Supplementary Material Fig. SM1), and in *atp*B–*rbc*L tree the subclade of specimens from Astrakhan+Volgograd Provinces was maximally supported (Fig. 2). This subdivision somewhat correlates with the geographical origin of specimens. This great heterogeneity might be explained by the fact that all specimens are from a marginal part of the species distribution, which is centered in Afghanistan, Iran, countries of the Middle Asia, and the Middle East.

The present analysis involved two specimens already studied by Afonina *et al*. (2014): from Mongolia (KM381997) and from Dagestan (KM381996); DNA was also re-extracted from the latter one (isolate OK4569). These specimens were referred by Afonina *et al*. (2014) to *S. caninervis*. However, in the present study they were resolved in the highly supported clade with the GenBank accession of *S. pseudohandelii* from Kazakhstan. The specimen from Dagestan fits well *S. pseudohandelii* in morphology (Figs. 2–3: P1), whereas the Mongolian

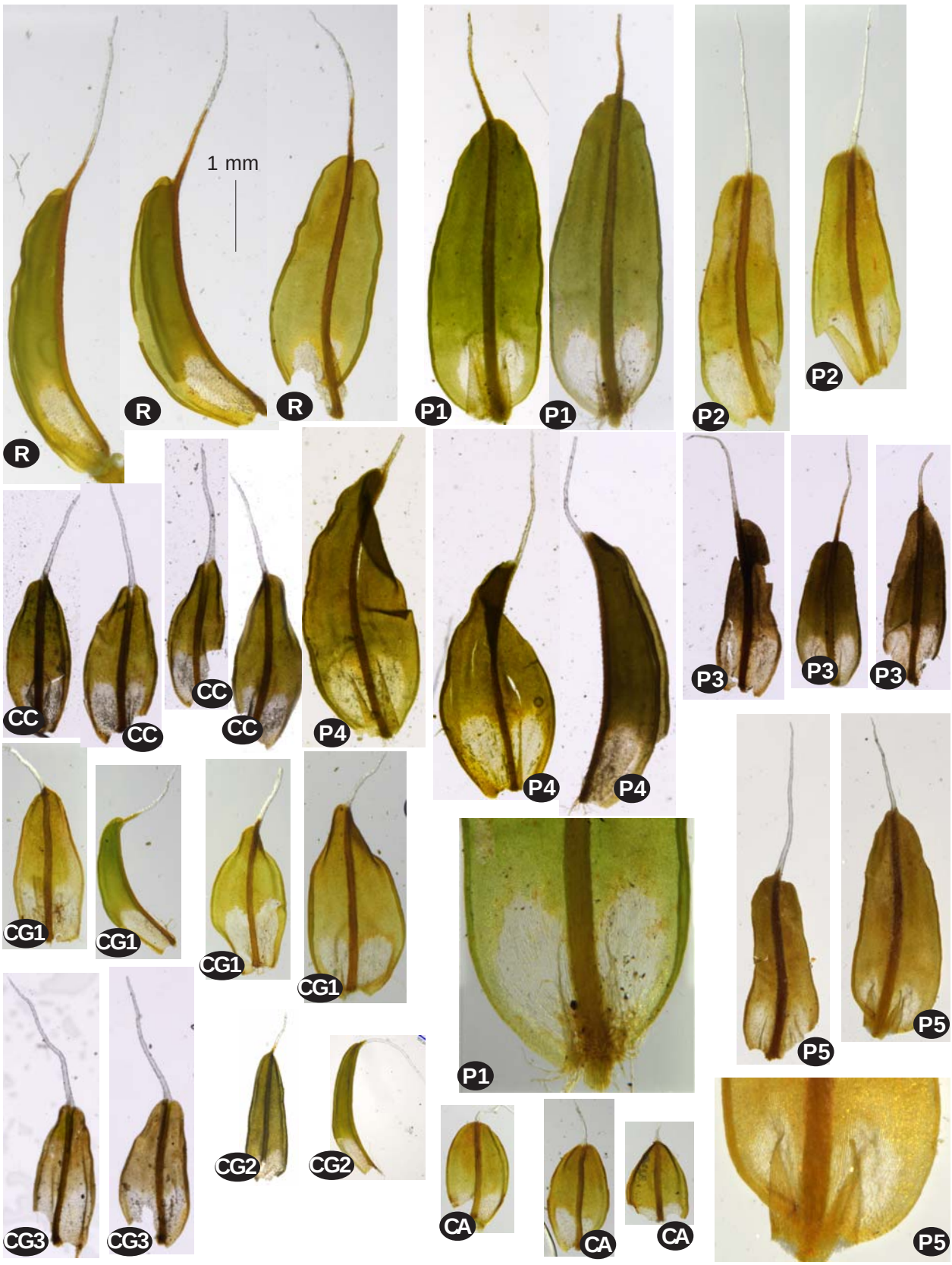

Fig. 2. Leaves of *Syntrichia* species: R: *Syntrichia ruralis* (Volgograd Prov., MHA9063462); P1–P5: *S. pseudohandelii*; (P1: Dagestan, OK4569; P2: Volgograd Prov., OK4564; P3: Astrakhan Prov., OK4565; P4: Mongolia, KM381997; P5: Dagestan, LE); CA: *S. caninervis* var. *astrakhanica* (from: Volgograd Prov., MHA9063478); CG: *S. caninervis* var. *gypsophila* (CG1: Volgograd Prov., MHA9063593; CG2: Volgograd Prov., MHA9063623; CG3: Astrakhan Prov., MHA9063356); CC: *S. caninervis* var. *caninervis* (from: Astrakhan Prov., MHA9063373).

