

CROSSIDIUM CRASSINERVIVM (POTTIACEAE, BRYOPHYTA),
A NEW SPECIES FOR RUSSIA

CROSSIDIUM CRASSINERVIVM (POTTIACEAE, BRYOPHYTA) – НОВЫЙ ВИД ДЛЯ РОССИИ

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Abstract

Crossidium crassinervium is a xeric species occurring in South Europe, North Africa, Middle East, Caucasus, countries of Central Asia (Tadjikistan and Turkmenistan), China, southern states of U.S.A., and Mexico. Here we report the first findings of *C. crassinervium* in Russia. It was collected in southern Siberia, in Khakassia, in the upper course of the Yenisey River and in Buryatia, East Sayan Mountains. The ITS sequences confirm the closest affinity of Siberian specimens to *C. crassinervium*, though they differ from those of European plants in a number of substitutions and indels comparable with the differences between European *C. crassineurum* and *C. aberrans*.

Резюме

Crossidium crassinervium – это ксерофильный вид, распространенный в Южной Европе, Северной Африке, на Ближнем Востоке, на Кавказе, в странах Средней Азии (Таджикистане и Туркменистане), в Китае, на юге США и в Мексике. Для России *C. crassinervium* приводится впервые по образцам из Хакасии и Бурятии. Российские образцы по ITS образуют умеренно поддерживаемую кладу вместе с европейскими образцами *C. crassinervium*, однако по этому маркеру имеются отличия между российскими и европейскими образцами этого вида, которые по числу замен и инделей сопоставимы с отличиями между европейскими растениями *C. crassinervium* и *C. aberrans*.

KEYWORDS: mosses, new record, nrITS

INTRODUCTION

The genus *Crossidium* Jur. includes 14 species (Brinda & Atwood 2026), with the worldwide distribution in xeric regions of all continents, excluding Antarctic. In regional floras of temperate and boreal regions of Northern Hemisphere the genus is usually poorly represented: only one species is reported from Russia (Ignatov *et al.*, 2025) and China (Li *et al.*, 2001), four species from North America (Delgadillo, 2007), and 7 species from Europe combined with Macaronesia (Hodgetts *et al.*, 2020). Two most widespread species of the genus in Northern Hemisphere are *Crossidium squamiferum* (Viv.) Jur. and *C. crassinervium* (De Not.) Jur.

Crossidium crassinervium is a xeric species with two varieties, var. *crassinervium* and var. *laevipilum* (Ther. & Trab.) Delgad., the latter sometimes treated at species level, e.g. in Flora Briofitica Ibérica (Cano, 2006). However, in the Checklist and country status of European bryophytes (Hodgetts & Lockhart, 2020) these varieties are not regarded, and the species is recorded from mainly South European countries and from Canary Islands. It is also known from Northern Africa and Middle East (Ros *et al.*, 2013), Chad (O'Shea, 2006), Cape Verde Archipelago (Sim-Sim *et al.*, 2024), Azerbaijan (Qasimov & Novruzov, 2017), and countries of Middle Asia (Mamatkulov, 1990). In China, it was recorded from several prov-

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inces by Tan & Zhao (1997); however, Li *et al.* (2001) did not include this species into their treatment of the genus in the Moss Flora of China. Later it was reported also from Shaanxi Province (Liu *et al.*, 2011). *Crossidium crassinervium* var. *crassinervium* is also known from the southern states of the U.S.A. (Delgadillo, 2007) and Mexico (Delgadillo, 1994).

Until now, *C. crassinervium* remained unknown in Russia. Savicz-Lyubitskaya & Smirnova (1970) in the “Handbook of mosses of the USSR, the Acrocarpous mosses” reported it, under the name *C. chloronotos* auct., for the Caucasus and Middle Asia, without detailed references. In the Check-list of mosses of East Europe and North Asia (Ignatov *et al.*, 2006) some references were given, *i.e.*, Simonov (1978) for Moldavia, Lyubarskaya (1986) for Azerbaijan, Mamatkulov *et al.* (1998) for Turkmenistan, and Mamatkulov (1975, 1990) for Tadjikistan.

