

TOWARD A NEW UNDERSTANDING OF *SYNTRICHIA SUBMONTANA*
(POTTIACEAE, BRYOPHYTA)

НОВОЕ ПОНИМАНИЕ *SYNTRICHIA SUBMONTANA* (POTTIACEAE, BRYOPHYTA)

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Abstract

Syntrichia submontana (Broth.) Ochyra has been previously reported from Tajikistan, Kyrgyzstan and Mongolia. It was considered to be dioicous, with sporophytes unknown. Our study of extensive herbarium collections from Mongolia, southern Siberia and the Caucasus, as well as some collections from China revealed that this species has a much wider distribution in Asia. Its sexual condition is polyoicous: autoicous plants are most frequent, with antheridia and paraphyses lacking perigonal leaves, forming a group just below the perichaetium, but occasionally also male, female and, more rarely, synoicous plants are found in the same tuft. Mature sporophytes are rare in Mongolian collections, but they are frequent in China, southern Siberia and the Caucasus. Peristomial basal membrane is very low, consisting of 1-2(-3) cell rows. *S. submontana* is similar in gametophytic characters to *S. sinensis* (Müll. Hal.) Ochyra, and their close relationship was confirmed by molecular study (*nrITS2*). A description of *S. submontana* is amended and supplemented by sporophyte characteristics. *Syntrichia longimucronata* (X.J. Li) R.H. Zander is synonymized with *S. submontana*. Descriptions, illustrations, distribution and ecological data are provided for *S. submontana* and *S. sinensis*. Our molecular data also found two distinct entities within the morphologically variable *S. laevipila* Brid., which tentatively confirms recognizing of *S. pagorum* Milde as a separate species. Specimens of *S. caninervis* var. *astrakhanica* Ignatov, Ignatova & Suragina from distant localities are also resolved in a clade separated from *S. caninervis* var. *caninervis*; thus the variety likely deserves being raised to the species level.

Резюме

Syntrichia submontana (Broth.) Ochyra была до настоящего времени известна из Таджикистана, Кыргызстана и Монголии. Вид считался двудомным, его спорофиты не были описаны. Изучение многочисленных гербарных образцов из Монголии, южной Сибири и с Кавказа, а также некоторых коллекций из Китая показало, что вид имеет гораздо более широкое распространение в Азии. Он является многодомным, при этом чаще всего представлены однодомные растения, у которых перигонии не почковидные, группа антеридиев и парафиз без покровных листочков располагается немного ниже перихеция, но иногда в той же самой дерновинке встречаются также женские, мужские и, реже, обоеполюе растения. Зрелые спорофиты редки в коллекциях из Монголии, но обычны в образцах из Китая, южной Сибири и с Кавказа. Перистом характеризуется низкой базальной мембраной, состоящей из 1-2(-3) рядов клеток. По признакам гаметофита *S. submontana* сходна с *S. sinensis* (Müll. Hal.) Ochyra, и их близкое родство подтверждается также молекулярными данными (*nrITS1-2*). Описание *S. submontana* исправлено и дополнено характеристической спорофитов. *Syntrichia longimucronata* (X.J. Li) R.H. Zander синонимизирована с *S. submontana*. Для *S. submontana* and *S. sinensis* приводятся описания, иллюстрации, обсуждается экология и распространение. Наши молекулярные данные также показывают, что внутри морфологически вариабельной *S. laevipila* Brid. есть две четких группы, что предположительно свидетельствует в пользу выделения *S. pagorum* Milde в качестве самостоятельного вида. Образцы *S. caninervis* var. *astrakhanica* Ignatov, Ignatova & Suragina из отдаленных местонахождений образовали кладу, отдельную от *S. caninervis* var. *caninervis*; таким образом эта разновидность, вероятно, заслуживает видового статуса.

KEYWORDS: mosses, Pottiaceae, *Syntrichia*, taxonomy, new synonyms, new records, Russia, Mongolia, China, ITS.

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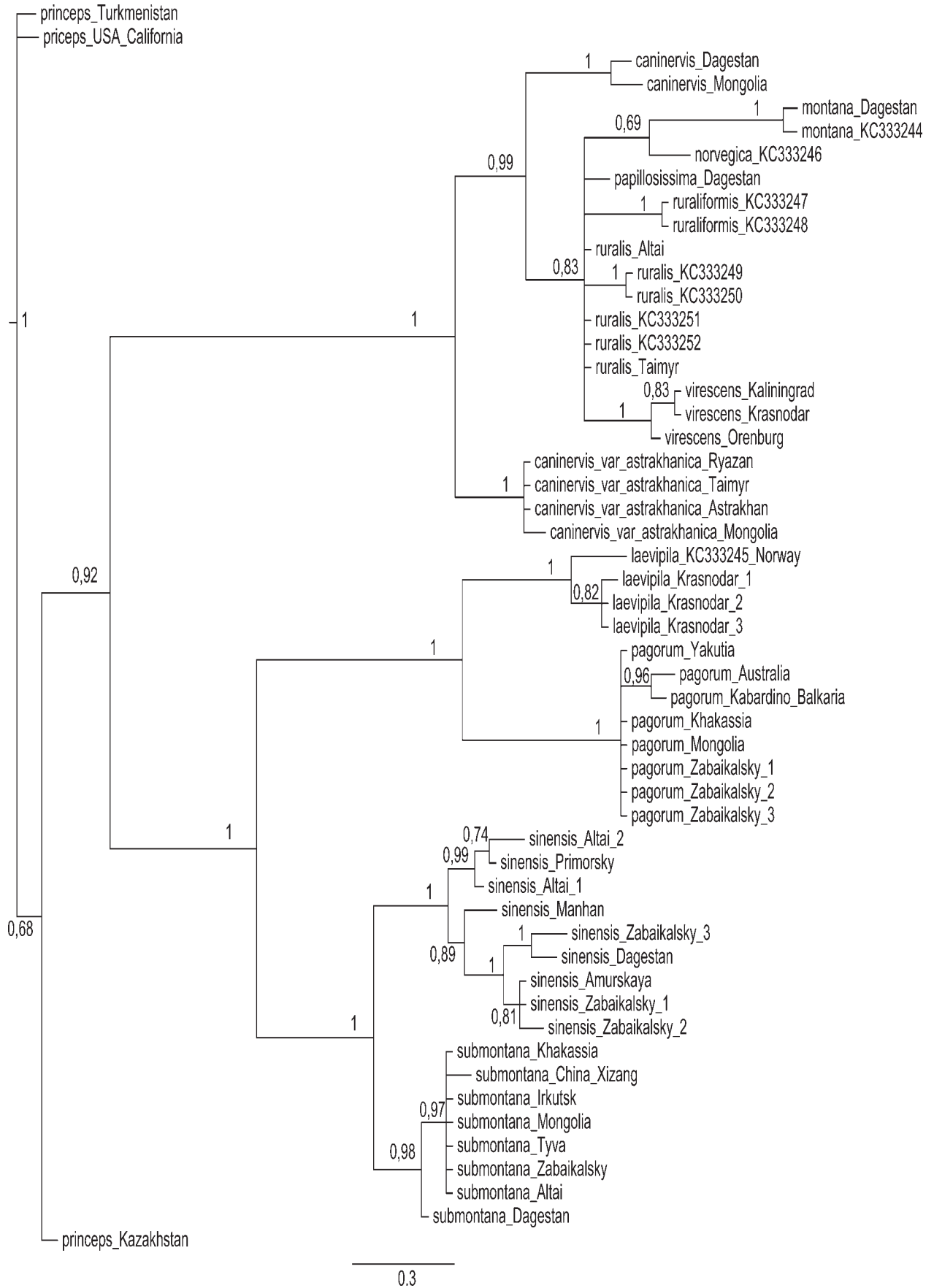


Fig. 1. Bayesian tree of *Syntrichia* based on 5.8rRNA and ITS2 sequence data. Posterior probabilities are shown at branches.

INTRODUCTION

The genus *Syntrichia* Brid. is known as a difficult one for species identification, and there have been controversial taxonomic approaches to some species and their groups. The genus has been a subject of a thorough taxonomic treatment of Kramer (1980) for Palearctic, Gallego (2005) for Mediterranean region and Macaronesia, and Mishler (2007) for North America. The group of species around *S. laevipila* has been additionally revised by Gallego et al. (2004, 2005) for Europe.

In the territory of Russia, 10 species and 2 intraspecific taxa of *Syntrichia* were listed (Ignatov, Afonina, Ignatova et al., 2006). However, some unresolved problems with specimen identification were revealed during moss flora exploration in the southern Siberia and the Caucasus. In particular, a number of specimens similar to *S. sinensis* (Müll. Hal.) Ochyra have been found to have leaves with an unusually long hair point, basal membrane of peristome lower than in this species, and naked perigonia (which are usually bud-like). For clarifying a relationship of these specimens and *S. sinensis* we undertook a combined molecular and morphological study of this group, involving also *S. laevipila* and *S. pagorum* Milde, as the 'atypical *S. sinensis*' also could be interpreted as very large forms of these species in case if sporophytes are lacking.

MATERIAL AND METHODS

Morphological studies were based on collections from LE, MHA, MW and PE.

For molecular study 9 specimens of "typical *S. sinensis*" and 8 specimens of "atypical *S. sinensis*" were selected, representing geographically distant localities of both. In addition, 11 specimens of *S. laevipila* s.l. (i.e., including *S. pagorum*) from different areas of Asiatic Russia and the Caucasus were studied, 3 specimens of *S. princeps* (De Not.) Mitt., and a number of other more distantly related species of the genus. GenBank data were borrowed for nine *Syntrichia* specimens, mostly of *S. ruralis* and closely related species. Totally 53 sequences were included in the analysis.