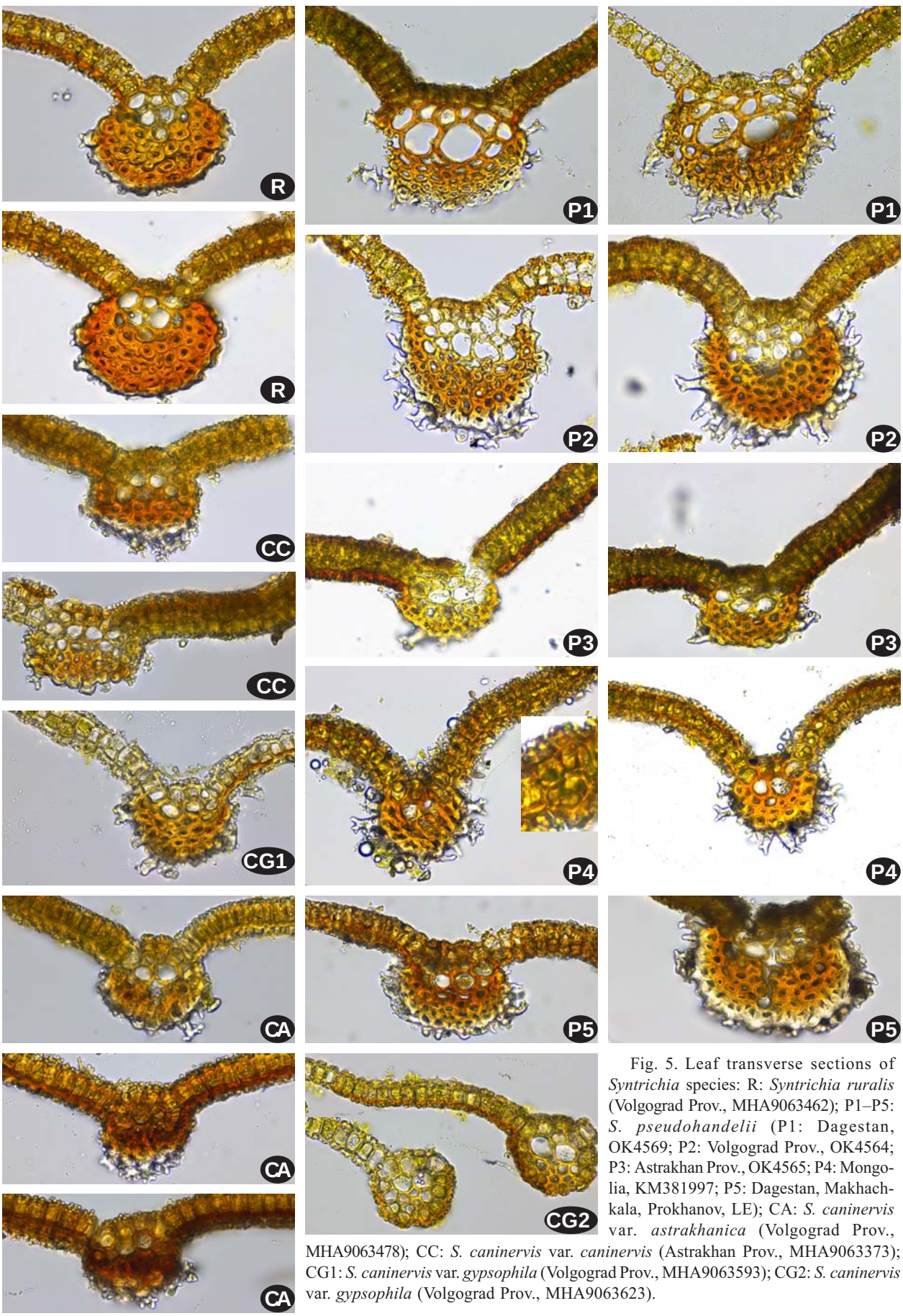

Fig. 5. Leaf transverse sections of *Syntrichia* species: R: *Syntrichia ruralis* (Volgograd Prov., MHA9063462); P1–P5: *S. pseudohandelii* (P1: Dagestan, OK4569; P2: Volgograd Prov., OK4564; P3: Astrakhan Prov., OK4565; P4: Mongolia, KM381997; P5: Dagestan, Makhachkala, Prokhanov, LE); CA: *S. caninervis* var. *astrakhanica* (Volgograd Prov., MHA9063478); CC: *S. caninervis* var. *caninervis* (Astrakhan Prov., MHA9063373); CG1: *S. caninervis* var. *gypsophila* (Volgograd Prov., MHA9063593); CG2: *S. caninervis* var. *gypsophila* (Volgograd Prov., MHA9063623).

plants do not differ in leaf shape and lamina structure from *S. caninervis* var. *gypsophila* (Figs. 4–5: P4). The only difference between the Mongolian plants and *S. caninervis* is the size of plants and leaves: they have stems ca. 2 cm tall and much larger leaves, to 3.8 mm long (Fig. 4: P4), i.e. being similar in this respect not to *S. caninervis* but to most other specimens of *S. pseudohandelii* and *S. ruralis* (Fig. 4: R, P1–2).

Since both accessions, KM381997 (Mongolia) and KM381996 (Dagestan) named by Afonina *et al*. (2014) as *S. caninervis,* are resolved here in the clade with four other accessions of *S. pseudohandelii* (two of them from GenBank), were refer them to that species. However, contrary to the statement of Kramer (2023) that *S. pseudoihandelii* is scarcely variable morphologically, we observed a considerable variability in size of leaves and plants in studied specimens. Moreover, the Mongolian specimen, which was proved by the studied molecular markers to belong to *S. pseudohandelii*, disagrees with its morphological circumscription. We have no explanation of this fact; a hybrid nature of these plants can be supposed.

