

THE GENUS *STREBLOTTRICHUM* (POTTIACEAE, BRYOPHYTA) IN RUSSIA

РОД *STREBLOTTRICHUM* (POTTIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

The genus *Streblotrichum* is revisited in Russia based on morphological study and the nuclear ITS and plastid *rps4* and *trnL-F* sequence data. It is shown that Russian specimens belong to four species. *Streblotrichum convolutum* and *Barbula jacutica* were already known in Russia; the latter is transferred to the genus *Streblotrichum*. *Streblotrichum enderesii* is newly recorded from Russia; it was revealed in collections from Urals, Altai, Yakutia, and Primorsky Territory. A new species, *S. taimyrense*, is described from North Siberia (Taimyr) based on differences in morphology and sequence data. Descriptions, illustrations, and ecological data are provided for all species; variability of *S. convolutum* is discussed. Key to identification for the species of *Streblotrichum* occurring in Russia is presented.

Резюме

Проведена таксономическая ревизия рода *Streblotrichum* для территории России с использованием молекулярно-филогенетического анализа ядерного ITS и хлоропластных участков *rps4* и *trnL-F*. Полученные данные показывают, что в России этот род представлен четырьмя видами. Два из них были известны ранее: это *S. convolutum* и *Barbula jacutica*; для последнего вида сделана новая комбинация в роде *Streblotrichum*. *Streblotrichum enderesii* впервые приводится для России; он был выявлен в гербарных коллекциях с Урала, Алтая, из Якутии и Приморского края. Растения с Таймыра, которые хорошо отличаются по морфологическим и молекулярным данным, описаны под названием *S. taimyrense*. Для всех видов приводятся описания, иллюстрации и данные об экологии; обсуждается вариабельность *S. convolutum*. Дан также ключ для определения видов *Streblotrichum*, встречающихся в России.

KEYWORDS: mosses, Pottiaceae, taxonomy, new species, new records, ITS, *rps4*, *trnL-F*.

INTRODUCTION

The genus *Streblotrichum* P. Beauv. was described in the famous “Prodrome...” by Palisot de Beauvois (1804), where it included four species, two of them belong now to *Trematodon* Michx. and *Tortella* (Müll. Hal.) Limpr. In 19th and 20th centuries, it was mostly submerged in a synonymy of *Barbula* Hedw., though some authors, e.g. Savicz-Lyubitskaya & Sminova (1970) acknowledged the differences of *S. convolutum* (Hedw.) P. Beauv. from other *Barbula* by recognition *Streblotrichum* as a genus of its own, in which they also included *S. enderesii* (Garov.) Loeske, *S. croceum* (Brid.) Loeske (now in *Hydrogonium* (Müll. Hal.) A. Jaeger), and *S. bicolor* (Bruch, Schimp. & W. Gümbel) Loeske (now in *Gymnobarbula* Jan Kučera).

Zander (2007) classified *Streblotrichum* in *Barbula*, accepting in North America only one species, *S. convolutum*, with infraspecific taxa, mentioning that in Europe

the genus is probably more diverse. However, no studies addressed specifically to this genus in Europe and Russia were conducted so far.

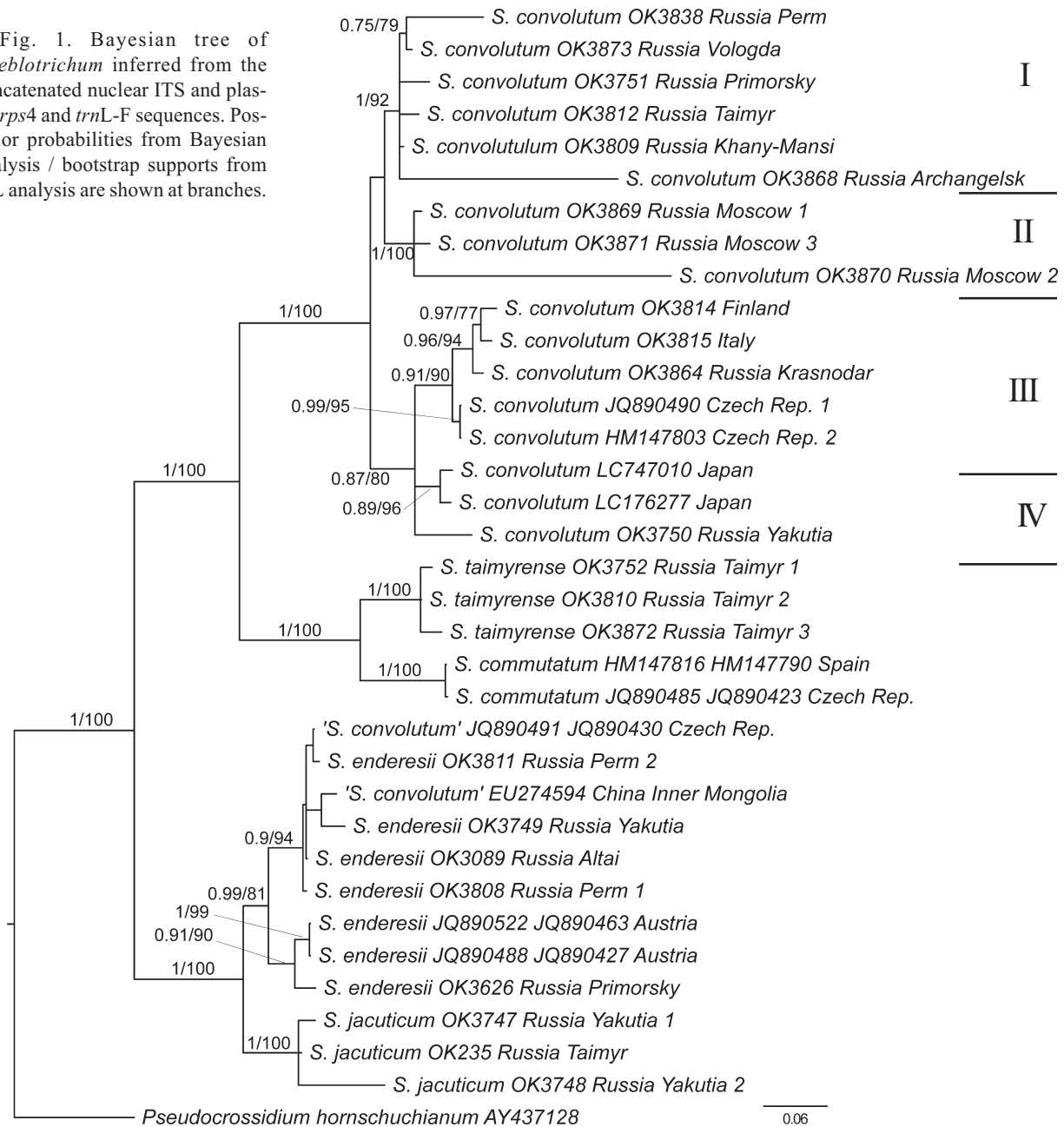
Meanwhile, molecular phylogenetic studies (Inoue & Tsubota, 2016; Bechteler *et al.*, 2023) found *Streblotrichum* not only well separated from *Barbula*, but isolated enough for being placed in monogeneric subfamily of Pottiaceae, Streblotrichoideae Y. Inoue & H. Tsubota.

In the course of preparing the genus treatment for the Moss Flora of Russia, a more complex morphological diversity was noticed in this genus. Thus we checked some more or less distinct groups of specimens with the molecular phylogenetic methods, which proved to be helpful in many previously studies of Pottiaceae (Werner *et al.*, 2005; Kučera *et al.*, 2020; Jimenez *et al.*, 2022), including, among others, those treated European species of *Streblotrichum* (Kučera *et al.*, 2013).

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Fig. 1. Bayesian tree of *Streblotrichum* inferred from the concatenated nuclear ITS and plastid *rps4* and *trnL-F* sequences. Posterior probabilities from Bayesian analysis / bootstrap supports from ML analysis are shown at branches.



## MATERIAL AND METHODS

### Molecular studies

We sequenced nuclear ITS, the most useful region for species level taxonomy in mosses, as it is also most copiously represented in GenBank, and also two plastid regions, *trnL-F* and *rps4*.

DNA extraction was done with the Qiagen Extractor. Amplification used primers L and B for ITS (White, 1990) and primers for plastid region *trnS-F* (Hernández-Maqueda *et al.*, 2008; Olsson *et al.*, 2009). However, only partial sequences of the latter long region, ca. 1800 bp, were used in the present analysis, namely *trnL-F* and *rps4*, ca. 1200 bp, as the sequences for the other parts of this region were not obtained for many samples. The sequencing protocols were essentially the same as

in previous studies (Gardiner *et al.*, 2005).

Obtained sequences were aligned using MAFFT v. 7.487 (Kato & Standley, 2013) E-INS-i strategy. Accession numbers and voucher data are in Appendix 1.

**Molecular analysis.** Preliminary tests demonstrated no supporting conflicts in trees based on only nuclear and only plastid markers, so the further analysis was undertaken for concatenated dataset. *Pseudocrossidium hornschuchianum* was used as a root, because in the groups placed closer in the phylogenetic tree of the family (*Scopelophila*, *Hyophila*), and some others (*Gymnostomum*, *Molendoa*) ITS differs so much that it was almost impossible to align.

Sequences were aligned using MAFFT v. 7.505 (2022/Apr/10) with the E-INS-i alignment strategy with other-

Appendix. Species of the genus *Streblotrichum* sequenced de novo for nrITS and plastid *rps4* and *trnL-F*.