Only ITS2 is included in the study by three reasons: (1) ITS1 was unavailable in GenBank for these species; (2) ITS1 sequences of species even within one genus cannot be unequivocally aligned; and (3) ITS2 has numerous substitutions, clearly correlating in most cases with the species as they are currently known based on morphology. Specimen vouchers and GenBank accessions are in Appendix 1.

Laboratory protocol was essentially the same as in previous moss studies, described in detail by, e.g., Gardiner et al. (2005). ITS sequences were aligned independently using MUSCLE (Edgar, 2004), and modified manually using BioEdit 7.0.9.0 (Hall, 1999).

For the rooting of trees *Syntrichia princeps* was chosen, because it was difficult to align ITS sequences of *Syntrichia* with any ITS sequences of related genera, e.g.,

Tortula Hedw., and sequences of *S. princeps* visually were the most distinct from other major groups of sequences. Supplementary analyses with the rooting on *S. norvegica* both by Bayesian methods and maximum parsimony in TNT (not shown) found *S. princeps* to be distant from *S. sinensis*–*S. laevipila* s.l.–complex, which is in the main focus of the present study.

Bayesian analyses were performed using MrBayes (Huelsenbeck et al. 2001), version 3.2.0, running in two parallel analyses, consisting each of six Markov chains of 10,000,000 generations with a sampling frequency of one tree each ten thousand generations and the chain temperature at 0.05. Parameters of the substitution model were estimated during the analysis (six substitution categories, a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites). Convergence of the analyses was evaluated using Tracer 1.4.1 (Rambaut & Drummond 2007) to check that ESS values were all greater than 200 (default burning). The consensus tree was then combined after first 25% of trees were discarded as a burn-in. All analyses were performed on the Cipress Science Gateway (<http://www.phylo.org/portal2>).

RESULTS

Phylogenetic analysis resulted in a Bayesian tree (Fig. 1) consisting of two well-supported clades, one including species of *S. ruralis*–*S. caninervis*–*S. virescens*–complex, and another composed of *S. sinensis*–*S. laevipila* s.l.–complex.

The species of the former clade will be the subject of a separate analysis. Here we just point out that this preliminary analysis of the group supports the elevation of *S. caninervis* var. *astrakhanica* to the species level.

Syntrichia sinensis–*S. laevipila* s.l.–clade consists of two maximally supported subclades. The first of them represents typical *S. sinensis* and a species in question, each forming a clade. Nine specimens of *S. sinensis* from geographically distant localities (from Primorsky Territory in Russian Far East, Inner Mongolia in China and westward to Dagestan in the Caucasus) form the clade with the posterior probability 1.00; another clade with the support 0.98 consists of six specimens of "atypical *S. sinensis*" from southern Siberia, one from Dagestan in the eastern part of Caucasus, one specimen of *S. submontana* from Mongolia and one specimen from Tibet, collected not far from the type locality of *S. longimucronata* (cf. Fig. 3). Being largely sympatric with *S. sinensis*, this taxon has also small, but fairly stable morphological distinction from it.

A second subclade is formed by specimens of *S. laevipila* s.l. The present Bayesian analysis subdivides them in two clades, both with support P=1.00. One of them includes dioicous plants, referred here to *S. pagorum*, while another comprises autoicous plants, corresponding to *S. laevipila* s. str. in its common circumscription. Within polytomy of six Siberian and Mongolian plants

of *S. pagorum*, a moderately supported (PP=0.96) nested clade occurs, composed by Central Caucasian and Australian plants. The *S. laevipila* s.str. subclade includes one Norwegian specimen clearly differentiated from three Caucasian specimens (though all three from a relatively restricted area).

DISCUSSION

As soon as it became clear that the plants of unknown *Syntricha* in question cannot be just a marginal phenotype of *S. sinensis*, an expanded search for appropriate name has been undertaken yielding a possible attribution of the former to *S. longimucronata* (X.J. Li) R.H. Zander. This species was described from Xizang Province of China (Li, 1981), and our plants in question were in agreement with its description in most gametophytic and sporophytic characters (*i.e.*, presence of central strand in stem and hydroids in costa, highly recurved leaf margins, long and weakly denticulate hair-point, low basal membrane of peristome, as well as autoicous sexual condition, though perigonia were not described in details). The only character which we did not observe in our plants was leaf marginal border “consisting of several rows of thick-walled, or sometimes elongated cells, yellowish or brownish” (Li *et al.*, 2001). Nevertheless, the illustration on p. 219 (Plate 132: 2) shows an unbordered leaf margin. This character is known to be variable in other species of *Syntrichia*, *i.e.*, *S. laevipila*, representing both clearly bordered and totally unbordered leaves in different specimens. In all collections from China available for our study, including a locality from Xizang Province, leaves were not bordered.

Another species name, which could be attributed to our plants was *S. submontana* (Broth.) Ochyra. This species was described from Issyk Kul Lake vicinity in Kyrgyzstan (Brotherus, 1931). The description indicates a dioicous sexual condition and absence of sporophytes in the type specimen. Later, *S. submontana* was reported also from several localities in Pamir Mts of Tajikistan (Mamatkulov, 1990). Sporophytes were not found as well in this area. This fact did not allow us to use this name for the plants, which were autoicous in most of our collections, and often bearing capsules. However, there was much in common in gametophytic structure between our plants and the description and illustrations of *S. submontana* (Brotherus, 1931; Savicz-Lyubitzkaya & Smirnova, 1970; Mamatkulov, 1990; Kramer, 1980). Among diagnostic characters of this species, erecto-patent spatulate leaves with rounded apices and narrowly recurved margins, long and weakly denticulate hyaline hair-point, weakly scabrous dorsal side of costa, presence of stem central strand and costal hydroids were listed.

In 1970, *S. mongolica* Boros was described from Mongolia. Shortly afterwards it was synonymized with *S. submontana* by Kramer (1980), despite the former species being described as autoicous. This synonymization was accepted by Abramov & Abramova (1983) and

Tsegmed (2001, 2010). Tsegmed (2010) in “Moss flora of Mongolia” describes *S. submontana* as a dioicous species with sporophytes unknown and with rather wide distribution in the country. We have studied a syntype of *S. mongolica* in LE and numerous Mongolian collections in MHA made by M.S. Ignatov during an expedition to Gobi-Altai area in 2001 and identified as *S. submontana*. These specimens were very similar to an “unknown species” from southern Siberia and the Caucasus in gametophytic characters, although the plants from Gobi were smaller and looked damaged with respect to unfavorable growth conditions in the dry area. According to Ignatov *et al.* (2004) this plant is one of the most common in the xeric environments and also commonly produces sporophytes, which naturally not always successfully come to maturity, thus often seen as immature ones. Our study of gametangia distribution revealed a wide variation in plant sexual condition. The most common result of study of a large specimen is that the female, male and autoicous plants occur in the same tuft; more rarely synoicous and sterile plants were found.

Very characteristic are the naked antheridia in *S. submontana*, sitting on stem among paraphyses, without perigonal leaves, contrary to bud-like perigonia of *S. sinensis* and many other species. The latter case, *i.e.*, when bud-like perigonia are developed on a separate very short branch, has been reported by Zander (1993) as the only possible in the description of *Syntrichia*. Thus, *S. submontana* is obviously an exceptional case in the genus.

Numerous collections from Mongolia helped us to understand why *S. submontana* was described as dioicous. Its sexual condition is variable, thus small collection from extreme environments may often have only one sex expressed, if any. The ITS sequence data of the polyoicous Mongolian specimen was identical with mainly autoicous plants from south Siberia and Caucasus.

The holotype of *Syntrichia (Tortula) submontana* has naked perigonia, grouped with paraphyses laterally near shoot apex and subapical innovations. This fact confirms the applicability of this name for plants under question. No female plants were seen in the holotype, although we hesitated to investigate every shoot due to paucity of material in the specimen. However, considering the variation of sex expression in bigger collections of the species, the absence of females both agrees with the original diagnosis and does not contradict the amended circumscription of the present study.

Curiously, *Syntrichia sinensis* has also been described originally as dioicous, likely due to the fact that perigonia are not always found in specimens of this species. They are rather inconspicuous being quite similar to young sterile innovations, albeit found in all sufficiently large collections we studied. The holotype of this species is the collection made in June 1894 by Giraldis from Schaaxi (‘Schen-si’), In-kia-puo (‘Iu-kia-po’ in proto-logue is an obvious misprinting, as it is clear from nu-

merous labels in H, S, FI for other species, and also Chen' text). It has been studied by Chen (1941) but then likely destroyed in Berlin during the 2d World War. Neither holotype, nor isotypes were located by Kramer (1980) and Gallego (2005), who at the same time did not substitute it by neotype. However, as the distinction between *S. submontana* and *S. sinensis* involves a character not described in the original description, thus neotypification of *S. sinensis* is proposed.

Müller (1896) originally described *Barbula* (*Syntrichia*) *sinensis* from one collection, but later, in the second part of the "Bryologia provinciae Schen-si Sinesis" (Müller, 1897, page 254) again labeled *Barbula* (*Syntrichia*) *sinensis* as 'nova species', and cited two more specimens. The second of them, from Lun-san-huo is annotated as a specific form, although without any formal recognition 'forma foliis tenuiter pungentibus', thus the first specimen, from Lao-y-san, collected by Giraldis in March 1896 is the reasonable candidate for the neotype. Fortunately this specimen is present in H-BR. Being in full agreement with the protologue, it is proposed here as the neotype of *S. sinensis*. The plants of the neotype have antheridia surrounded by perichaetial leaves, *i.e.*, having the structure common for the genus *Syntrichia*, except for *S. submontana*. At the same time, this neotype has leaves with a relatively long hair point, which somewhat disagrees with the most common current understanding of this species as one with a short hyaline awn (Savicz-Lyubitskaya & Smirnova, 1970; Kramer, 1980; Gallego, 2005; Mishler, 2007), although Li (2001) described the hair point as 'rather long'.