In Russia, we confirm the presence of *S. pseudohandelii* in the Caucasus (Dagestan Republic), Crimea, Astrakhan and Volgograd Provinces. Its records from Saratov Province and Stavropol Territory (Ignatova & Afonina, 2025) were erroneous.

Additional specimens examined: RUSSIA: **Crimea**: Solnechnaya Dolina settlement, 9.IV. 1976 *Luks & Kryukova* (LE); Azovo-Sivashsky Reserve, 10.VI.1950 *Parnassky* (LE); **Dagestan**: Makhachkala, 27.IX.1957 *Prokhanov 2664* (LE); Buinaksk Distr., Tolgi Valley, 28.V.2010 *Fedosov 10-2-433* (MHA9020890); same place and date, *Fedosov 10-4-4* (MW9022870). KAZAKHSTAN: Syr-Daryinskaya Prov., Karatau Mt., 9.VII.1931 *Samsel 83* (MW9022882). UZBEKISTAN: Tashkent Prov.: Zaaminsky Reserve 16.VI.1952 Nazarenko (LE); Bash-Kyzylsait River 22.VI.1954 *Nazarenko* (LE); Fergana Distr.: above Khamzaabad, 8.V.1986 *Townsend 86/107*, 6.V.1986 *86/170* (LE); Laidoukhan Canyon, 3.IV.1949 *Shafeev* (LE). TURKMENISTAN: Zapadny Kopetdag, c.fr., 13.X.1967, same, 26.X.1967 *Leontieva* (LE); Kopetdag, Bakhardensky Distr., 20.VII.1954; 24.VII.1954; 25.VII.1954; 28.VII.1954; *Markova* (LE); Krasnovodsk Prov., Boshoi Balkhan IV. 1971 *Koshkelova* (LE). KYRGYZSTAN: Frunse outskirts, 5.V.1959 *Golovanova* (MW9022879); Talassky Alatau, Talas outskirts, 23.VII.2016 *Seregin M-3729* (MW9116914). MONGOLIA: Khbdossky Aimak, Bulugun Somon, 17.IX.1948 *Grubov 5272* (LE); Govi-Altai Aimak, Altai somon, Aj Bogd Mt., 4.VII.2001 *Ignatov 01-664* (MHA9065482); same, 5.VII.2001 *Ignatov 01-667* (MHA9065479).