Species	Isolate	Locality	Voucher	ITS	trnS-F p.p.
<i>S. convolutum</i>	OK3751	Russia, Primorsky, Dalnegorsk	Ignatov & Ignatova 13-1542 MHA9005044	PQ728280	PQ793265
<i>S. convolutum</i>	OK3812	Russia, Taimyr	Fedosov 09-377 MW9003777	-	PQ793266
<i>S. convolutum</i>	OK3814	Finland	Ignatov & Ignatova 10-1046 (MHA)	PQ728281	PQ793267
<i>S. convolutum</i>	OK3864	Russia, Krasnodar, Utrish	Ignatov & Ignatova 05-437 MW9003757	PQ728282	PQ793268
<i>S. convolutum</i>	OK3815	Italy, Sicily	Kozhin s.n. 7 Sep 2010 MHA9003802	PQ728283	PQ793269
<i>S. convolutum</i>	OK3750	Russia, Yakutia, Ulakhan-Chistai	Ignatov & Ignatova 18-1768 MHA9005342	PQ728284	PQ793270
<i>S. convolutum</i>	OK3809	Russia, Khanty-Mansi, Neroika	Skuchas 14-753 MW9003764	PQ728285	PQ793271
<i>S. convolutum</i>	OK3869	Russia, Moscow 1, Zvenogorod	Ignatova, 25 Jun 2004 MW9003728	PQ728286	PQ793272
<i>S. convolutum</i>	OK3871	Russia, Moscow 3, Odinzovo	Ignatov & Ignatova, 21 Jun 2009 MW9003723	PQ728287	PQ793273
<i>S. convolutum</i>	OK3870	Russia, Moscow 2, Klin	Ignatov 14 Jun 1996 MW9003727	PQ741446-	PQ793274
<i>S. convolutum</i>	OK3868	Russia, Archangelsk, Pinega	Ignatov 3 Aug 1988 MHA9005031	-	PQ793278
<i>S. convolutum</i>	OK3838	Russia, Perm	Bezgodov 16 Aug 2023 #203 (MHA)	PQ728288	=
<i>S. convolutum</i>	OK3873	Russia, Vologda,	Karmazina 373-04 MW9003731	PQ728289	PQ793279
<i>S. jaciticum</i>	OK3747	Russia, Yakutia 1, Tarbagannakh	Ignatov 00-1060 MHA9005224	PQ728278	PQ793262
<i>S. jaciticum</i>	OK235	Russia, Taimyr, Fomich	Fedosov 08-628 MW9003806	PQ728279	PQ793263
<i>S. jaciticum</i>	OK3748	Russia, Yakutia 2, Rossomakha	Ignatov & Ignatova 17-899 MHA9025266	PQ741445	PQ793264
<i>S. enderesii</i>	OK3749	Russia, Yakutia, Lenskie Stolby	Ignatov 00-35 MHA9005063	PQ728273	PQ793258
<i>S. enderesii</i>	OK3808	Russia, Perm 1, Chusovaya	Bezgodov 16 Jul 2017 #187 MHA9026138	PQ728274	PQ793259
<i>S. enderesii</i>	OK3811	Russia, Perm 2, Chusovaya	Bezgodov 16 Jul 2017 #187 MW9090557	PQ728275	PQ793260
<i>S. enderesii</i>	OK3089	Russia, Altai, Topuchaya	Ignatov & Ignatova 21-28 (MHA)	PQ728276	-
<i>S. enderesii</i>	OK3626	Russia, Primorsky, Ussuri Reserve	Ishchenko A_31_2 (MHA)	PQ728277	PQ793261
<i>S. taimyrense</i>	OK3752	Russia, Taimyr 1, Khatanga	Fedosov 13-3-0725 MHA9005045	PQ728290	PQ793275
<i>S. taimyrense</i>	OK3810	Russia, Taimyr 2, Ereechka	Fedosov 13-3-0767 MW9003772	PQ728291	PQ793276
<i>S. taimyrense</i>	OK3872	Russia, Taimyr 3, Medwezhyha	Fedosov 05-396 MW9003809	PQ728292	PQ793277

wise default options, and afterwards checked for obvious inconsistencies manually. The analysis was performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012) with the GRT+G model, and run with 5 000 000 generations (reaching all PSRF equal to 1.000, and ESS > 2000). Partitioning followed the initially suggested partitions, nrns=4, nchain=6, temp=0.02.

Maximum likelihood analysis was performed at W-IQ-TREE server (Trifinopoulos *et al.*, 2016), 1000 replications and otherwise default parameter, 1000 replications. Substitution models were selected by the server: ITS1: TNe+G4; 5.8S RNA gene K2P+I; ITS2: TN+F+G4; *rps4* TPM3u+F+I+G4; *trnL-F* F81+F+I.

**Morphological studies** were conducted mainly on specimens from MW, MHA, partly from LE and BM.

## RESULTS

**Molecular phylogenetic analysis**

Molecular phylogenetic tree (Fig. 1) found in *Streblotrichum* two maximally supported clades. The first one is subdivided into two subclades: one includes three specimens of *S. jaciticum* and is maximally supported; another one, moderately supported (PP=0.99, BS=81), includes two specimens of *S. enderesii* from Central Europe (sequences from GenBank, deposited by Jan Kučera) five newly obtained sequences from four specimens from Russia, and two taken from GenBank, from Central Europe and China (submitted there as *S. convolutum*). Hereafter the latter subclade it is denoted as 'enderesii-clade'. This 'enderesii-clade' includes internal subclades with lower support, excepting one highly supported (PP=1, BS=99) clade that combines two specimens of *S. enderesii* from Austria.

The second clade of the genus *Streblotrichum* also has two maximally supported subclades. The smaller clade includes two smaller subclades, both maximally supported.

One of them includes two specimens of *S. commutatum* from Czech Republic and Spain (deposited to GenBank by Jan Kučera). Another includes three specimens from the northern Siberia, Taimyr; the latter are discussed below and described in 'Taxonomy' section as *S. taimyrense*. The larger clade includes 17 specimens of *S. convolutum*, it is subdivided into smaller clades, partly supported, roughly corresponding to the geographic origin of specimens: subclade I includes specimens from Asian Russia and NE European Russia; subclade II includes three specimens from Moscow region and is maximally supported albeit its plants were selected for the analysis as maximally different morphologically; subclade III is West European and includes also one specimen from the Russian part of the Caucasus; IV: three remaining specimens do not form a clade, but form a paraphyletic grade to the clade III, they include eastern plants: two from Japan and one from East Yakutia. This spatial differentiation should not be considered comprehensive until a denser sampling made, but it is likely interesting for further testing.

**Morphological observations**

Molecular delimitation of two groups, *S. taimyrense* and 'enderesii-clade' forced us to search morphological distinctions between the samples of these particular clades, as well as *S. convolutum* and *S. jaciticum*. Since we could not study sequenced specimens of *S. enderesii* from Austria, we used for comparison a specimen from Austria (Baumbartner, Exs. 293 of *Barbula flavipes*, Stiria). We also included the specimen with mature sporophytes, morphologically fitting *S. enderesii*, from which we failed to obtain DNA; it was collected in Perm Territory, on Chusovaya River bank, close to the locality of sequenced specimen (OK3808 and OK3811). A comparison of plants from four groups found in Russia by the molecular analysis, e.g. *Streblotrichum convolutum*, *S. taimyrense*, *S. jaciti-*