This problem is complicated also due to the fact, that in addition to '*Barbula* (*Syntrichia*) *sinensis*' Müller (1898) described also two other species, *Barbula* (*Syntrichiae albipilae*) *brachypila* Müll. Hal. and *Barbula* (*Syntrichiae rubripilae*) *erythrotricha* Müll. Hal. from about the same area. Later, P.-C. Chen (1941) in his monograph of East-Asiatic Pottiaceae reduced both of them into synonymy of *Syntrichia alpina* Jur., a European species, which however appeared to be illegitimate, and corresponds to the current understanding of *S. sinensis*. However, in a view of the segregation of *Syntrichia submontana* both taxa were checked, especially *Barbula erythrotricha*, as it has been described as having long hyaline hair-point, the character more characteristic to *S. submontana* than to at least the most common phenotypes of *S. sinensis* in Russia and Europe. Nevertheless, the perigonal structure of the plants, selected as lectotype by Chen (1941), it is not different from the neotype of *S. sinensis*, thus the earlier synonymization is simply confirmed here.

The studied syntype of *Barbula brachypila* has the same perigonal structure, and we are currently inclined to confirm this synonymization too, although the discussion below explains less definite situation in case of this name.

We found that specimens of *S. sinensis* from Russia show variation in hair-point length. Most specimens match the description of Gallego (2005), who estimates its length at 0.1-0.5 mm. At the same time, several specimens possessed leaves with longer hair-points, up to 0.9 mm long in upper leaves. Furthermore, three such specimens, one from Primorsky Territory and two from Altai, formed a separate subclade within *S. sinensis*-clade in the nrITS Bayesian tree (Fig. 1, see also Fig. 4: 11-13). According to the description (Müller, 1998), *B. brachypila* is characterized by costa excurrent in a short awn, whereas awns of *B. sinensis* and *B. erythrotricha* are described as "*foliorum pilo plus minus longo tenui denticulato*". We have studied 3 specimens of *B. sinensis* and 3 specimens of *B. erythrotricha* from H-BR identified by Carl Müller, as well as a specimen of *B. brachypila* cited in protologue from LE. All these specimens of *B. erythrotricha* and *B. sinensis*, as well as other specimens from Schen-si identified by V.F. Brotherus (H-BR) possess awns 0.6-0.8 mm long, while they are shorter, up to 0.4 mm, in the specimen of *S. brachypila* (see Fig. 5). In other essential characters, *i.e.*, peristome basal membrane height (3-6 cells high) and autoicous sexual condition with bud-like perigonia, all studied specimens are uniform and fit well the concept of *S. sinensis* accepted by most authors.

The molecular data suggest a slight differentiation between long- and short-awned phenotypes, but this problem cannot be solved with the present sampling and limited study of Chinese material. Therefore we are accepting *S. sinensis* in a broad sense at the moment, in agreement with Chen (1941), Kramer (1980), Gallego (2005), Li *et al.* (2001), pending the solution in a specifically addressed study.

Although not specifically addressed to other groups of *Syntrichia*, the present analysis highlights a need of additional study of *S. laevipila*-complex. Recent publications of Gallego *et al.* (2004, 2005) demonstrated a continuous variation of morphological and molecular characters within *S. laevipila* s.l., including *S. pagorum*, which was recognized by, *e.g.*, Crum & Anderson (1981) and Stone (1971). Our molecular phylogenetic analysis however found two maximally supported clades that are hundred-percent congruent with the sexual condition, a character often used as a main one for differentiation of *S. laevipila* and *S. pagorum*. The present limited sampling precludes a convincing conclusion, but calls attention to further studies.

Tree topology suggests also a need of more narrow species distinction in *S. caninervis*-group, as *S. caninervis* var. *astrakhanica*, a taxon described only recently (Ignatov *et al.*, 2002), constitutes another lineage, not closely related to var. *caninervis* (Fig. 1). It seems that the former is no less widespread in Russia than the latter. The re-evaluation of the type of *S. caninervis*, described from Tibet in China, will be essential, as both taxa occur in nearby Mongolia.

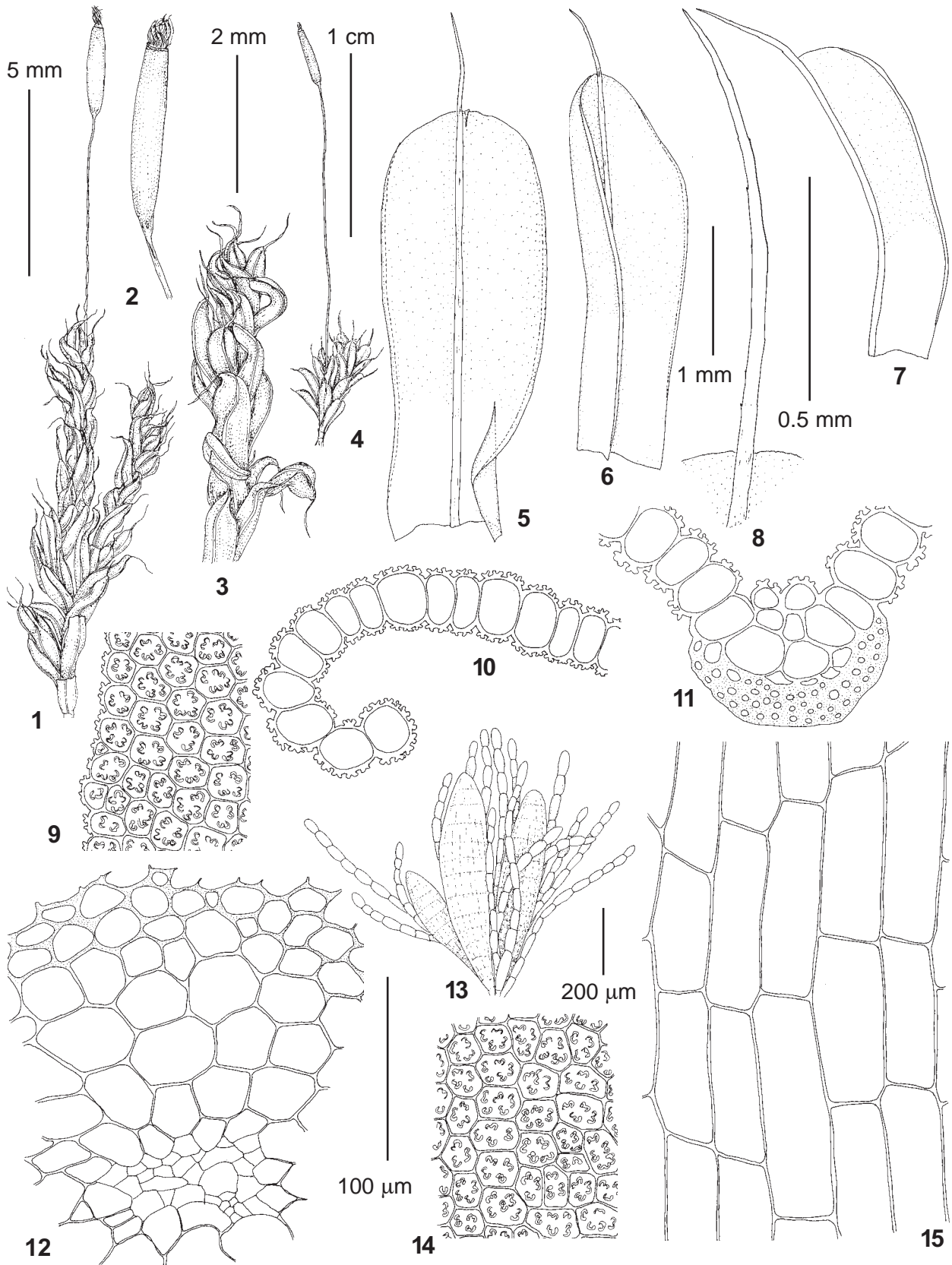


Fig. 2. *Syntrichia submontana* (Broth.) Ochyra (from: Russia, Zabaikalsky Territory, Sokhondinsky Biosphere Reserve, Agutsa River, Afonina A3510, LE): 1, 3 – habit, dry; 2 – capsule; 4 – habit, wet; 5, 7 – leaves; 6 – perichaetial leaf; 8 – leaf hair-point; 9 – cells at leaf margin in distal part; 10 – leaf transverse section at margin; 11 – transverse section of costa; 12 – stem transverse section; 13 – antheridia and paraphyses without perigonal leaves; 14 – median laminal cells; 15 – basal laminal cells. Scale bars: 1 cm for 4; 5 mm for 1; 2 mm for 2, 3; 1 mm for 5-7; 0.5 mm for 8; 200 μ m for 13; 100 μ m for 9-12, 14-15.