Syntrichia caninervis

Kramer (2023) keyed out *S. caninervis* var. *caninervis* as having 'lamina towards the leaf tip ±completely with two (to three) layers'. Among its other distinctive morphological characters, he listed broad-ovate to ovate-lingulate leaves, awns hyaline from the base, costae with substereids or stereids with wide lumens, and laminal cells with dense, thick, horseshoe-shaped or dumbbell-shaped papillae. Within this species, he also recognized var. *gypsophila* having leaf laminae with bistratose portions to various extent, occasionally being totally unistratose, var. *abranchesii* differing from the latter only in absence of hyaline awns and known only from the type locality in Spain, and var. *astrakhanica* characterized by the presence of axillary gemmae on rhizoids.

Syntrichia caninervis s.l. occurs in xeric steppe areas of South-East European Russia, East Caucasus, and Crimea; in Asian Russia it is also confined to the dry areas with calcareous bedrocks in Altai, Taimyr, and Yakutia (Ignatova & Afonina, 2025); it was also reported from one locality in Buryatia (Ellis *et al.*, 2019). However, its intraspecific variability in the country has never been in the focus of special studies, and only var. *astrakhanica* was reported in addition to the type variety.

In 2023–2024, we explored the moss flora of two protected areas in Cis-Caspian lowland around salt lakes Elton and Baskunchak. Among others, 11 and 16 specimens of *S. caninervis* s.l. were identified in collections from these localities, respectively. Among them, about an equal number of specimens were referred to var. *caninervis* and to var. *gypsophila*: 6/5 in Elton and 8/7 in Baskunchak. In specimens referred to the type variety, leaf laminae were bistratose at large portion from costa to margins, but always with several rows of unistratose cells at margins. In another group of specimens identified as var. *gypsophila*, leaf laminae were predominantly unistratose with very few or single bistratose strips one cell wide or, rarer, lamina is unistratose throughout.

Only few transitional morphotypes between these two variants were observed (Fig. 5: CG1). Almost all leaves of both varieties were similar in shape and size: ovate to ovate-lanceolate, ca. 2.0–2.5 mm long, with hyaline awns equal or longer than laminae, densely spinose, hyaline from the base. Most these specimens had similar structure of costae: with moderately large guide cells, occasionally with hydroids, 2–3 layers of substereids or stereids with wide lumens, and with high, pedicellate, branched at tips papillae on dorsal surface (Fig. 5: CC and CG1).

However, one specimen strongly deviating in morphology was revealed in collections from Elton area (Volgograd Province); it is shown in Figs. 4–5 as CG2. It was collected on a slope of a dam at the bank of Elton Lake, in sparse forb community with rather dense moss cover of *Bryum caespiticium* Hedw. and *Syntrichia ruralis.* This specimen (*Ignatov et al. 23-161*, MHA9063623, isolate 4579) was also first identified as *S. ruralis* because its costae looked smooth dorsally, its leaves were lingulate (Fig. 4: CG2), and its leaf laminae were totally unistratose. But when leaf transverse sections were made, it appeared that they lack stereids and are formed of substereids with wide lumens (Fig. 5: CG2). Also, their awns were hyaline from the base, without reddish coloration below, which agrees better with *S. caninervis*. A peculiar was its dorsal surface of costa: it was covered with horse-