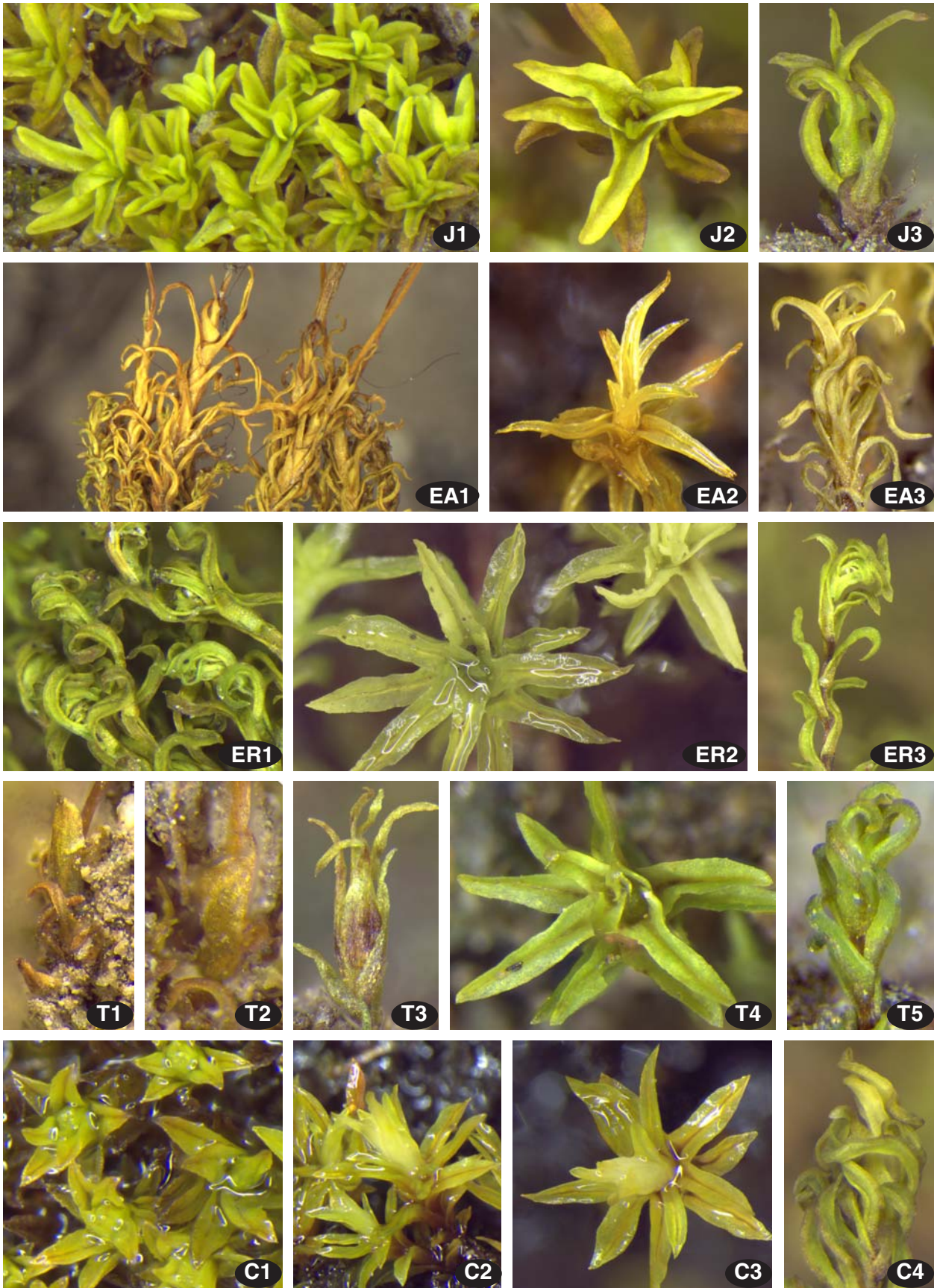


Fig. 2. Habit of *Streblotrichum* species: **J**: *S. jacuticum*, OK3748 (J1–J3); **EA**: *S. enderesii*, Baumbartner, Exs. 293 of *Barbula flavipes*, Stiria (Austria) (EA1–EA3); **ER**: *S. enderesii* from Russia, OK3811 (ER1); OK3089 (ER2), OK3808 (ER3); **T**: *S. taimyrense*: type (T1–T2) and OK3872 (T3–T5); **C**: *S. convolutum*, OK3814 (C1–C2), OK3838 (C3–C4).





Fig. 3. A comparison of leaves, their transverse sections and basal cells of *Streblotrichum* species. **J**: *S. jacuticum*, OK3748; **EA**: *S. enderesii*, Baumbartner, Exs. 293 of *Barbula flavipes*, Stiria (Austria); **ER**: *S. enderesii* from Russia, OK3811 and OK3089; **T**: *S. taimyrense*, OK3872; **C**: *S. convolutum*, OK3838. Scale bars: 0.5 mm for leaves; 100  $\mu\text{m}$  for basal leaf cells; 50  $\mu\text{m}$  for leaf transverse sections.

*cum* and species from ‘enderesii-clade’, and also Austrian specimen of *S. enderesii*, is shown in Figs. 2–6, regarding particular morphological characters, in addition to a subsequent species description in the section ‘Taxonomy’.

**The plant habit** (Fig. 2) is contrastingly different in Austrian specimen of *S. enderesii*, which has much narrower leaves and a somewhat crisped appearance. *Streblotrichum jacuticum* is conspicuous due to rounded leaf apices, and in well-developed plants this feature leaves no doubt that they belong to this species. However, when *S. jacuticum* grows by scattered individuals or in inappropriate habitats, its leaves are narrower, becoming less different from some Arctic blunt-leaved phenotypes of *S. taimyrense* and, occasionally, also *S. convolutum*. The widespread phenotype of *S. convolutum* which possesses dense, bright yellow-green, extensive tufts, bearing only few sporophytes, is usually easy to recognize in the field; this feature is unique for *S. convolutum*. However, *S. convolutum* has many other phenotypes, occasionally having loose tufts; such plants may be confused with other species of the genus, such as representatives of ‘enderesii-clade’ from Russia (Fig. 2).

**Leaf shape** (Fig. 3) is most distinct in *S. jacuticum* due to rounded leaf apices; leaves of *S. enderesii* from Austria are narrow, with margins recurved to 3/4 of the leaf length, whereas the representatives of other clades have shorter leaves with margins recurved at short distance in mid-leaf. Basal laminal cells are most distinct in *S. jacuticum*: they have length to width ratio 3–6:1 in well-developed leaves, which is higher than in all other species, ca.1.5–3:1. In plants of ‘enderesii-clade’ from Russia leaves are longer tapering to apex than usually takes place in *S. convolutum*, but not always: in some cases *S. convolutum* (especially tall plants growing in wet conditions) have leaves gradually tapering to apex.

**Distal leaf cells** (Fig. 4) are variable in size in *S. convolutum*, being most commonly 8–10  $\mu\text{m}$ , but occasionally larger; they bear two or, more commonly, four papillae per cell. Papillae may look round and solid or c-shaped; the latter are more conspicuous upon the surface of larger cells, over 10–13  $\mu\text{m}$ , which occur plants of *S. convolutum* growing in wet habitats. In plants of ‘enderesii-clade’ from Russia cells are generally larger than in *S. convolutum*, up to 17  $\mu\text{m}$ . Round papillae occur in the



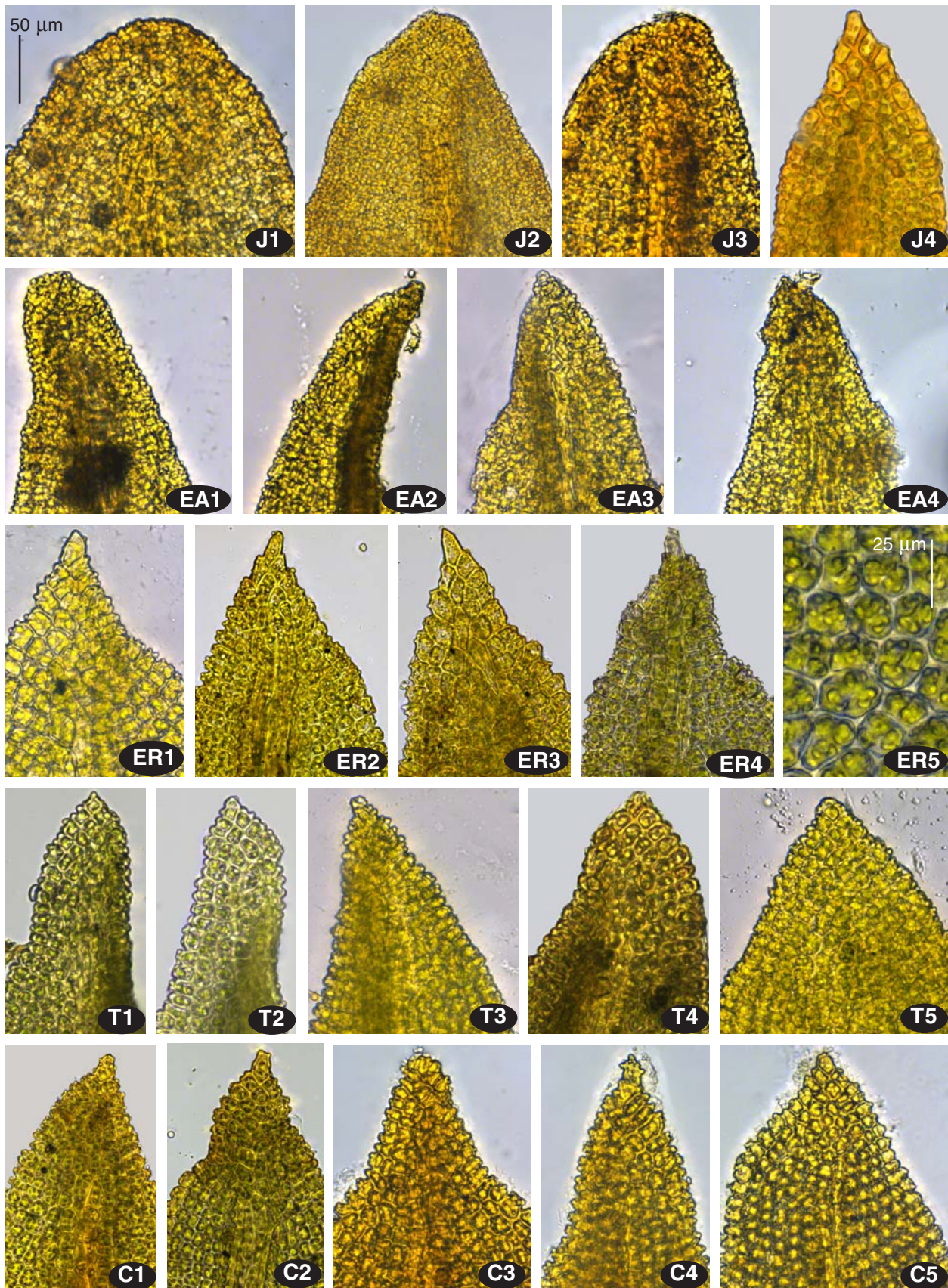


Fig. 4. Leaf apices of *Streblotrichum* species. **J**: *S. jacuticum*, OK3748 (all); **EA**: *S. enderesii*, Baumbartner, Exs. 293 of *Barbula flavipes*, Stiria (Austria) (all); **ER**: *S. enderesii* from Russia, OK3811 (ER1); OK3089 (ER2), OK3089 (ER3), OK3626 (ER4), OK3089 (ER5); **T**: *S. taimyrense*, OK3872 (all); **C**: *S. convolutum*, OK3870 (C1–C2), OK3838 (C3–C5). Scale bar 50 µm for all except ER5 (25 µm).