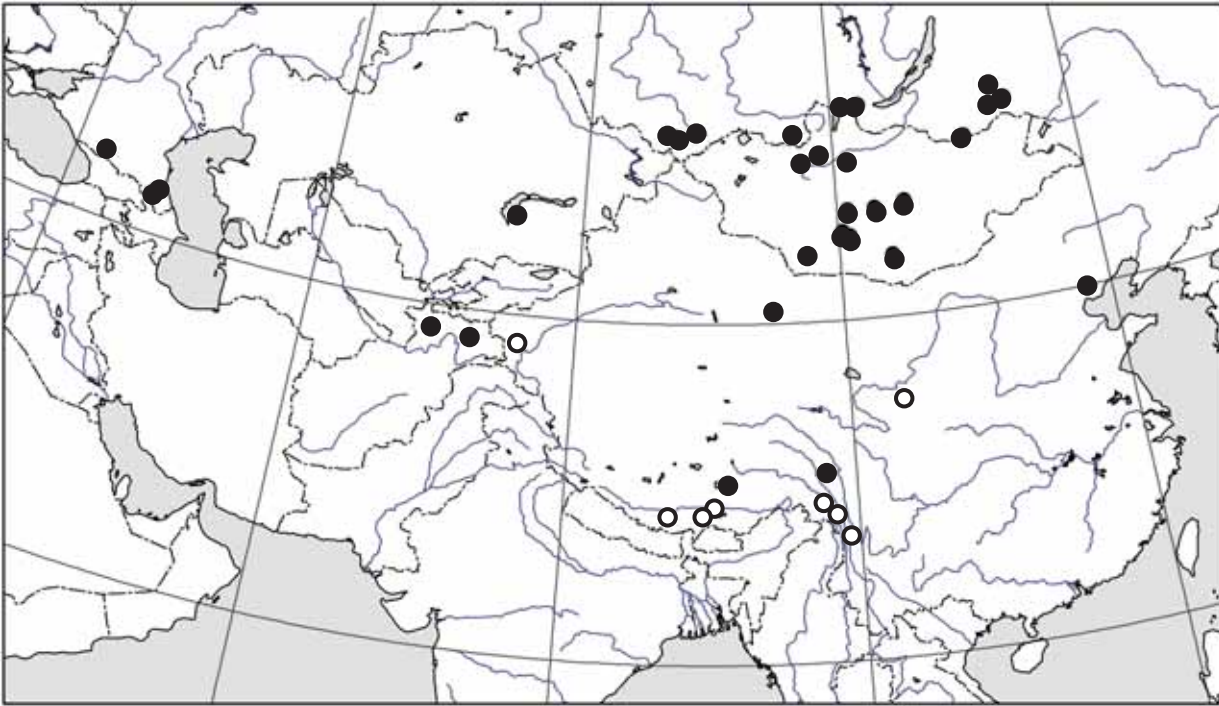


Fig. 3. Distribution of *Syntrichia submontana* (Broth.) Ochyra, based on specimens studied (solid circles) and literature data for *S. longimucronata* from Li *et al.* 2001 (open circles).

TAXONOMIC TREATMENT

Syntrichia submontana (Broth.) Ochyra, *Fragm. Florist. Geobot.* 37: 213. 1992. — *Tortula submontana* Broth., *Trudy Bot. Sada Akad. Nauk S.S.S.R.* 42(2): 168. 1931. Holotype: Turkestan. Ur-Tokai – Kutemaldy. 1896 7/6 leg. V.F. Brotherus (H 3148373).

Syntrichia mongolica Boros, *Trans. Brit. Bryol. Soc.* 6: 70. f. 1–2. 1970. Type: Mongolia or. In rupestribus silicat. prope Baronurt. Alt. ca. 1000 m. 23.VIII.1967. R. Moldvai (isotype in LE!). Synonymized by Kramer (1980).

?*Syntrichia longimucronata* (X.J. Li) R.H. Zander, *Bull. Buffalo Soc. Nat. Sci.* 32: 269. 1993. — *Tortula longimucronata* X.J. Li, *Acta Bot. Yunnan.* 3: 107. f. 4. 1981. Type: 'China, Xizang, Jia-li Co., D.-D. Tao 5313a' (holotype in HKAS, not seen).

Figs. 2-3, 5: 2-3, 8

Plants medium-sized, in rather loose turfs, dull green, yellowish- or brownish-green in upper part, reddish brown below. Stem 0.5-2.0 mm, erect, simple or irregularly branched, loosely tomentose throughout, with weak central strand, thickened cortical cells in 2-3 layers and weakly differentiated hyalodermis. Leaves contorted or twisted when dry, spreading to weakly recurved when moist, oblong-elliptic to oblong-lingulate, 2.0-3.5×0.6-1.2 mm, not constricted at midleaf, weakly keeled in upper part, sometimes with longitudinal folds, rounded at apex; margins recurved from above leaf base to near apex, unbordered, smooth or crenulate distally due to bulging cells; costa strong, 65-90 μ m wide at base, weakly tapering distally, reddish-brown, smooth on dorsal side, excurrent in an awn 0.5-1.5 mm long, weakly and distant-

ly denticulate, reddish-brown at base and hyaline at most of its length or, occasionally, yellowish or brownish at most length except small apical portion; costa in transverse section with one layer of guide cells, two layers of smaller adaxial cells, ventral surface papillose, abaxial stereid band of 3(-4) layers, with hydroids; leaf lamina unistratose; upper and median laminal cells rounded-quadrate or hexagonal, thin-walled, 12.5-20×(10-)12-20 μ m, papillose, with 3-6 papillae per cell, papillae bifurcate, not pedicellate, 2.5 μ m high; basal laminal cells forming a clearly differentiated hyaline area, rectangular, smooth, thin-walled, sometimes weakly collenchymatous, basal juxtacostal cells 50-115×17.5-35 μ m, basal marginal cells shorter and narrower. Polyicous: male, female, autoicous and, more rarely, synoicous plants are occasionally found in same or different collections. Perichaetial leaves similar to stem leaves, but sometimes inner perichaetial leaves smaller and narrower than stem leaves. In autoicous and male plants, antheridia and paraphyses in clusters just below perichaetium or below shoot apex, perigonal leaves lacking. Seta erect, reddish brown, 1.0-2.0 cm long, spirally twisted to the right distally. Urn reddish brown, 2.5-3.5×0.7-0.8 mm, cylindrical, straight or slightly curved; operculum long conical, 1.2-1.4 mm long; peristome 0.9-1.4 mm high, with basal membrane of 3-6 cell rows. Spores 12-15 μ m, finely papillose.

Taxonomy. By studying the isotype of *Syntrichia mongolica*, we confirm Kramer (1980)' conclusion on the identity of this species with *S. submontana*. Although we did not see type material of *S. longimucronata*, we presume its identity with *S. submontana* basing on: (1)

coincidence with description and illustrations, (2) same ITS2 sequence and the presence of naked antheridia in specimen from the area near the type locality.

Variation. The most variable character of *S. submontana* is sexual condition of plants. Collections from southern Siberia and the Caucasus, as well as from China and some areas of Mongolia, are autoicous and bear mature sporophytes. However, some plants with only female gametangia are also found in the same specimens. At the same time, Mongolian samples from harsh environments are mostly polyoicous, with a mixture of female, male, autoicous and, more rarely, synoicous plants in the same specimen. According to the description of *S. submontana* (Brotherus, 1931; Mamatkulov, 1990), specimens from Middle Asia were only dioicous.

There is some variation in hair-point color: in most specimens from Russia and Mongolia hair-points are hyaline, with a small basal portion brownish, while in a specimen from Xizang and a few ones from Transbaikalia hair-points are brownish-colored on most of their length, with only small distal portion being hyaline.

We did not observe the leaf marginal border in any studied specimen, but, as its presence is reported for *S. longimucronata* (Li, 1981; Li *et al.*, 2001), this character may show variation.

Differentiation. Collections from Russia which we attribute now to *Syntrichia submontana* were previously mostly identified as *S. sinensis*. They are similar to the latter species in size of plants, leaf shape and size, presence of stem central strand and hydroids in costa, and autoicous sexual condition. At the same time, plants with mature sporophytes could be easily recognized even under stereomicroscope: they differ in the height of basal membrane of peristome (very low, 1-2 cell rows in *S. submontana* vs. higher, 3-6 cell rows in *S. sinensis*, see Fig. 5: 1-2) and, in most cases, in the hair-point length (0.5-1.5 mm in *S. submontana* vs. 0.1-0.3 mm in *S. sinensis*). Leaf margins are more strongly recurved almost to the apex in *S. submontana*, whereas they are less recurved in proximal 1/2-2/3 of leaf length in *S. sinensis*. There is also a stable difference in structure details of male inflorescences. In *S. submontana*, perigonial leaves are lacking and antheridia with paraphyses form a compact group just below the perichaetium (Fig. 5: 3), more rarely at some distance below. In *S. sinensis*, perigonia are bud-like, covered by small, obtuse perigonial leaves (Fig. 5: 4), usually situated at some distance below perichaetia. If the plants of *S. submontana* are dioicous, male inflorescences are also naked, lateral or subterminal. The most difficult case is if sporophytes are lacking or immature, perigonia are not found and awns exceed 0.5 mm: such plants can be attributed both to *S. submontana* and to long-awned *S. sinensis*. In this case, leaf margin recurvation (longer in *S. submontana*) can be helpful, but such plants cannot be identified with certainty.

Ecology. The species grows in similar habitats to *S.*

sinensis, but generally in more xeric areas. In Transbaikalia, it prefers dry cliffs and rock outcrops at slope bases, boulders and rocks in open birch forests, more rarely it grows on trunk bases of birch and elm trees and once it was found on woody roof of a shed. In Altai it was collected on dry rocks and cliff crevices, both open and forested, once it was found on soil along a road and at base of birch trunk. In Dagestan it grows exclusively on dry calcareous rocks and cliffs, contrary to *S. sinensis* which is often found also on trees in this area. Elevations range was documented between 600-1200 m in Transbaikalia, 450-2100 m in Altai and 1700-2300 in the Caucasus.