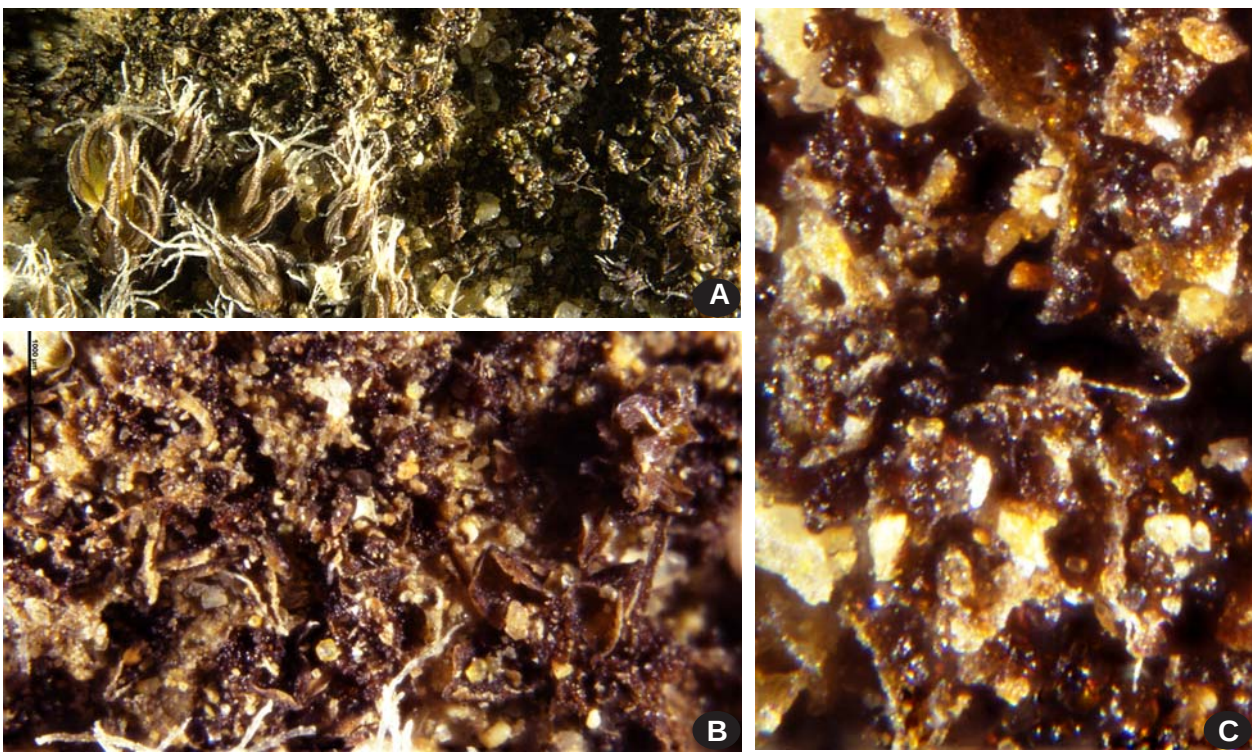

Fig. 4. *Syntrichia caninervis* tuft, partly formed by a well developed plants with long hyaline awns (A, below), while another part (A, above and magnified in B and C) is formed by apparently damaged plants, bearing numerous gemmae; some plants in gemmiferous part of the tuft look more recovered and have small hyaline awns that are serrate in a way similar to the well developed plants, and dorsal side of their costae are also bearing papillae characteristic for the species.

shoe-shaped papillae similar to the papillae on leaf lamina. In the molecular phylogenetic trees inferred from all three studied markers, it was resolved within *S. caninervis*-clade (Figs. 1–3), and we refer it *S. caninervis* var. *gypsophila* due to unistratose leaf laminae. This case is similar to the case with Mongolian specimen (MHA9065478), which appeared in molecular phylogenetic trees within *S. pseudohandelii* but fit *S. caninervis* in morphology. However, another explanation can be suggested here: growth in severe environments on the bank of salty lake, on strongly saline substrate, may cause such changes in leaf development. The plants were small, with leaves even smaller than in most studied specimens of *S. caninervis,* including var. *astrakhanica* (Fig. 4), but they formed normally developed sporophytes.

Syntrichia caninervis var. *astrakhanica* was described in 2002 from the Bogdo Mountain area, near the Baskunchak Lake, Astrakhan Province and was also reported from two other localities in Astrakhan Province and one in Volgograd Province (Ignatov *et al*., 2002). Presence of multicellular axillary gemmae in *S. caninervis* was never mentioned in literature earlier, but we found the remarks on herbarium labels of *Tortula desertorum* made by A.A. Abramova, who pointed that there were brood bodies on these plants and, in one case, that the plants were depauperate (Astrakhan Province, Dasang, 1952, unknown collector (S.D. Erpert?), LE; Kasakhstan, Guriev Province, Novobogatinsky Distr., 8.VIII.1951, Nepli, LE).