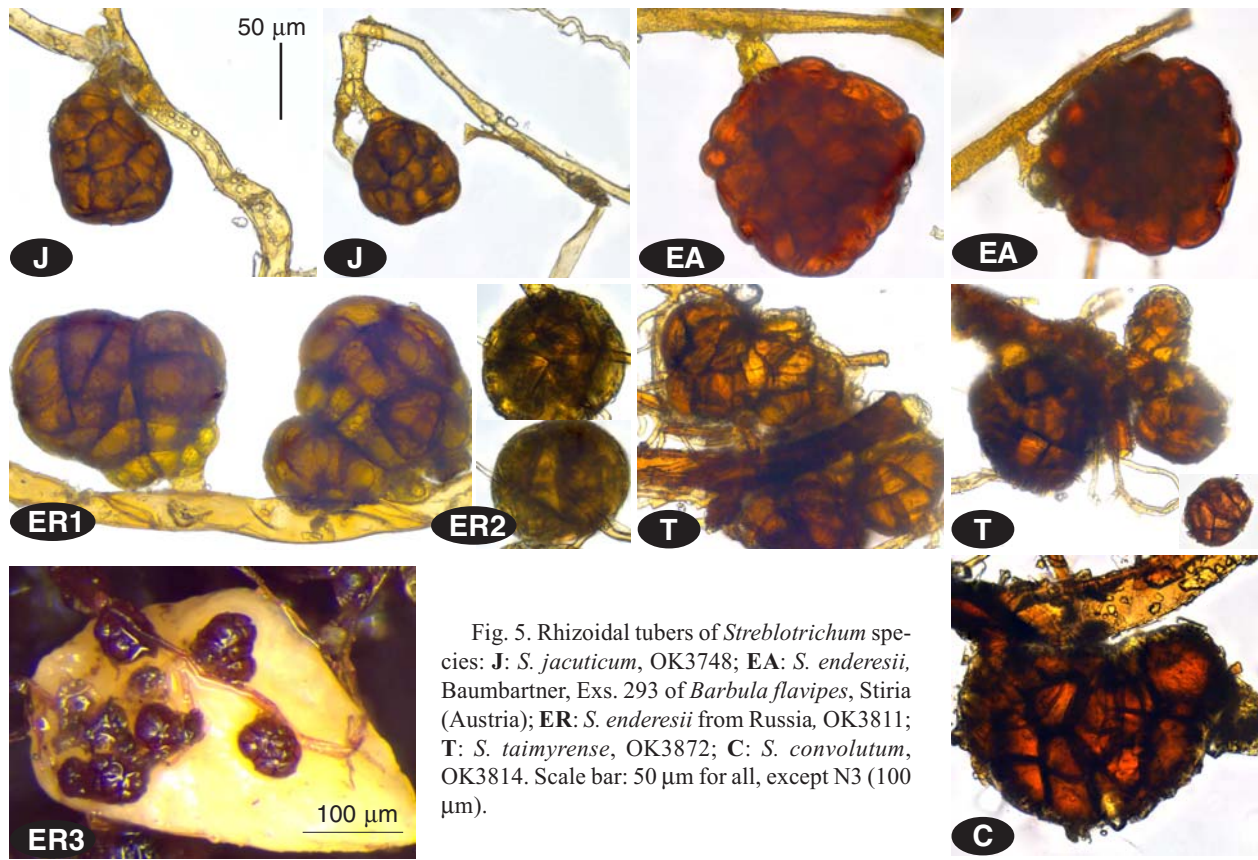


Fig. 5. Rhizoidal tubers of *Streblotrichum* species: J: *S. jacuticum*, OK3748; EA: *S. enderesii*, Baumbartner, Exs. 293 of *Barbula flavipes*, Stiria (Austria); ER: *S. enderesii* from Russia, OK3811; T: *S. taimyrense*, OK3872; C: *S. convolutum*, OK3814. Scale bar: 50 µm for all, except N3 (100 µm).

lower part of leaf, where they are especially conspicuous in the transition to leaf base where cells are smooth. In *S. taimyrense* laminal cells are smaller, (5–)6–9(–10) µm, papillae are smaller and denser, sometimes looking solid, and the marginal denticulation is usually inapparent. The mentioned differences partly depend on plant habitat, as harsh conditions reduce plant size and in some groups also cell size. Consequently, the papillae often look solid in *S. taimyrense*, though not always: e.g., in Fig. 4 T5 papillae are less branched, unlike clearly c-shaped papillae in *S. convolutum* and ‘enderesii-clade’.

*Streblotrichum jacuticum* has small, acute leaves in the lower parts of stems; in such leaves cells are comparatively large, 9–14 µm, while in larger leaves with rounded apices they are only 5–8 µm, i.e., like in *S. taimyrense*.

Leaf margins in plants of ‘enderesii-clade’ are in about a half specimens wavy or ‘eroded’, though in other samples leaf margins do not differ from those in *S. convolutum*. A similar ‘eroded’ leaf margins occasionally occur in *S. convolutum*, too (especially in tall plants growing in wet conditions).

**Rhizoidal tubers** (Fig. 5) are possible to find in all species of *Streblotrichum*, though in some samples they are relatively few. Their size is variable. In mature tubers the outer cells are convex, while in young ones they are flat, and smaller rhizoidal tubers are usually perfectly round (Fig. 6ER). Size of rhizoidal tubers approaches 120–200 µm in most samples, but in *S. taimyrense* they were smaller, up to 130 µm, maybe due to a limited num-

ber of observations. The more definite is the smaller tuber size in *S. jacuticum*, 70–100(–120) µm (Fig. 5J), based on rather abundant material. The abundance of tubers varies in plants from ‘enderesii-clade’; in specimens from Primorsky Territory (OK3626) and from Urals (OK3811) tubers are enormously abundant.

**Perichaetial leaves, capsules, setae** (Fig. 6). Capsules in *Streblotrichum*, as well as in many other genera of Pottiaceae, have an ability to shorten after dehiscence and operculum removal. Capsules at the same stage of maturity are usually more or less equal within a sample; they also do not differ considerably between species. Peristome teeth are spirally twisted to the right; their surface is densely papillose. Thus, capsule shape, size and peristome characters are not distinctive between species of *Streblotrichum*. However, the setae and perichaetial leaves provide useful diagnostic characters. Setae of *S. convolutum* in most cases are conspicuously stramineous, whereas in *S. jacuticum* and *S. taimyrense* they are reddish. Plants of ‘enderesii-clade’ from Russia were in most cases sterile. We used for comparison an old specimen of *S. enderesii* from Austria (EA) and a not sequenced specimen from Perm Territory (ER), collected close to the localities of specimens OK3708 and OK3811 (see Discussion below). In these specimens the color of setae is more like ochre, i.e. yellow in general, but not stramineous. It is noteworthy that in some northern populations from limestone, setae of *S. convolutum* is sometimes slightly or conspicuously reddish (e.g., in OK3868).



Fig. 6. Capsules, setae and perichaetia of *Streblotrichum* species. J: *S. jacuticum*, OK3748; EA: *S. enderesii*, Baumbartner, Exs. 293 of *Barbula flavipes*, Stiria (Austria); ER: *S. enderesii* from Russia, Perm Territory, 12.VIII.2005, *Bezgodov 196*, MHA9131969; T: *S. taimyrense*, OK3872; C: *S. convolutum*, OK3838. Scale bars: 1 mm for all.

Perichaetial leaves in *S. convolutum* are formed by the sheathing base with only a short apiculus. These perichaetial leaves are sometimes well exposed, in other cases hidden among subperichaetial innovation shoots. In other species inner perichaetial leaves are suddenly contracted into acumen. The most distinct from *S. convolutum* is *S. jacuticum*, where acumina are longer than basal parts of perichaetial leaves. In *S. taimyrense* and plants of ‘enderesi-clade’ acumina of perichaetial leaves are from about a quarter to a half of basal part of the leaf in length.

#### DISCUSSION

The present study confirmed the distinction of *Streblotrichum jacuticum* from *S. convolutum*, providing additional evidence by molecular data. Morphological differences of these species include shape of stem leaves and perichaetial leaves, seta color, and size of rhizoidal tubers (Figs. 3J, 3C, 4J, 4C, 5J, 5C, 6J, 6C). The differences of *S. jacuticum* from North American *Barbula eustegia* Card. & Thér. was discussed by Ignatova (2001); they include setae color (reddish vs. yellow), spore size (11–14  $\mu\text{m}$  vs. 7–10  $\mu\text{m}$ ) and shape of stem leaves (variable in shape, often with shoulder vs. uniform, gradually

narrowed upwards). There is also some resemblance in color of setae, shape of perichaetial leaves and, to some extent, of stem leaves between *S. jacuticum* and *Barbula cheniana* Redf. & B.C. Tan. The latter species was considered to be endemic of China, where it is widely distributed (Li *et al.*, 2001). It was also recently found in Japan (Inoue *et al.*, 2019). However, in *Barbula cheniana* the border between smooth basal cells and papillose mid-leaf cells in stem leaves is described as often V-shaped, which is not the case for *S. jacuticum*; illustrations of *B. cheniana* in Li *et al.* (2001) and in Inoue *et al.* (2019) show stem leaves without shoulders, with greater length/width ratio than in *S. jacuticum*. A detailed comparison of specimens is needed to clarify the relationship between these species.