Distribution. The distribution of *Syntrichia submontana* includes mountain areas of China (Xizang, Yunnan, Shaanxi, Sichuan, Gansu, Hebei and Xinjiang Provinces), Mongolia (almost throughout the country), Kyrgyzstan and Tajikistan. In Asiatic Russia, the species is common in southern part of Zabaikalsky Territory and was also found in western part of Irkutsk Province and Buryatia, in Tyva and in several localities in Altai Republic, mostly in rather xeric areas along tributaries of Chuya River and Chulyshman Rivers. It is also common at places in eastern Caucasus (Dagestan) and found once in Karachaevo-Cherkessian Republic.

Specimens examined: **CHINA:** Kansu occidentalis, ad fluv. Bardun-fischii, 11.V.1886, *Potantin s.n.* (LE); [Hebei Prov.], Weichang, X. 1899, *Palibin s.n.* (LE); prov. Kansu occ., ad. fl. Solomo vallis fl. Bardun, 16.V.1886, *Polunin s.n.* (LE); Prov. Szechuan, Mt. Omei, Ching-ding, ca 3000 m. ad rupes regions subalpinae, subskiophila, Photophila. c.sp., VIII. 1942, *Chen s.n.* (LE); Xizang (31°18.5'N, 97°58.54'E), 3.VIII.2001, *Miwa & Y. Yia 3825* (PE). **MONGOLIA:** Kosogol Lake, 2.VII.1902, *Elenkin s.n.* (LE); Hangai, 20.VII.1972, *Tsogt & Kukkk 32* (LE); Selenginsky aymag, Buteleeliyn nuruu Ridge, 25.VIII.1974, *Tsegmed 2171* (LE); Ubsu-Nurski aymag, Turgen Ridge, 7.VIII.1973, *Tsegmed 380* (LE); Arkhangai Aimag, Sumein-am Mt., 9.VII.1970, *Tsogt s.n.* (MHA); Bayankhongor Aimag, 43 km W of Bayan-Undur somon, 27.VIII.1972, *Tsogt & Kukkk 393* (MHA); Bayan-Hongor Province, between Ikh-Bogd and Baga-Bogd Mts, Ignatov 01-652 (MHA); Khangai Mts, Egiin-Daba pass, Chulutu-gol River, 5.VIII.1973, *Golubkova & Tsogt s.n.* (MHA); Khangai, 7 km N of Tarialei somon, 22.VII.1972, *Tsogt & Kukkk 32* (MHA); Bulgan Aimag, Khutag somon, Altaid River mouth, 7.VIII.1974, *Tsegmed 1768* (MHA); Omnogovi Province, Gurvansaikhan National Park, *Ignatov 01-658, 01-661, 01-654* (MHA); Ovorhangai Province, 10 km N of Arvanheir, Ongi River, *Ignatov 01-651, 01-656* (MHA); Dungovi Province, Aerdaenaedalai somon, *Ignatov 01-660* (MHA).

ASIATIC RUSSIA: Irkutsk Province: Tunkinsky District, Sayan Mts, Nilova pustyn', 30.V.1902, *Elenkin s.n.* (LE); western shore of Baikal Lake, Bolshie Koty, 11.IX.1981, *Filin s.n.* (MW); Slyudyanka District, Kultuk, *Kosovich-Anderson B-741* (MHA). **Republic of Buryatia:** East Sayan Mts, upper Oka River, Dodo-Zahna village, 2.VII.2008 (with *S. sinensis*), *Afonina 00708* (LE); Arshan Settlement (51°46'N, 102°27'E), 1100 m alt., 15.VIII.1993, *Shevyreva & Konovalova s.n.* (MHA). **Zabaikalsky Territory** (selected specimens): Aksha District, Tsagan-Olui Settlement, 12.X.1909, *Mikhno s.n.* (LE); near Aginskoe Settlement, left bank of Aga River (51°07'N, 114°40'E), 15.VII.2006, *Afonina 4706* (LE); right bank of Ingoda River 5

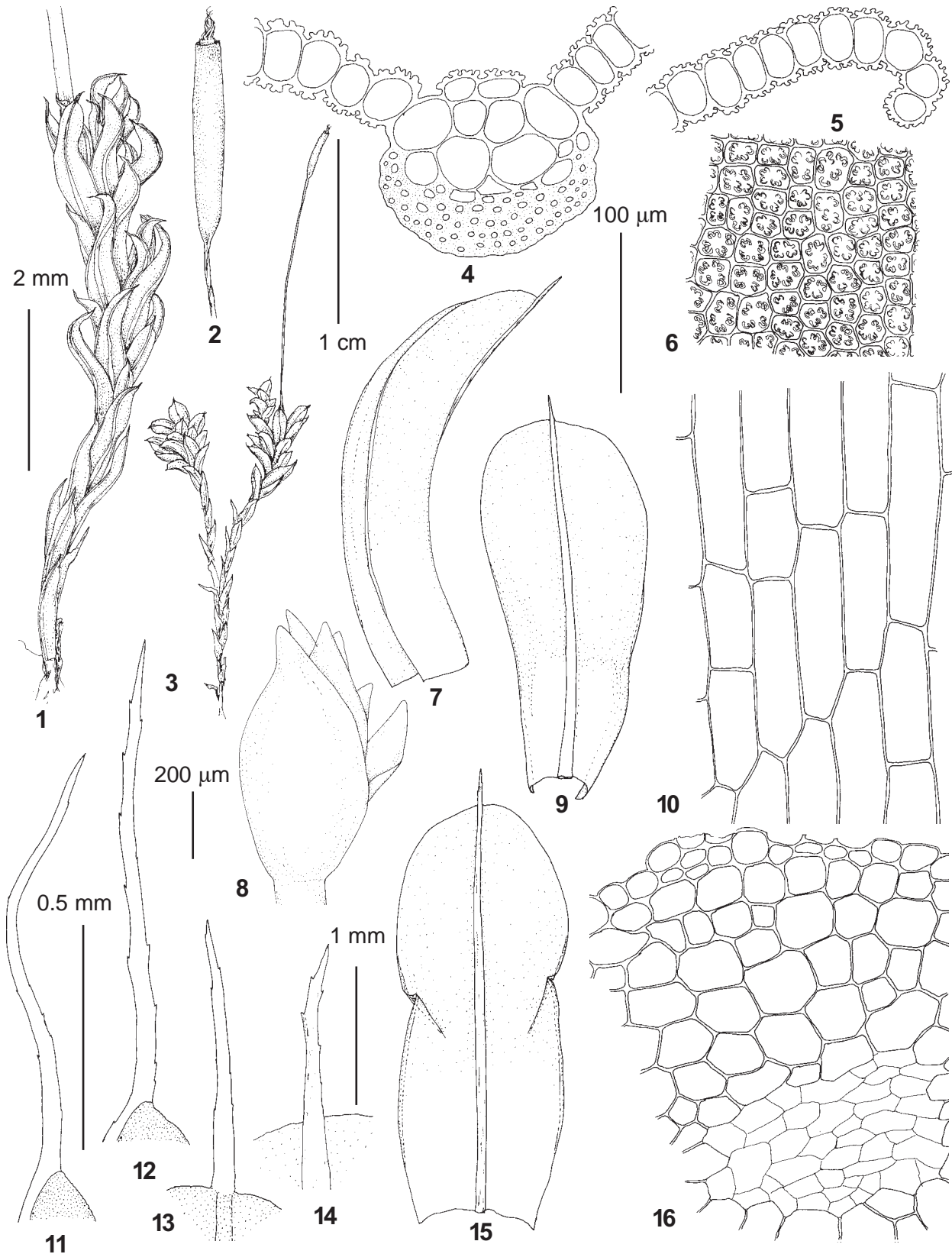


Fig. 4. *Syntrichia sinensis* (Müll. Hal.) Ochyra (1-10, 14-16 – from: Russia, Dagestan, Gunib, Ignatov & Ignatova #09-255, MW; 11 – from: Russia, Altai, Chermal, Ignatov & Ignatova 34/109, MHA; 12 – from: Russia, Primorsky Territory, Chandolaz, Ignatov et al. 06-2825 MHA; 13 – from: Russia, Altai Republic, Teletzkoe Lake, 3.VI.1989, Ignatov s.n. (MHA). 1 – habit, dry; 2 – capsule; 3 – habit, wet; 4 – transverse section of costa; 5 – leaf transverse section at margin; 6 – median laminal cells; 7, 9, 15 – leaves; 8 – bud-like perigonium; 10 – basal laminal cells; 11-14 – leaf hair-points; 16 – stem transverse section. Scale bars: 1 cm for 3; 2 mm for 1-2; 1 mm for 7, 9, 15; 0.5 mm for 11-14; 200 µm for 8; 100 µm for 4-6, 10, 14.

km S of Darasun railway station (51°52'N, 113°43'E), 658 m alt., on rocks, 14.VII.2007, *Afonina 05107* (LE); National Park "Alhanay" (50°50'N, 113°22'E), 1048 m alt., 24.VII.2007, *Afonina 08307* (LE); Sokhondinsky Reserve, Enda River (49°26'39"N, 110°50'55"E), 1162 m alt., 24.VIII.2011, *Afonina 5911* (LE); same place, 24.VIII.2011, *Afonina 6011* (LE); Enda River, Khukhe-Baytsa Creek (49°28'17"N, 110°51'58"E), 1214 m alt., 27.VIII.2011, *Afonina 7511* (LE); **Tyva Republic**: Erzinsky District, Tara-Khol' Lake, 13.IX.2003, Korobkov s.n. (LE). **Altai Republic**: Argut canyon, 23.VII.1903, *Krylov s.n.* (LE); Ongudai District, Malyj Yaloman Creek (50°28'N, 86°33'E), 900 m alt., 31.VII.1991, *Ignatov & Ignatova 25/119* (MHA); Chulyshman River valley, Yazula (50°38'N, 88°58'E), 1700 m alt., 25.VI.1989, *Ignatov 0/1547* (MHA); Ongudai District, Chuya River, Belyj Bom, Sadaklar Creek (50°22'10"N, 87°02'20"E), 920 m alt., *Seregin & Seregina M-2222* (MW); Kosh-Agach District, Severo-Chuisky Mt. Range, Chibit, Oroj Creek (50°15'00"N, 87°29'30"E), 2060 m alt., *Seregin & Seregina M-2164* (MW). **CAUCASUS**: **Dagestan**: Charoda District, Gunukh (42°13'N, 46°41'E), 2200 m alt., *Abakarova & Ignatov 11-2012* (MHA); Charoda District, Uruk-Sota (42°18'N, 46°46'E), 2300 m alt., *Ignatov & Abakarova 11-7* (MHA); Gunib District, Gunib (42°25'N, 46°55'E), 1760 m alt., *Ignatov & Ignatova 09-568, 09-542* (MHA). **Karachaevo-Cherkessian Republic**, Gudgora, (43°43'N, 42°19'E), 2200 m alt., on soil in cracks of rock, 14.VII.2010, *Ukrainskaya s.n.* (LE).