Later Afonina *et al.* (2014) proposed that *S. caninervis* var. *astrakhanica* deserves elevation to the species level because it was resolved separately from two other specimens of *S. caninervis* in the molecular phylogenetic analysis. That paper aimed to solve another problem around *Syntichia sinensis*, and its distinction from *S. submontana* was demonstrated, but *S. caninervis* was not discussed in details. However, in the present study, two specimens (from Dagestan and Mongolia) called *S. caninervis* by Afonina *et al*. (2014) were resolved apart from *S. caninervis*-clade but together with four specimens of *S. pseudohandelii* (see discussion above). Regarding four samples called '*S. caninervis* var. *astrakhanica*' by Afonina *et al*. (2014), two of them have rhizoidal gemmae; these are the samples from Astrakhan (KM381998) and Ryazan (KM382036) Provinces. However, in the specimens from Taimyr Autonomous District (KM382037) and Mongolia (KM381997) gemmae are absent and leaf laminae are predominantly bistratose, so they apparently represent *S. caninervis* var. *caninervis*.

In the present study, four accessions of '*S. caninervis* var. *astrakhanica*' from the dataset of Afonina *et. al*. (2014) were supplemented by four GenBank accessions of *S. caninervis* s.l. and nine newly generated sequences of this species; the latter represented all three varieties of *S. caninervis* known in Russia. In the obtained molecular phylogenetic tree based on nr ITS, they all were resolved in one clade without any clear subdivisions (Fig.

1). It rejects an assumption about a separate species status of var. *astrakhanica* which was apparently based on erroneous identifications of some specimens.

In the treatment of *Syntrichia* in the Moss Flora of Russia (Ignatova & Afonina, 2025), *S. caninervis* var. *astrakhanica* is also reported from Kalmykia, Ingushetia in the East Caucasus, Saratov, and Voronezh Provinces. This variety was also found in France (Skrzypczak, 2006) and Estonia (Leis & Kannukene, 2007). In its collections from Russia, a considerable variation of plants is observed. In the original description, the main diagnostic characters of var. *astrakhanica* included small size of plants, leaves 0.5–0.9 mm long, with predominantly unistratose lamina, often with short hyaline awns and weakly papillose laminal cells (especially in leaves around apical clusters of gemmae). Such specimens were collected several times in Astrakhan Province. However, in other collections from the vicinities of Elton and Baskunchak Lakes, as well as from other localities plants approaching in habit to typical *S. caninervis* var. *gypsophila* but having gemmae in leaf axils were also found. In some specimens such plants were mixed with 'typical' *S. caninervis* var. *astrakhanica* having much smaller, 'depauperate' plants with more numerous gemmae (Fig. 4). The latter were occasionally collected along the roads, in placed where they could be trampled, and one can assume that copious production of gemmae is caused just by the mechanical damage or growth in extremely severe conditions. Since gemmae were sometimes found in leaf axils of large, 'normal' plants (e.g., in specimen from Ryazan Province, MW9022890), they can occur more often in *S. caninervis* but be scarce, hidden between leaves and remain not recognized. They are easily observed only when they are abundant and plants look depauperate.

We also revisited herbarium collections in MHA and MW and found that both var. *caninervis* and var. *gypsophila* occur in the other areas of lowland European Russia and Caucasus. However, in Bashkortostan, Altai Republic, and Taimyr only var. *caninervis* was revealed. In Yakutia, var. *caninervis* was collected in Oimyakon District, Ust-Nera surroundings and in the lower course of Yana River, whereas in Central Yakutia, Khangalassky District, only var. *gypsophila* was identified. Specimens from Buryatia are fairly scarce, but they also belong to var. *gypsophila.* In all cases, *S. caninervis* was collected in places with limestone bedrocks: on xeric slopes with steppe vegetation in Ust-Nera surroundings and in Yana River basin, and on dry, open limestone cliffs and xeric slopes to Lena River in Khangalassky District. In the latter locality, it was collected only on the S-faced left bank of Lena River, but not on Lenskie Stolby on the opposite, N-faced bank, where huge limestone cliffs and steppe slopes occur. In Buryatia, it grew on S-faced dry rocky slope with *Caragana jubata*. In Altai, it was found in its xeric south-eastern area, Kosh-Agach District, where it grew on dry rock outcrops and rocky slopes. In Taimyr, it was collected on cliff ledges covered with calcareous finesoil on dry slopes.