Three specimens Taimyr resolved in a maximally supported clade sister to *S. commutatum* and distinct in morphology apparently require a segregation in a separate species. It is described below in the ‘Taxonomy’ section as *Streblotrichum taimyrense*. The distinctions of *S. taimyrense* from *S. convolutum* include smaller laminal cells (mostly 6–9  $\mu\text{m}$  vs. 10–12  $\mu\text{m}$ ) and larger spores



(11–14  $\mu\text{m}$  vs. 8–10  $\mu\text{m}$ ). Spores of *S. convolutum* were studied from different regions (see Specimens examined of *S. convolutum*). Also, reddish seta, which is characteristic for *S. taimyrense*, is rare in *S. convolutum*, and their perichaetial leaves are different (Figs. 5, 9 & 10).

A comparison of *Streblotrichum taimyrense* and *S. commutatum* is more difficult. These two species are most closely related according to molecular phylogenetic data, and they also have some common morphological features. Both species have small laminal cells and reddish setae. However, perichaetial leaves in *S. commutatum* are described as obtuse or shortly apiculate, whereas in *S. taimyrense* perichaetial leaves have a conspicuous triangular acumina ca. 1/3 of leaf base in length or slightly shorter. Regarding spore size, all publications that describe *S. convolutum* and *S. commutatum* (often as a infraspecific taxon of the former species) provide the spore size in combined description being 8–10  $\mu\text{m}$ , despite Juratzka (1874) in the original description noted that spores of *S. commutatum* are slightly larger. Also, *S. commutatum* is described as a species larger than *S. convolutum*, whereas *S. taimyrense* is a small plant. And finally, the distinctions in ITS and *rps4* sequences are numerous, and there is no unique substitutions in plastid sequences for *S. taimyrense* + *S. commutatum*. Therefore we describe *S. taimyrense* (see below) as a new species, though most closely related to *S. commutatum*.

*Streblotrichum taimyrense* has variable leaf apices, obtuse or acute. Superficially this species resembles *S. jacuticum* and Arctic forms of *S. convolutum*, which also occasionally have rounded leaf apices, but their placement in *S. convolutum* is proved by sequencing. Rather often, albeit not always, papillae in *S. taimyrense* look round, similar to *Molendia* or *Gymnostomum*, and this feature might be useful for identification of sterile plants.

The most unexpected result of the present study is a revealing of 'enderesii-clade'. Plants from different regions of Russia, including Urals, Altai, Yakutia, and Primorsky Territory appeared to have subidentical sequences with GenBank accessions from Czech Republic and China, and also with the European *S. enderesii*. This species was not previously recorded from Russia. Savicz-Lyubitskaya & Smirnova (1970) mentioned that it occurs in Ukraine and Middle Asia. In the check-list of East Europe and North Asia (Ignatov *et al.*, 2006) it was also reported from these regions based on publications of Bachurina & Mel'nichuk (1988) for Ukraine, Lazarenko (1938) for Uzbekistan, and Mamatkulov *et al.* (1998) for Kyrgyzstan.

The main character differentiating *Streblotrichum enderesii* from *S. convolutum* is shape of perichaetial leaves: in the former species they are abruptly contracted into long, narrowly triangular to subulate acumina and have stronger costae, while in the latter one they are obtuse or short apiculate; *S. enderesii* also has narrower stem leaves with margins recurved beyond the mid-leaf. Unfortunately, most

sequenced specimens from Russia from 'enderesii-clade' were scarce and sterile, except for specimen OK3749 from Yakutia, in which one perichaetium with broken off capsule was found, and its perichaetial leaves had long, triangular acumina. Two isolates were obtained from one sterile specimen collected on the bank of Chusovaya River in Perm Territory, North Urals. However, we failed to extract DNA from the third specimen from the same area, also scarce but bearing several mature sporophytes. This specimen fitted well *S. enderesii* in having perichaetial leaves with long, triangular acumina and stem leaf margins recurved to 2/3–3/4 the leaf length (Fig. 6ER3); it was correctly identified by its collector A.G. Bezgodov but never published before. Regarding morphological characters of other sequenced specimens from Russia resolved in a clade with *S. enderesii* from Austria, they possess only small differences from *S. convolutum*, i.e. narrower acute leaf apices, larger leaf cells, and, in some cases, uneven or weakly dentate upper leaf margins. This is hardly helpful for separating them from large morphotypes of the latter species growing in wet conditions. On the other hand, these specimens do not differ significantly in leaf shape and leaf margins recurvation from specimens from Switzerland presented in detailed photos at [https://www.swissbryophytes.ch/index.php/de/bilder?taxon\\_id=nism-649](https://www.swissbryophytes.ch/index.php/de/bilder?taxon_id=nism-649). Thus, based on the evidence from obtained molecular phylogenetic data and taking into account the fact that most sequenced specimens were not optimally developed, as well as presence of typical plants of *S. enderesii* with sporophytes in Urals, we refer sequenced specimens of 'enderesii-clade' just to this species.

#### TAXONOMY

***Streblotrichum*** P. Beauv., Mag. Encycl. 9(5[19]): 317. 1804.

*Plants* small to medium-sized, in dense or loose tufts, green or yellow-green. *Stems* usually unbranched, evenly foliate. *Leaves* straight, curved, flexuose or contorted when dry, patent when wet, long-ligulate or oblong lanceolate, base broadened and sheathing or not distinctly sheathing, upper part flat or keeled, laminae between costa and margin flat or arching-recurved; margins plane or weakly recurved below, rarely recurved almost throughout; apex broadly acute to rounded, entire or apiculate; *costa* vanishing 1–6 cells below the apex, papillose on dorsal and ventral surfaces, in transverse section with dorsal stereid band, ventral stereid band weak or often absent in weaker developed plants; *laminal cells* rounded-quadrate, densely papillose on both leaf surfaces, with low C-shaped papillae; basal cells rectangular, smooth, at transition to upper lamina papillae are remote and round. *KOH reaction* yellow-orange to reddish. *Specialized asexual reproduction* by large, spheric to elliptic, red-brown rhizoidal tubers. *Dioicous*. *Perichaetial leaves* with sheathing bases, tightly embracing the seta base, distally obtuse or contracted into narrow acumina. *Male plants* small, among female ones. *Setae* long, stramineous, reddish-yellow or

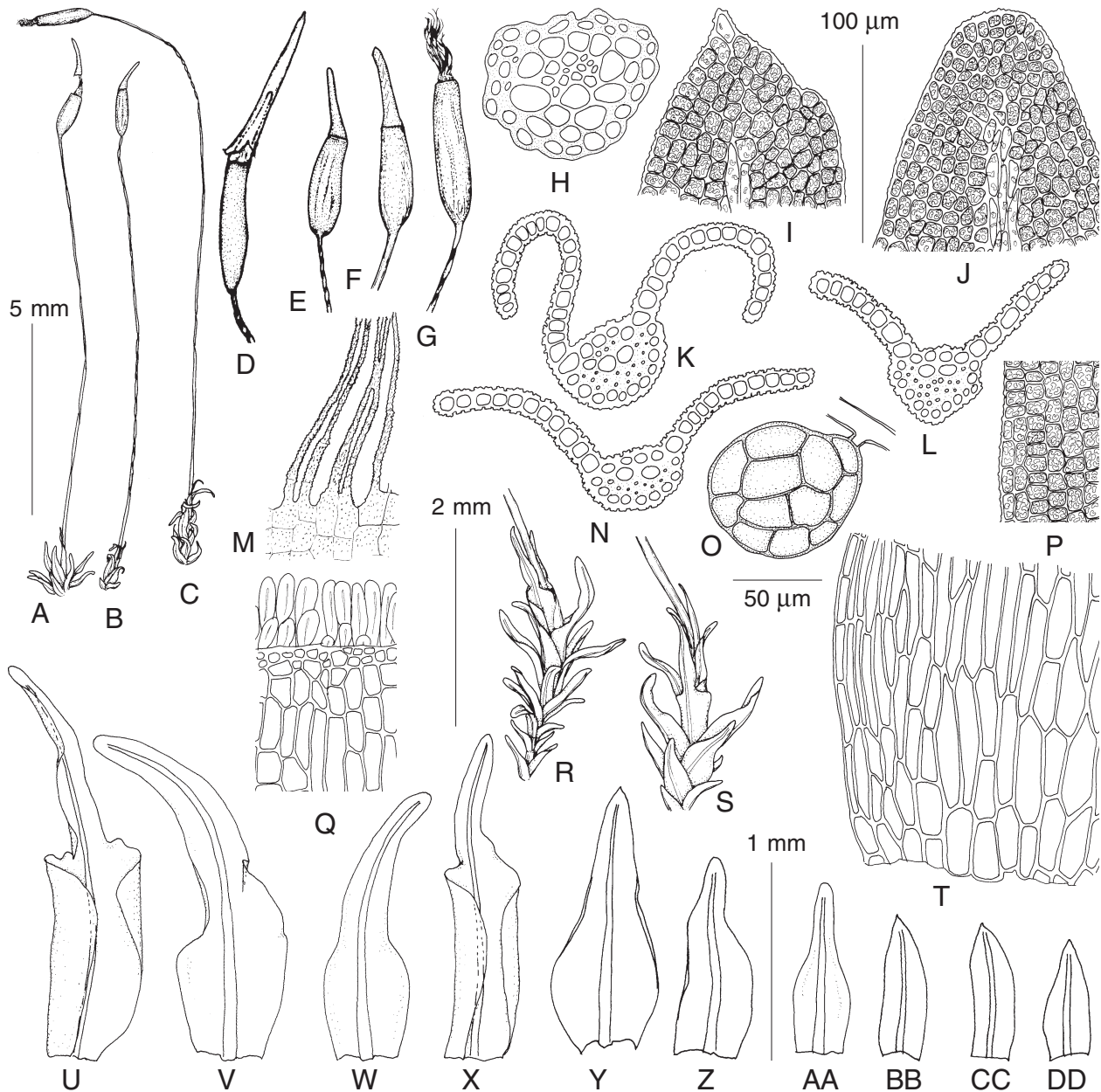


Fig. 7. *Streblotrichum jacuticum* (from: Russia, Yakutia, Ust-Maya Distr., Allakh-Yun, 24.VIII. 2000, Ignatov 00-1060, MHA9005223). A–C, R–S: abit, dry; DG: capsules; H: stem transverse section; I–J: upper laminal cells; K–L, N: leaf transverse sections; M: peristome; O: gemma; P: mid-leaf cells; Q: annulus & exothecium; T: basal laminal cells; U–X: perichaetial leaves; Y–DD: stem leaves. Scale bars: 5 mm for A–C; 2 mm for D–G, R–S; 1 mm for U–DD; 50  $\mu$ m for O; 100  $\mu$ m for H–N, P–Q, T.