Syntrichia sinensis (Müll. Hal.) Ochyra, Fragm. Florist. Geobot. 37: 213. 1992. – *Barbula sinensis* Müll. Hal., Nuovo Giorn. Bot. Ital., n. s. 3: 100. 1896. – *Tortula sinensis* (Müll. Hal.) Broth., Nuovo Giorn. Bot. Ital. 13: 279. 1906. Neotype: China interior, Provincia Shen-si sept., in monte Lao-y-san, Mart. 1896, legit Rev. Jos. Giraldis, determ. Prof. C. Müller sub n. 1382 (H-BR 4205016).

Barbula alpina Bruch & Schimp., Bryol. Eur. 2: 101. 1842, nom. illeg. [non *Barbula alpina* Steud., Nomencl. Bot. 2: 71. 1824.]. – *Tortula alpina* (Bruch & Schimp.) Bruch., Musci Frond. Exsic.: 163. 1843. – *Syntrichia alpina* (Bruch. & Schimp.) Jur., Laubm.-Fl. Oesterr.-Ung.: 1939. 1882.

Barbula brachypila Müll. Hal., Nuovo Giorn. Bot. Ital., n.s. 5: 181. 1898.

Barbula erythrotricha Müll. Hal., Nuovo Giorn. Bot. Ital., n.s. 5: 181. 1898. Lectotype (designated by Chen, 1940): China interior, Provincia Shen-si sept., in monte Lao-y-huo prope Schan-gen-ze, 12 Mart. 1897, legit Rev. Jos. Giraldis, determ. Prof. C. Müller sub n. 1800 (H-BR 4205010).

Figs.4, 5: 1, 4-7

Plants small to medium-sized, in dense or loose tufts, dark green above, reddish-brown below. Stem 4-15 mm, erect, irregularly branched, weakly tomentose, with central strand, sclerodermis of 1-2 layers of cells with slightly thickened brownish walls and weakly developed hyalodermis. Leaves densely arranged, appressed and spirally twisted when dry, generally spreading or patent when moist, lingulate-spathulate, not or weakly constricted at midleaf, 2.0-3.5×0.7-1.5 mm, apex rounded; margins en-

tire, plane in distal part and weakly recurved at proximal 1/2(-2/3) or only at mid-leaf; costa strong, reddish-brown, 60-90 µm wide at base, weakly tapering distally, smooth on dorsal side, ending in a short or, occasionally, moderately long, 0.1-0.5(-0.8) mm, weakly denticulate reddish-brown awn, strongly convex dorsally, in transverse section with one layer of guide cells, two layers of smaller adaxial cells, ventral surface papillose, abaxial stereid band of 3-4 cell layers, with hydroids; lamina unistratose, upper and mid-lamina cells round-quadrate or hexagonal, 12.5-20×(10-)12-20 µm, with 6-8(-12) papillae per cell, bifurcate, not pedicellate, 2.5 µm high; basal juxtacostal cells rectangular, 50-115×17.5-35 µm, thin-walled, sometimes weakly colenchymatose, forming a clearly differentiated hyaline area, basal marginal cells shorter and narrower, chlorophyllose. Autoicous. Inner perichaetial leaves smaller and narrower than stem leaves (ca. 1.5×0.6 mm). Antheridia bud-like, perigonal leaves with blunt apices, perigonia situated at some distance below perichaetium. Seta erect, reddish brown, 1-1.5 cm long, spirally twisted. Capsule reddish brown, 2.5-3.5 mm, cylindrical, straight or slightly curved; operculum long conical, 1.2-1.4 mm long; basal membrane of 3-6 rows of cells, 0.09-0.16(-0.2) mm high. Spores 12-18 µm, finely papillose.

Variability. *Syntrichia sinensis* possesses a considerable variability of leaf hair-point (see also discussion on p. 16). In all specimens from Europe available for our study length of hair-points do not exceed 0.5 mm in perichaetial leaves and they are usually shorter, 0.1-0.3 mm, in stem leaves. It is in an agreement with descriptions by European authors, e.g., Gallego, 2005). At the same time, in specimens from China hair-points are often longer, up to 0.8 mm. In Russia, specimens with short hair-points are much more frequent; only few long-pointed collections were made in the Russian Far East, Khakassia and Altai (in the latter mostly at places with milder and wetter climate).

Differentiation. Differences from *S. submontana* are discussed under the latter species. A combination of short awns (to 0.3 mm in most cases), mostly reddish-brown, and comparatively low basal membrane of peristome (consisting of 3-6 rows of cells) readily separates it from fruiting *S. laevipila* s. str., which is characterized by longer (0.5-1.0 mm) and mostly hyaline awns and higher basal membrane (10-20 rows of cells). However, it is more difficult to separate sterile plants of *S. sinensis* from dioicous and always lacking sporophytes *S. pagorum*; most helpful characters are recurved leaf margins to 2/3 the leaf length in *S. sinensis* vs. mostly plane or only weakly recurved at mid-leaf margins of *S. pagorum*, as well as absence of brood leaves in *S. sinensis* vs. their frequent occurrence in *S. pagorum*, formed in abundance in axils of upper leaves and on the top of shoot.

Ecology. The species occurs in mesic to rather xeric environments. In Siberia, it largely prefers rocks, espe-