Selected specimens examined:

Syntrichia caninervis* var. *caninervis

EUROPEAN RUSSIA: **Crimea**: Sudak, 1.VI.1975 *Soklakova* (MW9022866); Bakhchisarai Distr., 18.V.1955 *Melnichuk* (MHA9058722). **Dagestan**, Buinaksk Distr., Tolgi valley, 28.V.2010 Fedosov 10-2-473 (MW9113244). **Kalmykia**: Iki-Burul Distr., 10.V.2009 Ukrainskaya (LE). **Astrakhan Province**: Akhtubinsk Distr., Bogdo-Baskunchak Nature Reserve, 7.V.2024 *Ignatov & Ignatova 24-1* (MW9134248); Bolshoe Bogdo Mt., 23.VI.1952 *Nepli* (LE). **Volgograd Province**: Ilovlinsky Distr., 20.V.1984 *Belyanina* (MW9022869); Elton Lake, 10.VI.1923 *Ilyun & Grigoriev* (LE); same place, 1914 *Savicz-Lyubitskaya* (LE). **Rostov-na-Donu Province**: Myasnikovsky Distr., Nedvigovka, 9.V.2005 *Sereda* (MHA9020883). **Belgorod Province**: Valuiki Distr., VIII.1977 *Bedenko* (LE). **Samara Province**: Samara Distr., 28.III.1926, *Sprygin* (LE). **Voronezh Province**: Kamenka Distr., 15.III.2014 *N.N. Popova 47* (MHA9020898). **Orenburg Province**: Kuvandyk Distr., 31.V.2004 *Spirina & Zolotov* (MHA9020901). **Bashkortostan**: Abzelilovo Distr., 20.VII.2013 *Baisheva 23-13-8* (MHA9022913). ASIAN RUSSIA: **Altai Republic**: Kosh-Agach Distr.: Chegan-Uzun, 10.VIII.2012 *Ignatov & Ignatova 12-353* (MW9022877); same place, 25.VII.1966 *Bardunov* (MHA9118988). Kuraisky Range, Tabozhok Creek, 23.VI.2021 *Ignatov &Ignatova 21-594* (MW9092162). **Krasnoyarsk Territory**: Taimyr Municipal Distr., Kzyl-Khaya Mt., 15.VIII.2007 *Fedosov 07-408* (MW9022884); Fomich River, 27.VII.2008 *Fedosov 08-304* (MW9022885). **Yakutia**: Oimyakon Distr., Topol Creek, 5.VIII.2015 *Ignatov & Ignatova 15-1515* (MW9022889); Verkhoyansk Distr., 7.VII.2007 *Isakova* (MHA9020886).

Syntrichia caninervis* var. *gypsophila

EUROPEAN RUSSIA: **Dagestan**: Buinaksk Distr., Tolgi valley, 28.V.2010 *Fedosov 10-4-5 (*MW9022871). **Kabarino-Balkaria**: Nalchik, 4.VI.2002 *Kharzinov 262* (MW9022872). **Stavropol Territory**: Pyatigorsk, 28.IV.1963 *Kozlova* (LE). **Kalmykia**: Priyutnoe Distr., 21.V.2010 *Ukrainskaya* (LE). **Astrakhan Province**: Bogdo-Baskunchak Reserve, 5.V.2002 *Suragina* (MW9022867); Dosang, 8.X.1949 *Erpert* (LE). **Volgograd Province**: Pallasovka Distr., Elton Lake, 1.V.2023 *Ignatov et al. 23-92* (MHA9063487). **Rostov-na-Donu Province**: Myasnikovsky Distr., 11.VIII.2005 *Sereda* (LE) **Voronezh Province**: Boguchary Distr., 4.V.2014 *N.N. Popova 52* (MHA9020900). ASIAN RUSSIA: **Yakutia**: Khangalassky Distr., Elanka, 1.VIII.2016 *Ignatov & Ignatova 16-81* (MW9077278). Buryatia: Okinsky Distr., Belyi Irkut River, 12.VII.2015 *Afonina 1615* (LE).

Syntrichia caninervis* var. *astrakhanica

EUROPEAN RUSSIA: **Astrakhan Province**: Krasnoyarsk Distr., Dosang, 20.IX.1951 Erpert (LE); Akhtubinsk Distr., Bogdo-Baskunchak Nature Reserve, 13.VII.2002 *Suragina* (MHA9020918). **Kalmykia**: Priyutnoe Distr., 21.V.2010 *Ukrainskaya* (LE). **Volgograd Province**: Svetloyarsk Distr., Tinguta, 3.VI.1996 Matveev (MHA9020919). **Voronezh Province**: Borisoglebsk Distr., 23.XI.2014 *N.N. Popova 46* (MHA9012903). KAZAKHSTAN: Guriev Province, Novobogatink Distr., 8.VIII.1951 *Nepli* (LE).