reddish. *Capsules* erect, cylindric. *Opercula* conic and tapered to rostrum, altogether usually as long as the urn. *Annuli* well-developed, readily revolvable. *Perisome teeth* split into ca. 32 filiform branches, spirally twisted, papillose on both surfaces. *Spores* small.

1. *Streblotrichum jacuticum* (Ignatova) Ignatova, comb. nov. — *Barbula jacutica* Ignatova, *Arctoa*, 10: 161. f. 1–2. 2001.

**Type:** East Siberia, Republic Sakha/Yakutia, Ust-Maya District, Allakh-Yun, Tarbagannakh, 61°06'N – 138°10'E, 1000 m alt., along old road, 24.VIII.2000 M. Ignatov 00-1060 (holotype MHA!).

**Description.** *Plants* in loose tufts or growing by individual plants. *Stems* 1–3 mm long, upper leaves larger and crowded. *Leaves* differentiated in size and shape, upper leaves 1.2–1.6×0.3–0.5 mm, with differentiated ovate base, rather abruptly contracted to lanceolate acumen, apically broadly rounded; lower leaves ca. 0.5×0.15 mm, oblong-ovate, apically acute; laminae between costa and margin strongly arching-recurved; margins plane or recurved at transition from base to acumen, entire; *costa* in upper stem leaves leaves up to 70  $\mu$ m wide, in transverse section ventral stereid band small in lower part of better developed leaves, otherwise absent; upper and median *laminal cells* 6–9(–10)  $\mu$ m in leaves with round-



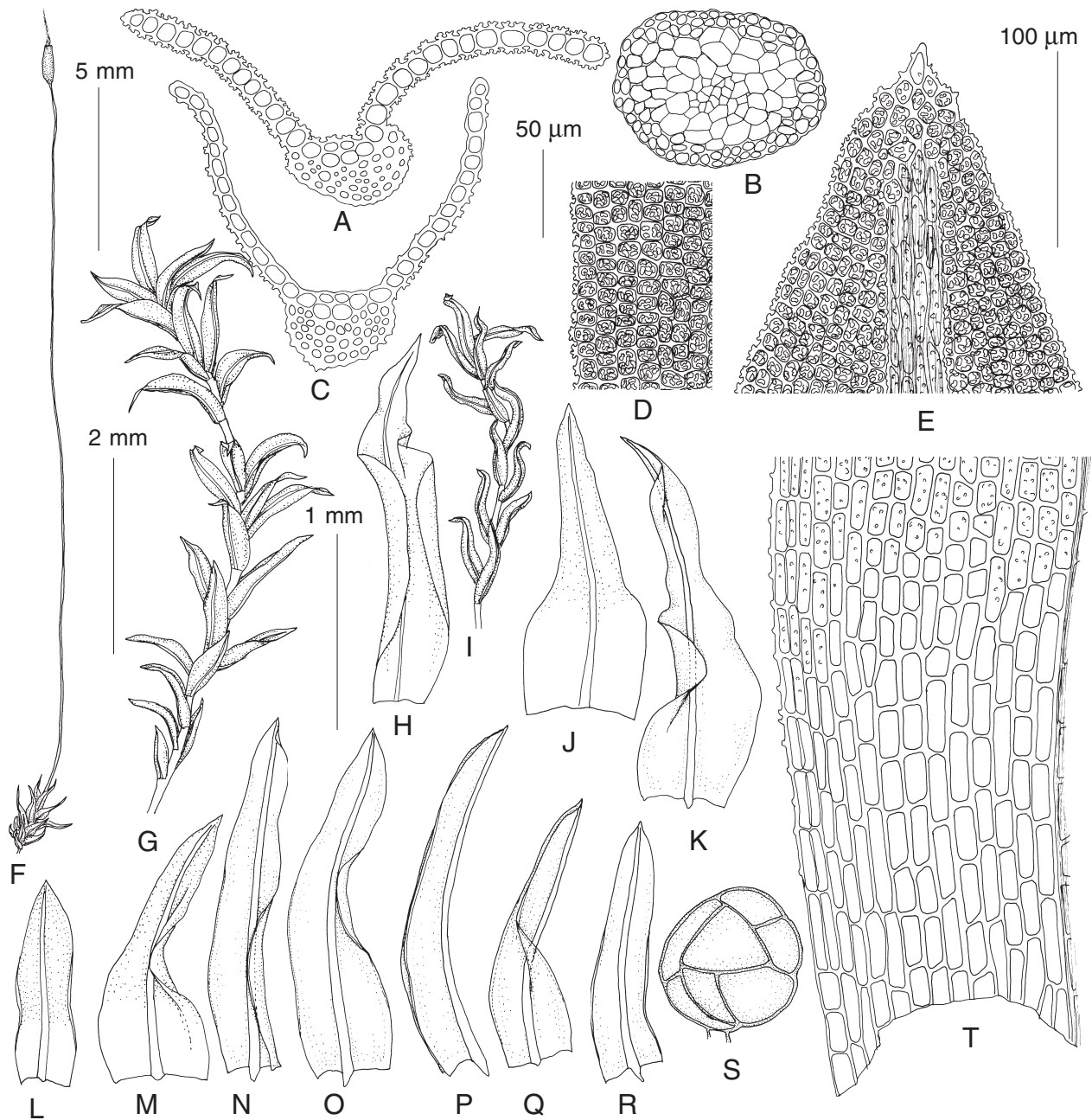


Fig. 8. *Streblotrichum enderesii* (from: Russia, Perm Territory, Lysva Distr., Chusovaya River, 12.VIII.2005, *Bezgodov 196*, PPU, MHA9131869). A, C: leaf transverse sections; B: stem transverse section; D: mid-leaf cells; E: upper laminal cells; F, I: habit, dry; G: habit, wet; H: inner perichaetial leaf; J–K: outer perichaetial leaves; L–R: stem leaves; S: gemma; T: basal laminal cells. Scale bars: 5 mm for F; 2 mm for G, I; 1 mm for H, G–R; 50 µm for A–C, S; 100 µm for D–E, T.

ed apex, in smaller acute leaves near stem base cells larger, to 12–13 µm, densely papillose, papillae C-shaped; basal cells in larger leaves to 30–65×8–14(–20) µm, with length to width ratio 2.5–7:1. *Rhizoidal tubers* 70–100(–120) µm. Perichaetial leaves up to 2.0×0.7 mm, with broad base moderately tightly appressed to seta, contracted to a linear acumen, in inner perichaetial leaves as long as the basal part. *Setae* 10–16 mm, red. *Capsules* 0.9–1.3×0.4 mm. *Spores* 11–14 µm.

**Distribution and ecology.** This species is known from two localities in Yakutia and one locality in Anabar Plateau

in the southern Taimyr. The type collection was gathered of humus-rich soil bank along abandoned roadside near the tree line; it includes only few plants. Subsequently we found a large population of this species, where it is occurring here and there over 5 km of the valley of a small creek Segenyakh (also called Rossomakha) in Sette-Daban Range in East Yakutia, at 450–600 m elev. This is a calcareous area, with large *Andreaeobrym* population in the upper course of this creek (Ignatov *et al.*, 2016). In this area a population of *S. convolutum* was also found, but the latter species grows mostly along the cross-country road, whereas *S. jacuticum*