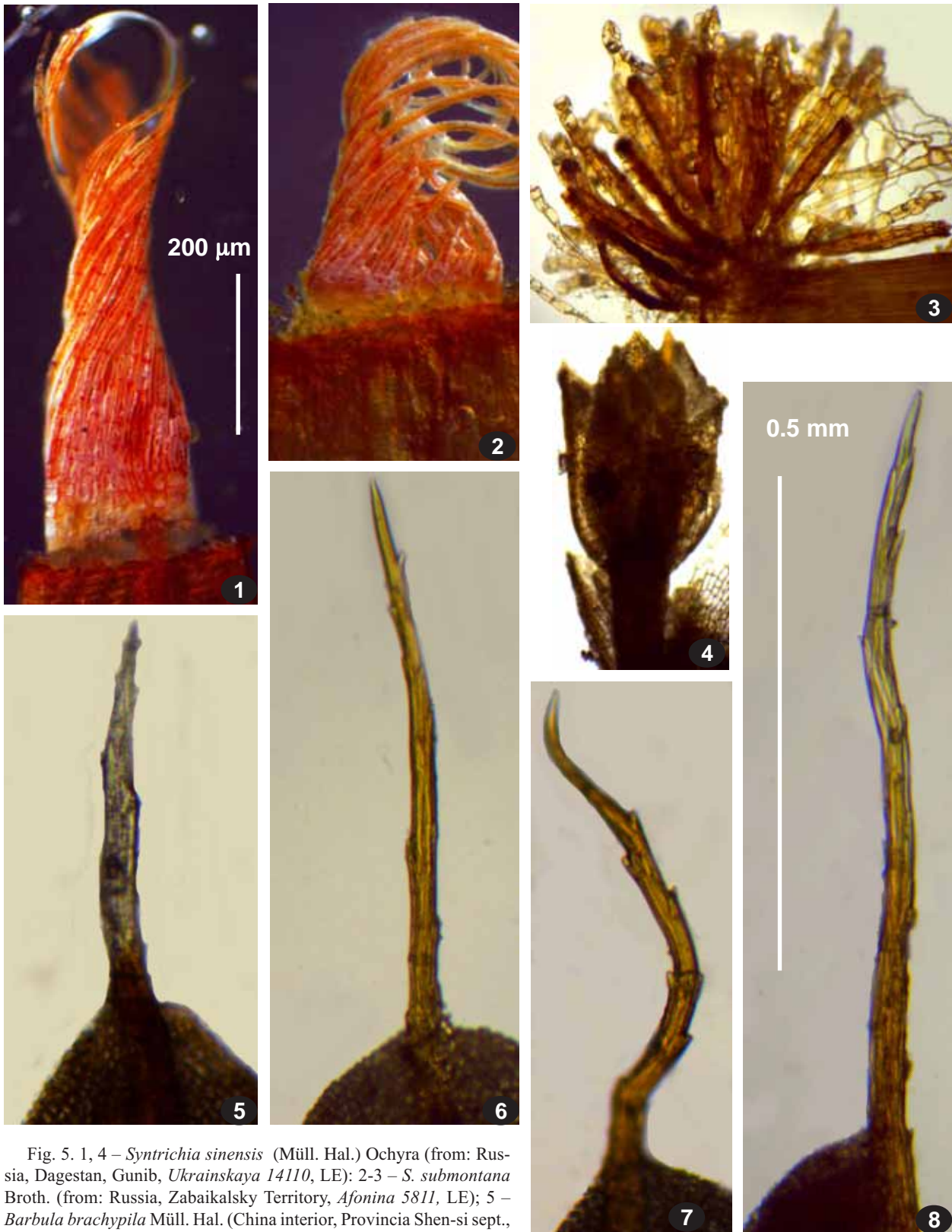


Fig. 5. 1, 4 – *Syntrichia sinensis* (Müll. Hal.) Ochyra (from: Russia, Dagestan, Gunib, *Ukrainskaya 14110*, LE); 2-3 – *S. submontana* Broth. (from: Russia, Zabaikalsky Territory, *Afonina 5811*, LE); 5 – *Barbula brachypila* Müll. Hal. (China interior, Provincia Shen-si sept., prope In-Kia-po, 23 Aug. 1846, legit Rev. Jos. Giralddi, determ. Prof. C. Müller sub n. 1804, LE); 6 – neotype of *Barbula sinensis* Müll. Hal. (China interior, Provincia Shen-si sept., in monte Lao-y-san, Mart. 1896, legit Rev. Jos. Giralddi, determ. Prof. C. Müller sub n. 1382, H-BR 4205016); 7 – lectotype of *Barbula erythrotricha* Müll. Hal. (China interior, Provincia Shen-si sept., in monte Lao-y-huo prope Schan-gen-ze, 12 Mart. 1897, legit Rev. Jos. Giralddi, determ. Prof. C. Müller sub n. 1800, H-BR 4205010); 8 – holotype of *Tortula submontana* Broth. (Turkestan, Or-Tokai – Kutemaldu, 7.VI.1898 leg. & det. V.F. Brotherus, H 3148373). 1-2 – peristomes; 3-4 – perigonia; 5-8 – distal portions of leaf with hair-point. Scale bars: 0.5 mm for 5-8; 200 μ m for 1-4.

cially rock outcrops in open forests, more rarely in open places. It was collected mostly at middle elevations (500-900 m in Zabaikalsky Territory, to 1400 m in Buryatia, 400-1000 m in Altai Mts, and 1100-2200 m in the Caucasus). In Manhan Mountains in Inner Mongolia, China, however, *S. sinensis* is a common epiphyte and in Altai Mts there are also collections from *Salix*, *Populus*, *Sorbus*, and *Betula*. Even more common this species is on trees in Dagestan: on *Juglans*, *Pyrus*, *Prunus*, *Salix* and *Carpinus*.

Distribution. *Syntrichia sinensis* has its main distribution in Central and Northern Asia, including China (Li *et al.*, 2001), Japan (Noguchi & Iwatsuki, 1988), Mongolia (Tsegmed, 2010), Kazakhstan, Turkmenistan, Tajikistan and Kyrgyzstan (Mamatkulov *et al.*, 1998; Ignatov, Afonina, Ignatova *et al.*, 2006), with its northern limit in continental part of the southern Russian Far East and southern Siberia from Transbaikalia to Altai Republic, being not rare in Transbaikalia and Altai. In the Caucasus, *S. sinensis* was reported from Georgia (Chikovani & Svanidze, 2004), Armenia (Manakyan, 1995), and Azerbaijan (Lyubarskaya, 1986). In Europe it is known from Germany (Düll & Meinunger, 1989), Austria (Köckinger *et al.*, 2008), Poland (Ochyra *et al.*, 2003) and Mediterranean countries (Cyprus, Italy, France, NE Spain, Slovenia, Tunisia and Turkey: Gallego, 2005; Pavletić, 1955; Ros *et al.*, 2013). *Syntrichia sinensis* also occurs in a restricted area in North America, Rocky Mountains in Colorado and New Mexico, where it was only recently discovered (Mishler, 2007).

Selected specimens examined: Specimens collected by J. Giraldi in Schen-si Province, China: sub *Barbula sinensis* Müll. Hal.: in monte Lao-y-san Mart 1896, det. C. Müller 1382 (H-BR 4205016); in monte Fui-Kio-san, 18 Oct. 1896, det. C. Müller 1805 (H-BR 4205015); in monte Kuan-tou-san, 5 Nov. 1896, det. C. Müller 1810 (H-BR 4205019); in monte Tui-Kio-san, 20 Oct. 1896, det. Brotherus (H-BR 4205017); in monte Tui-Kio-san, 7 Sept. 1896, det. Brotherus (H-BR 4205021); in monte Tui-Kio-san, 19 Oct. 1896, det. Brotherus (H-BR 4205022); in monte Tui-Kio-san, 17 Sept. 1896, coll. det. Brotherus (H-BR 4205024); sub *Barbula erythrotricha* Müll. Hal.: Lao-y-huo prope Schan-gen-ze, 12 Mart 1897, det. C. Müller 1800 (H-BR 4205010); in loco dicto Zu-lu, 27. Okt. 1896, det. C. Müller 1803 (H-BR 4205012, FI); in loco non notato, Sept 1896, det. C. Müller 1802 (H-Br 4205011, FI); prope In-Kia-po, 25 Aug 1896, det. Brotherus (H-Br 4205001); in monte Kuan-tou-san, Oct. 1897, det. Brotherus (H-Br 4205014); in monte Kan-y-san (calena Sao-y-san), 2 May 1899, det. Brotherus (H-Br 4205020); prope In-Kia-po, 16 Oct. 1897, det. Brotherus (H-Br 4205002, FI); Zu-lu, 13 Oct. 1898, det. Brotherus (H-Br 4205003, FI); Sao-y-san, 1897, det. Brotherus (H-Br 4205000); in monte Miao-Wang-san, Jul. 1899, det. Brotherus (H-Br 4205005); Han-sun-fu, Oct. 1899, det. Brotherus (H-Br 4205006); Han-sun-fu, Sept. 1898, det. Brotherus (H-Br 4205007, FI); prope In-Kia-po, 27 Mart 1896, det. Brotherus (H-Br 4205008, FI); prope In-Kia-po, 22 Oct 1897, det. Brotherus (H-Br 4205009, FI); sub *Barbula brachypila* Müll. Hal.: prope In-Kia-po, 23 Aug. 1896, det. C. Müller 1804 (LE).

CHINA: Inner Mongolia: NE of Huhhot, Yingshan Mountains, Manhan Mt., *Ignatov 08-510* (MW). **MONGOLIA:** Khubsugul aimag, RENCHINKHUMBE somon, Arasain gol River, Ulaankhal Mt., *Enkhzhargal 1753* (MHA); Khubsugul aimag, Tsagaan nuur somon, Darkhat depression, *Enkhzhargal 1200* (MHA).

ASIATIC RUSSIA: Altai Republic: Teletskoe Lake, 3.VI.1989, *Ignatov 87* (LE, MHA); Chulyshman River valley 8-10 km upstream Chulcha River mouth, *Ignatov & Ignatova 12-460* (MW); Chulcha River valley, *Ignatov 9/20* (MHA); Ongudai District, Malyj Yaloman, 4.VIII.2000, *Ignatova s.n.* (MW); Ongudai District, Chuya River, Belyj Bom, Sadaklar Creek, *Seregin & Seregina M-2228* (MHA); Katun River valley 2 km upstream Bijka Creek, *Ignatov & Ignatova 34/54* (MHA); Shebalino District, Katun River valley 10 km upstream Chemal, *Ignatov & Ignatova 34/118* (MHA); Shebalino District, Katun River valley near Ust-Sema, *Ignatov & Ignatova 24/52* (MHA). **Khakassia:** Shirinsk District, Efremenko Settlement, 6.VI.1970, *Vasil'ev s.n.* (LE). **Irkutsk Province:** western shore of Baikal Lake, Bol'shie Koty, 11.IX.1981, *Filin s.n.* (MW). **Buryatia:** Kyahta District, vicinity of Chikoy Settlement, 2.VI.1985, *Bardunov s.n.* (IRK, LE); East Sayan Mts, upper of Oka River, Dodo-Zhahna village, 2.VII.2008 (with *S. longimucronata*), *Afonina #0708* (LE). **Zabaikal'sky Territory:** Akscha District, Bukukun Settlement, 2.III.1910, *Mikhno s.n.* (LE); Gazimurovsky Zavod, limestone outcrops, 23.VIII.1963, *Bardunov s.n.* (IRK, LE); Nerchinsky Zavod District, Serebryanka Creek, 1.IX.1963, *Bardunov s.n.* (IRK, LE); Nerchinsky Zavod, 7.VIII.1989, *Bardunov s.n.* (IRK, LE); Duldurga District, National park "Alkhanay", 8.VII.2006, *Afonina # 1606* (LE); Nizhny Tsasuchei, rocks along bank of Onon River, 18.VII.2006, *Afonina 5306* (LE); Kyra District, 8 km NW of Mangut Settlement, 25.VII.2006, *Afonina 7306* (LE); right bank of Ingoda River 5 km S of Darasun railway station (with *S. longimucronata*), 14.VII.2007, *Afonina 05107* (LE) Kyra District, Sokhondinsky Reserve (with *S. longimucronata*), 24.VIII.2011, *Afonina 6011* (LE); Sretensk District, Kyrenga River, 19.VII.2012, *Afonina 1812* (LE); Gazimuro-Zavodsky District, circa 12 km SW of Batakan Settlement, 23.VII.2012, *Afonina 3512* (LE); Kalar District, right bank of Vitim River near hassing point "Vitim River", 29.VI. 20013, *Afonina 0113* (LE). **Amurskaya Province:** Zeisky Nature Reserve, Tukuringra Mt. Range, *Dudov & Kotel'nikova 2013_Br_0341* (MW). **Primorsky Territory:** Suchuan River Basin, Ekaterinovka Settlement, 4.IX.1913, *Komarov s.n.* (LE); Chernigovsk District, Lunza Settlement, 3.X.1934, *Lazarenko s.n.* (LE); Partizansk District, Lozovyy Range, Chandolaz Mt., *Ignatov et al. 06-2778* (MW); Lozo District, Gavrilov Klyuch, *Ignatov 07-73* (MW); Chuguevka District, Izvilinka River 5 km downstream Berezhnyaki, *Ignatov 07-500* (MHA). **CAUCASUS: Adygeya:** Malaya Laba, Pastbischnyi Range, 27.VIII.1945, *Karpov s.n.* (LE); **Dagestan:** Gunib, 25.V.2009, *Ukrainskaya 14286* (LE); same place, surroundings of Mountain botanical garden, *Ignatov & Ignatova 09-680, 09-582, 09-213, 09-255* (MW); Gunib District, Keger, *Ignatov & Abakarova 11-153* (MW); Charoda District, Gunukh, *Ignatov & Abakarova 11-4, 11-159* (MW); Charoda District, Uruk-Sota, *Ignatov & Abakarova 11-334* (MHA); Tsudakhar, Sana Creek, *Ignatov & Abakarova 11-385* (MHA). **Kabardino-Balkaria:** Cherek-Balkarsky River valley, Verkhnyaya Balkaria, *Ignatov et al. 05-1862* (MW); Cherek-Bezengiysky, 3 km upstream Bezengi, 3.VIII.2004, *Ignatov et al. s.n.* (MHA). **Karachaevo-Cherkessian Republic:** Dolina narzanov, 12.VII.2010, *Ukrainskaya 14716* (LE); Teberdinsky Nature Reserve, Shumka