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Supplementary materials: Fig. SM1. Maximum likelyhood phylogenetic tree for *Syntrichia ruralis* and *S. caninervis* groups based on nuclear ITS region, Dataset #2:

https://kmkjournals.com/upload/PDF/Arctoa/35/Arctoa_35_108_121_Fig_SM1.pdf

Appendix 1. Specimens of *Syntrichia* and Genbank accession data for sequenced samples.

Taxa	Isolate	Geolocation	Voucher specimen	Collection date	GenBank accession numbers ITS	*rpl*16	*atp*B–*rbc*L
S. caninervis var. *caninervis* --	OK4584	Russia: Altai Republic	Ignatov & Ignatova 21-594, MHA9131061	23.VI.2021	--	PZ537443	
S. caninervis var. *caninervis* PZ537461	OK4578	Russia: Altai Republic	Ignatov & Ignatova 12-364, MHA9118991	10.VIII.2012	--	PZ537438	
S. caninervis var. *caninervis*	OK687	Russia: Taimyr	Fedosov 05-547, MW9022887	4.VII.2005	KM382037	PZ537425	PZ537448
S. caninervis var. *caninervis* PZ537457	OK4570	Russia: Yakutia	Ignatov & Ignatova 15-1515, MHA9020887	5.VIII.2015	PZ540513	PZ537434	
S. caninervis var. *caninervis*is	OK4571	Spain	Munos K937, MHA9058725	25.III.2005	PZ540514	PZ537435	PZ537458
S. caninervis var. *caninervis*	OK4184	Russia: Astrakhan Prov.	Ignatov & Ignatova 24-132, MHA9063599	9.V.2024	PZ540506	PZ537427	PZ537450
S. caninervis var. *astrakhanica*	OK634	Russia: Astrakhan Prov.	Suragina s.n., MHA	3.V.1997	KM381998	PZ537421	PZ537444
S. caninervis var. *astrakhanica*	OK4181	Russia: Astrakhan Prov.	Ignatov & Ignatova 24-116, MHA	9.V.2024	PZ540505	PZ537426	PZ537449
S. caninervis var. *astrakhanica* PZ537447	OK677	Russia: Ryazan Prov.	Volosnova s.n., MW9022891	4.VIII.2009		KM382036	PZ537424
S. caninervis var. *astrakhanica*	OK4575	Russia: Astrakhan Prov.	Ignatov & Ignatova 24-154, MHA9063334	10.V.2024	PZ540516	PZ537437	PZ537460
S. caninervis var. *gypsophila*	OK636	Mongolia	Ignatov 01-669, MHA9065476	29.VI.2001	KM381999	PZ537422	PZ537445
S. caninervis var. *gypsophila*	OK4566	Russia: Astrakhan Prov.	Ignatov & Ignatova 24-104, MHA9063291	8.V.2024	PZ540509	PZ537430	PZ537453
S. caninervis var. *gypsophila*	OK4567	Russia: Volgograd Prov.	Ignatov et al. 23-255, MHA9063724	3.V.2023	PZ540510	PZ537431	PZ537454
S. caninervis var. *gypsophila*	OK4568	Russia: Astrakhan Prov.	Ignatov & Ignatova 24-86, MHA9063356	8.V.2024	PZ540511	PZ537432	PZ537455
S. caninervis var. *gypsophila*	OK4573	Russia: Astrakhan Prov.	Ignatov & Ignatova 24-85, MHA9063381	8.V.2024	PZ540515	PZ537436	PZ537459
S. caninervis var. *gypsophila*	OK4579	Russia: Volgograd Prov.	Ignatov et al. 23-161, MHA9063623	1.V.2023	PZ540517	PZ537439	PZ537462
S. pseudohandelii	OK637	Mongolia	Ignatov 01-663, MHA9065478	9.VII.2001	KM381997	PZ537423	PZ537446
S. pseudohandelii	OK4564	Russia: Volgograd Prov.	Ignatov et al. 23-124, MHA9063498	2.V.2023	PZ540507	PZ537428	PZ537451
S. pseudohandelii	OK4565	Russia: Astrakhan Prov.	Zemlyanskaya s.n., MHA9020912	9.V.1997	PZ540508	PZ537429	PZ537452
S. pseudohandelii	OK4569	Russia: Dagestan Rep.	Ignatov & Abakarova 11-102, MHA9118263	11.IV.2011	PZ540512	PZ537433	PZ537456
S. ruralis	OK3083	Russia: Altai Republic	Ignatov & Ignatova 21-467, MHA9132003	21.VI.2021	PZ540519	--	--
S. ruralis	OK4580	Mongolia	Ignatov 01-663, MHA9065478	9.VII.2001	--	PZ537440	--