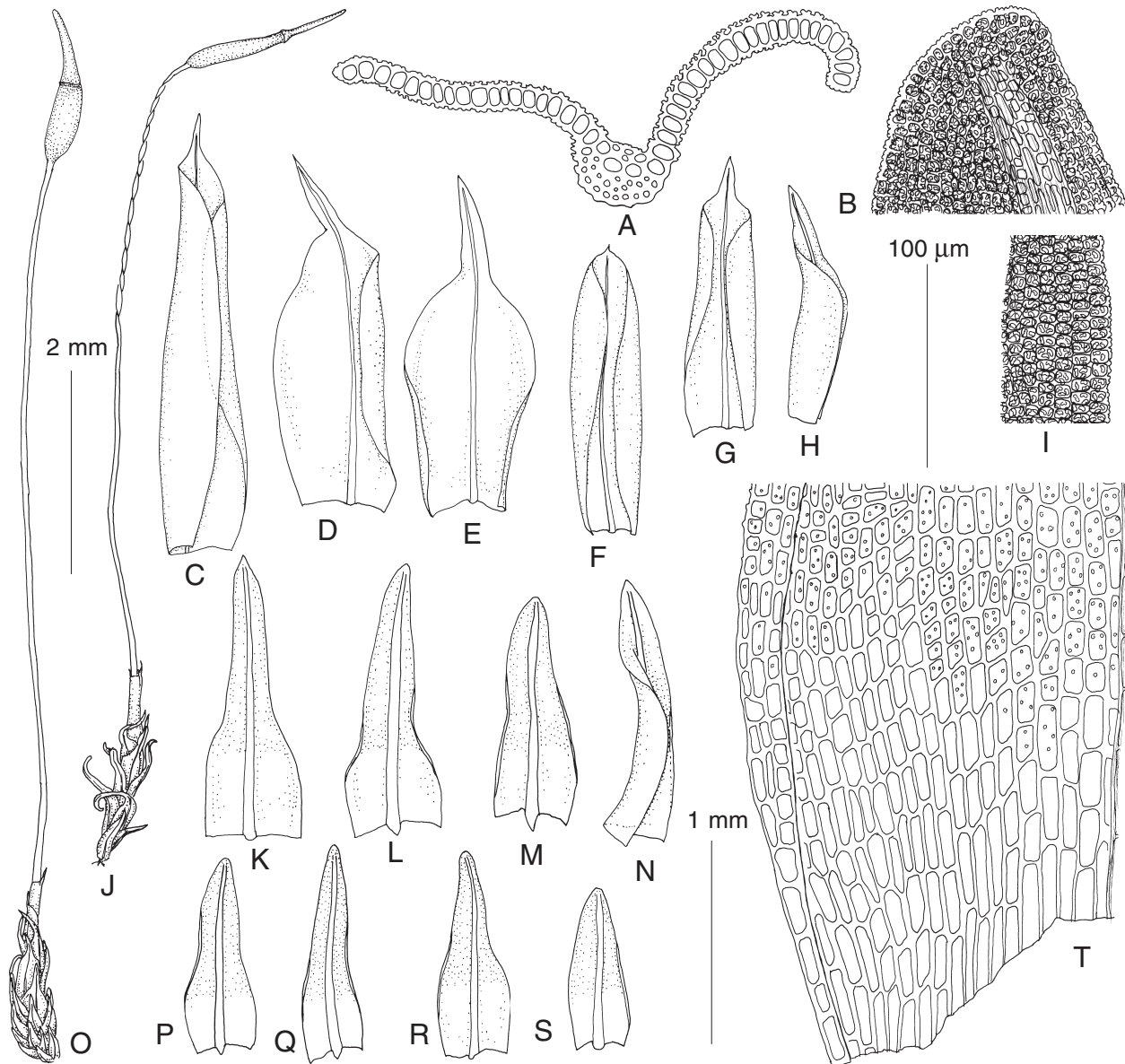


Fig. 9. *Streblotrichum taimyrense* (from holotype). A: leaf transverse section; B: upper laminal cells; C–G: perichaetial leaves; H: subperichaetial leaf; I: mid-leaf cells; J: habit, dry; K–N, P–S: stem leaves; O: habit, wet; T: basal laminal cells. Scale bars: 2 mm for J, O; 1 mm for C–H, K–N, P–S; 100  $\mu$ m for A–B, I, T.

is not weedy at all, occurring on somewhat eroded banks in floodplain and on bare soil patches at forest edges along old, little used forest roads and trails.

*Specimens examined:* see Table 1.

2. *Streblotrichum enderesii* (Garov.) Loeske, Hedwigia 49: 30. 1909. — *Barbula enderesii* Garov., Bryol. Austr. Excurs. 37. 1840.

Figs. 2E2, 3E2, 4E2, 5E2, 6E2, 8.

**Description.** Plants small or medium-sized, in loose tufts, green or yellow-green. Stems 2–10 mm long, evenly foliate. Leaves 1.0–1.5 × 0.2–0.35 mm, ovate-oblong, broader base moderately differentiated or not differentiated, sometimes with indistinct constriction above the base, with parallel margins in the middle and gradually

tapered to triangular apical part in larger leaves, or rounded and apiculate at apex in smaller leaves; laminae between costa and margin plane or moderately arching-recurved; margins plane, or recurved in lower half and plane above, or recurved at transition from base to acumen; in larger leaves often slightly undulate, wavy and coarsely denticulate; costa 30–50  $\mu$ m wide near the base, in transverse section usually without ventral stereid band or, rarely, with 1–2 cells with narrow lumen; upper and median laminal cells in larger leaves 11–17  $\mu$ m, in smaller leaves 8–11  $\mu$ m, densely papillose, papillae C-shaped; basal laminal cells in larger leaves to 40–65 × 10–20  $\mu$ m, with length to width ratio 2–4(–5):1, in smaller leaves basal cells fewer, short rectangular, with length to width ratio 1.3–3:1. Rhizoidal tubers 150–220  $\mu$ m, scattered



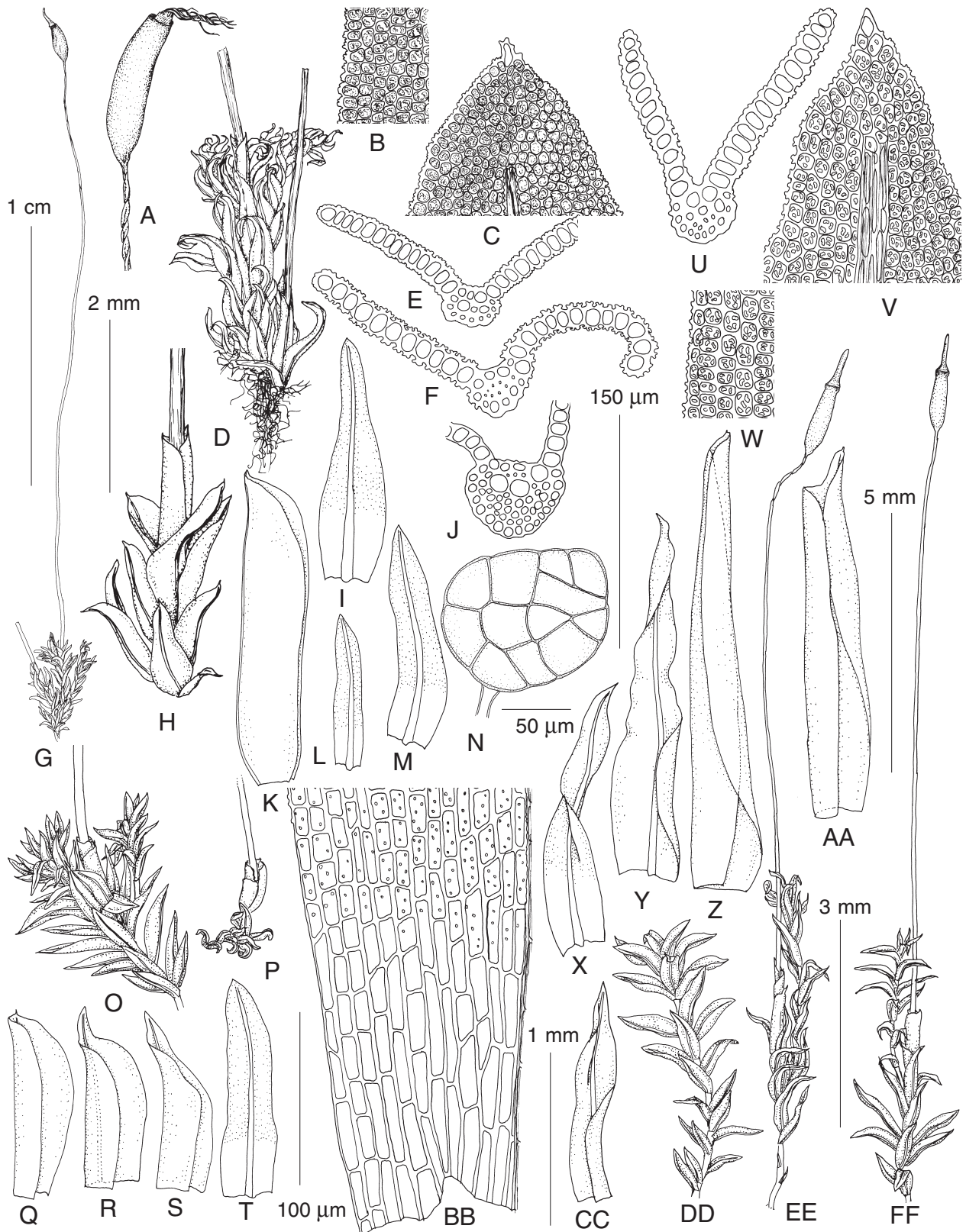


Fig. 10. *Streblotrichum convolutum* (A–N: ‘convolutum-morphotype’, from Russia, Moscow Province, Klin, 14.VI.1996, Ignatov s.n., MW9003727, isolate 3870; O–T: ‘convolutulum-morphotype’, from Russia, Primorsky Territory, Ignatov & Ignatova 13-1542, MHA9005044, isolate OK3751; U–FF: ‘sardoa-morphotype’, from Russia, Moscow Province, Zvenigorod, 25.VI.2004, Ignatova s.n., MW9003728, isolate OK3869). A: capsule; B, W: mid-leaf cells; C, V: upper leaf cells; D, P, EE: habit, dry; E–F, J, U: leaf transverse sections; G–H, O, DD, FF: habit, wet; I, L–M, T, X–Y, CC: stem leaves; K, Q–S, Z–AA: perichaetial leaves; N: gemma; BB: basal leaf cells. Scale bars: 1 cm for G; 5 mm for FF; 3 mm for DD–EE; 2 mm for A, D, H, O–P; 1 mm for I–M, Q–T, X–AA, CC; 150 µm for E–F, J, U; 100 µm for B–C, V–W, BB; 50 µm for N.

or exceedingly abundant. *Perichaetial leaves* up to 2×0.6 mm, with broad base more or less tightly appressed to seta, contracted to triangular-lanceolate acumen about twice shorter than the basal part. *Setae* 10–16 mm, reddish-yellow. *Capsules* 1.1–1.3×0.4 mm. *Spores* 8–10 µm.