Creek, *Ignatov & Ignatova 05-1041* (MW); Verkhnyaya Teberda, *Onipchenko 45/95* (MW); Karachaevsk surroundings, 4.V.2001, *Onipchenko s.n.* (MW).

ACKNOWLEDGEMENTS

Authors are greatly indebted to curators if FI, H and PE for specimen loans, to Alexander E. Fedosov for the help with the Bayesian analysis, to Mikhail Kozhin for assistance in mapping *Syntrichia submontana*, to M.T. Gallego for providing her publications, and to J. Kučera and R.H. Zander for valuable comments and correction of English of the manuscript. The work was partially supported by RFBR № 13-04-01427, 14-04-01424 and RAS program “World Life, Current State and Development”.

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Appendix 1. Genbank accession numbers and voucher specimen data of *Syntrichia* specimens other than taken from Genbank.

<i>S. caninervis</i>	Dagestan	Russia, Dagestan, <i>Ignatov & Abakarova 11-102</i> (MHA)	KM381996
<i>S. caninervis</i>	Mongolia	Mongolia, <i>Ignatov 01-663</i> (MHA)	KM381997
<i>S. caninervis</i>			
var. <i>astrakhanica</i>	Astrakhan	Russia, Astrakhan Province, 3.V.1997, <i>Suragina s.n.</i> (MHA)	KM381998
<i>S. caninervis</i>			
var. <i>astrakhanica</i>	Mongolia	Mongolia, <i>Ignatov #01-669</i> (MHA)	KM381999
<i>S. caninervis</i>			
var. <i>astrakhanica</i>	Taimyr	Russia, Taimyr, <i>Fedosov 05-547</i> (MW)	KM382037
<i>S. caninervis</i>			
var. <i>astrakhanica</i>	Ryazan	Russia, Ryazan 4.VIII.2009 <i>Volosnova s.n.</i> (MHA)	KM382036
<i>S. laevipila</i>	Krasnodarsky 1	Russia, Krasnodar Territory, <i>Ignatov & Ignatova 05-598</i> (MW)	KM382000
<i>S. laevipila</i>	Krasnodarsky 2	Russia, Krasnodar Territory, <i>Ignatov & Ignatova 05-68</i> (MW)	KM382001
<i>S. laevipila</i>	Krasnodarsky 3	Russia, Krasnodar Territory, <i>Ignatov & Ignatova 05-466</i> (MW)	KM382002
<i>S. montana</i>	Dagestan	Russia, Dagestan, <i>Fedosov 10-2-335</i> (MW)	KM382003
<i>S. pagorum</i>	Australia	Australia, 18.XII.1993, <i>Streimann 53305</i> (MHA)	KM382004
<i>S. pagorum</i>	Kabardino-Balkaria	Russia, Kabardino-Balkaria, <i>Ignatov et al. 05-1540</i> (MW)	KM382005
<i>S. pagorum</i>	Khakassia	Russia, Khakassia, Abakan, <i>Ignatov & Spirina 11-5033</i> (MHA)	KM382006
<i>S. pagorum</i>	Mongolia	Mongolia, <i>Ignatov 01-768</i> (MHA)	KM382007
<i>S. pagorum</i>	Yakutia	Russia, Yakutia, Lenskie Stolby, 20.VIII.2001, <i>Krivoshapkin s.n.</i> (MW)	KM382008
<i>S. pagorum</i>	Zabaikalsky 1	Russia, Zabaikalsky Territory, 9.VIII.2011, <i>Afonina s.n.</i> (LE, MHA)	KM382009
<i>S. pagorum</i>	Zabaikalsky 2	Russia, Zabaikalsky Territory, <i>Afonina 1711</i> (LE, MHA)	KM382010
<i>S. pagorum</i>	Zabaikalsky 3	Russia, Zabaikalsky Territory, <i>Afonina 1011</i> (LE)	KM382011
<i>S. papillosissima</i>	Dagestan	Russia, Dagestan, <i>Abakarova 11-168</i> (MHA)	KM382012
<i>S. princeps</i>	California	U.S.A., California, 5.VIII.1989, <i>Ignatov s.n.</i> (MHA)	KM382013
<i>S. princeps</i>	Kazakhstan	Kazakhstan., Aksu-Dzabagly, IV.1979, <i>Neshataeva s.n.</i> (MHA)	KM382014
<i>S. princeps</i>	Turkmenistan	Turkmenistan, Syunt-Khasardag, 13.IV.1989, <i>Levitskaya s.n.</i> (MHA)	KM382015
<i>S. ruralis</i>	Altai	Russia, Altai Republic, Bogoyash, <i>Ignatov 36/266</i> (MHA)	KM382016
<i>S. ruralis</i>	Taimyr	Russia, Taimyr, Ereechka, <i>Fedosov 13-3-0905</i> (MW)	KM382017
<i>S. sinensis</i>	Altai 1	Russia, Altai Republic, Teletskoe Lake, 3.VI.1989, <i>Ignatov s.n.</i> (MHA)	KM382018
<i>S. sinensis</i>	Altai 2	Russia, Altai Republic, Chermal, <i>Ignatov & Ignatova 34/109</i> (MHA)	KM382019
<i>S. sinensis</i>	Amurskaya	Russia, Amurskaya Province, <i>Dudov & Kotel'nikova 2013 Br 0341</i> (MW)	KM382020
<i>S. sinensis</i>	Dagestan	Russia, Dagestan, <i>Abakarova & Ignatov 11-361</i> (MHA)	KM382021
<i>S. sinensis</i>	Primorsky	Russia, Primorsky Territory, Chandolaz, <i>Ignatov et al. 06-2825</i> (MHA)	KM382022
<i>S. sinensis</i>	Zabaikalsky 1	Russia, Zabaikalsky Territory, <i>Afonina 5306</i> (LE)	KM382023
<i>S. sinensis</i>	Zabaikalsky 2	Russia, Zabaikalsky Territory, <i>Afonina 7206</i> (LE)	KM382024
<i>S. sinensis</i>	Zabaikalsky 3	Russia, Zabaikalsky Territory, 7.VII.1989, <i>Bardunov s.n.</i> (LE)	KM382025
<i>S. sinensis</i>	China	China, Inner Mongolia, Manhan Mt., <i>Ignatov 08-510</i> (MHA)	KM382026
<i>S. submontana</i>	Altai	Russia, Altai, Malyj Yaloman, <i>Ignatov & Ignatova 25/119</i> (MHA)	KM382027
<i>S. submontana</i>	Dagestan	Russia, Dagestan, <i>Abakarova & Ignatov 11-477</i> (MHA)	KM382028
<i>S. submontana</i>	Tyva	Russia, Tyva, 13.IX.2003, <i>Korobkov s.n.</i> (LE)	KM382029
<i>S. submontana</i>	Zabaikalsky	Russia, Zabaikalsky Territory, <i>Afonina 1110</i> (LE)	KM382030
<i>S. submontana</i>	Irkutsk	Russia, Irkutsk Province, Baikal Lake, 14.IX.1982, <i>Filin s.n.</i> (MW)	KM382031
<i>S. submontana</i>	China	China, Xizang, <i>Miwa & Y. Yia 2004080324</i> (PE)	KM382032
<i>S. submontana</i>	Khakassia	Russia, Khakassia, Abakan, <i>Ignatov & Spirina 11-5042</i> (MHA)	KM382038
<i>S. submontana</i>	Mongolia	Mongolia, Gurban-Saikhan, <i>Ignatov 01-658</i> (MHA)	KM382039
<i>S. virescens</i>	Kaliningrad	Russia, Kaliningrad Province, 10.VII.2005, <i>Dolnik s.n.</i> (MHA)	KM382033
<i>S. virescens</i>	Krasnodarsky	Russia, Krasnodar Territory, <i>Ignatov & Ignatova 05-206</i> (MHA)	KM382034
<i>S. virescens</i>	Orenburg	Russia, Orenburg Province, 3.V.2005, <i>Notov s.n.</i> (MHA)	KM382035