**Distribution and ecology.** This mainly European species was already known in Asia (Uzbekistan and Kyrgyzstan, see Discussion above). Its finding in geographically distant localities in Russia extends considerably its known distribution area. On Chusovaya River *S. enderesii* was collected on soil bank in the forest with high forbs in wet depression between limestone cliffs. In Altai it grew on eutrophic meadow with *Trollius asiaticus* on E-facing slope. In Yakutia it was found below high limestone cliffs near the bank of Lena River, on soil banks above pebble bar, and in Ussurijsky Reserve it grew on concrete foundation of destroyed building at the bank of a stream.

*Specimens examined:* Table 1.

3. ***Streblotrichum taimyrense*** Ignatova & Ignatov, species nova. Figs. 2T, 3T, 4T, 5T, 6T, 9.

**Diagnosis:** Differs from *S. convolutum* in larger spores, 11–14 µm vs. 8–10; perichaetial leaves with triangular-lanceolate acumina up to half the leaf base length vs. obtuse, with short apiculi; and smaller laminal cells, 6–8(–10) µm vs. 8–10 µm.

Type: [Russia], Krasnoyarsk Territory, Taimyr Distr., Khatanga settl. outskirts, Ereechka river upper course, Nyamakit-Daldyn creek mouth, Ereechka river valley 1 km downstream Nyamakit-Daldyn mouth. Eroded slope of 1-st terrace, on loamy ground. 02.VIII.[20]13. Coll. Fedosov V.E. 13-3-0725 (holotype MHA9005045).

**Description.** *Plants* small, growing usually as scattered individuals or in loose tufts, yellow-green or brown-green. *Stems* 1–3 mm long, evenly foliate or upper leaves somewhat crowded, central strand present. *Leaves* in upper stem parts 1.2–1.5(–1.8)×0.3–0.5 mm, from a distinctly differentiated, broader bases gradually or ±abruptly narrowed into lanceolate, broadly acute or blunt acumina; laminae between costa and margins plane or moderately arching-recurved; margins plane, or recurved in lower half and plane above, or recurved at transition from base to acumen, entire; *costa* 30–50 µm wide near leaf base, in transverse section with dorsal stereid band, usually without ventral stereid band, or occasionally with few thick-walled cells ventrally from guide cells; upper and median *laminal cells* 6–8(–10) µm, densely papillose, papillae C-shaped in larger cells or almost round in smaller cells; basal laminal cells rectangular, 30–45×10–15 µm, with length to width ratio 2–3(–4):1. *Rhizoidal tubers* 60–120 µm. *Perichaetial leaves* up to 2×0.8 mm, with broad base more or less tightly appressed to seta, contracted to triangular-lanceolate acumen 0.2–0.5 of the basal part in length. *Setae* to 8 mm, reddish-yellow. *Capsules* 0.8–1.0×0.3 mm. *Opercula* 0.6–0.8 mm long. *Spores* 11–14 µm.

**Distribution and ecology:** The species is known by three specimens from Taimyr, in the area ca. 60 km across. The plants grow on eroded slopes to rivers. Substrates are mostly calcareous.

*Specimens examined:* Table 1.

4. ***Streblotrichum convolutum*** (Hedw.) P. Beauv., Prodr. Aetheogam. 89. 1805. — *Barbula convoluta* Hedw., Sp. Musc. Frond. 120. 1801. Figs. 2C, 3C, 4C, 5C, 6c, 10.

*Plants* small or medium-sized, in dense or loose tufts, green, yellow-green or brownish-yellow. *Stems* (2–)3–7(–20) mm long, evenly foliate. *Leaves* in upper parts of stem 0.8–2.3×0.2–0.55 mm, ovate-lanceolate or oblong-ovate, the larger with better differentiated broader base, from which gradually tapered to acute or rounded, usually shortly apiculate apices; laminae between costa and margin plane or moderately arching-recurved; margins plane or, rarer, slightly recurved at places in lower half of leaf, entire or ‘denticulate’ because of outer cell walls bulging beyond the general leaf outline; *costa* 30–65 µm wide near the base, in transversal section with dorsal stereid band and occasionally also with a small ventral stereid band; upper and median *laminal cells* 8–10(–12) µm, densely papillose, papillae C-shaped; basal laminal cells rectangular, 35–70×9–15 µm, with length to width ratio (2–)3–7:1. *Rhizoidal tubers* 150–200 µm. *Perichaetial leaves* 1.7–2.7×0.8 mm, with broad base more or less tightly appressed to seta, obtuse or shortly and bluntly apiculate. *Setae* 10–16 mm, stramineous, rarely slightly reddish and very rarely rather deeply reddish. *Capsules* 1.1–1.3×0.5 mm. *Spores* (7–)8–10(–11) µm.

**Distribution and ecology:** The species was described from ‘whole Europe’, and is currently known almost throughout Holarctic and also in Mexico and New Zealand. In Russia it is known from many regions, but most collections are sterile, therefore a somewhat indefinite, considering possible confusing with *S. neglectum*. Nevertheless, the most common phenotype is readily recognizable, as the plant is forming dense, pure tufts, when collecting appearing as a solid piece of ground with mosses upon it. However, if tufts are loose, it is more difficult to separate *S. convolutum* from other species of the genus. *Streblotrichum convolutum* grows on bare soil in ruderal habitats, on eroded slopes, gravely river bars, rocky covers along railroads. The rarely used, almost abandoned roads is a rather suitable habit for this species in forest zone, as well as in Arctic.

*Selected specimens examined:* **RUSSIA: Altai Republic:** Tetselskoe Lake, Chulyshman River, 5.VII.1966, *Bardunov s.n.* (MHA9005074). **Krasnodar Territory:** Anapa Distr., Malyj Utrish, *Ignatov & Ignatova 05-437* (MW9003757). **Perm Territory:** Vishersky Reserve, 19.VI.1995, *Bezgodov 212* (MW9003749); same place, *Bezgodov 211* (MW9003748); 7.VIII.1995, same place, 19.VI.1995, *Bezgodov & Selivanov 212* (MW9003749). **Republic Sakha/Yakutia:** Tomponsky Distr., Nadezhda Creek, *Ignatov & Ignatova 16-984* (MHA9022648). **Sakhalin Province:** Sakhalin Island, Tym’ River, *Ignatov & Teliganova 06-441* (MHA9005067); **Archangelsk Province:** Kargopol Distr., 4.VII.2001, *Churakova 1513* (MW9003732);



Konosha Distr., 26.VII.2001, *Churakova 1498* (MW9003733). **Vologda Province:** Sokol Distr., 22.IX.1990, *Ignatov s.n.* (MW9003740). **Moscow Province:** Odintsovo Distr., Zvenigorod Biostation of MSU, 25.VI. 2004, *Ignatova s.n.* (MW9003728). **MONGOLIA:** *Enkhchagal 634* (MHA9065040).

**Variation:** *Streblotrichum convolutum* is heterogeneous genetically (Fig. 1), showing some geographic races, which probably evolved in semi-natural environments in different regions. However, its recent spreading as a weed probably makes any segregation problematic. Three phenotypes are recognizable in Russia, as shown in Fig. 10.

(1) dense tufts, comprising even greenish-yellow 'lawns' with solitary sporophytes, which seta bases are embraced by sheathing bases of the perichaetial leaves (Fig. 10A–N).

(2) loose tufts, where numerous innovations hide the perichaetia, which are difficult to see in the field with a handlens, as they need certain preparation under the stereomicroscope; these plants are sometimes quite tall, have more distant and less rigid leaves; it is likely that such variation is environmentally dependent: samples of phenotype '1' and '2' collected in Moscow Province close to each other in wet and dry habitat were found to be identical in DNA sequences (Fig. 10U–FF).

(3) low tufts with exposed perichaetia, which differ from '1' in the perichaetial leaves that are loosely appressed to the seta (Fig. 10G–T); this phenotype was observed in the Russian Far East (OK3751).

However, these more or less contrastingly different habits shows no correlation with the sequence data, thus the recognition of any infraspecific groups in Russia based on the present material is impossible.

#### KEY TO SPECIES IDENTIFICATION OF *STREBLOTTRICHUM* SPECIES IN RUSSIA

1. Perichaetial leaves contracted into acumina of 1/2–1/3 of the the total leaf length ..... 2
- Perichaetial leaves contracted into acumina shorter than 1/3 of the total leaf length ..... 3
2. Seta red; apices of perichaetial leaves rounded ..... 1. *S. jacuticum*
- Seta stramineous-yellow, apices of perichaetial leaveacute or acuminate ..... 2. *S. enderesii*
3. Stem leaves obtuse or bluntly acute; perichaetial leaves contracted into narrow acumina; spores 11–14  $\mu\text{m}$ . ..... 3. *S. taimyrense*
- Stem leaves acute, apiculate, rarely obtuse; perichaetial leaves obtuse or shortly apiculate; spores (7–)8–10(–11)  $\mu\text{m}$  ..... 4. *S. convolutum*

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