In 2011, M. Ignatov and U. Spirina gathered some moss specimens in Khakassia in the course of a field trip devoted mainly to paleontological studies. This collection was labeled and partly identified, but this work was not completed. It was revisited in 2025 by A.G. Bezdodov in the course of exploration of Khakassian mosses. Among others, a specimen of a recently described *Didymodon baicalensis* Ignatova & Ignatov was found, which included an admixture of a very small *Pterygoneurum*-looking moss without sporophytes, represented by tiny bud-like plants having ovate leaves with long hyaline hair-points. Microscopic observation revealed multicellular filaments on the ventral side of costa, a characteristic of the genus *Crossidium*. The lack of very thick-walled, hyaline cells in the upper part of leaves, however, excluded *C. squamiferum*, the only species of the genus reported from Russia (Ignatov *et al.*, 2025). These plants were tentatively referred to *C. crassinervium*. Subsequent revision of Siberian specimens identified as *C. squamiferum* in MW, MHA and NSK revealed two additional specimens resembling that from Khakassia; they were collected in two localities in the vicinity of Mondy Settlement in Buryatia. However, all these specimens did not fully fit the descriptions and illustrations of this species, *C. crassinervium*, and its varieties given by Cano (2006) and Heyn & Herrnstadt (2004). Therefore, the DNA barcoding method with the nr ITS was applied to clarify the species identity.

MATERIAL AND METHODS

Morphological studies

The photographs were taken under Olympus CX43 light microscope with the Infinity 1–2 camera. Z-stacks of several images were generated using HeliconFocus 4.50 (Kozub *et al.*, 2008), and stereomicroscope Nikon SMZ-25, with Z-stacking with NIS.

Molecular phylogenetic analysis

Nuclear ITS region was used for assessing affinities of the *Crossidium* specimens from Khakassia and Buryatia.

Laboratory work followed the protocol described by Gardiner *et al.* (2005). Most similar sequences for further phylogenetic analysis were selected and downloaded from GenBank using BLAST search. Yielded selection of *Crossidium* accessions and those representing other relatives of *Crossidium* was limited to include the reliably alignable ITS sequences with percent identity of 92 or just below. It included two accessions of *C. crassinervium*, two of *C. aberrans* Holz. & E.B. Bartram, two of *C. squamiferum*, and also single accessions of *Tortula revolvens* (Schimp.) G. Roth, *T. brevissima* Schiffn., *Pterygoneurum ovatum* (Hedw.) Dixon and *P. subsessile* (Brid.) Jur. Original ITS sequences were added: *C. squamiferum* (isolate TF19) to check repeatability of GenBank accessions of that species, and that of *Stegonia pilifera* (Brid.) H.A. Crum & L.E. Anderson (isolate TF27) to expand the outgroup selection. Data on sequenced samples is provided in Specimen examined of *C. crassinervium*, and next to them.

Sequences were aligned manually using BioEdit (Hall, 1999). Indel data were scored using the simple indel coding (SIC) approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1. (Müller, 2005) and added to the datasets prepared to Bayesian inferences. Bayesian analyses in MrBayes 3.2.7. (Ronquist *et al.*, 2012) were set for 2.5 million generations and sampling frequency one tree each 500 generations, average standard deviations of split frequencies were checked to have decreased below 0.01 after first 250 thousand generations. The chain temperature was set at 0.02 in all analyses and GTR model with sampling throughout the model space (setting nst = mixed) was used. Convergence of the analyses was assessed via ESS values, checked using Tracer v.1.7.2. (Rambaut *et al.*, 2018) to be higher than 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. ML trees were computed in IQ-tree (Trifinopoulos *et al.*, 2016) via the web server <https://www.hiv.lanl.gov/content/sequence/IQTREE/iqtree.html> with 1000 generations of ultrafast bootstrap and automatic assessing of the best fit nucleotide substitution model; indel data were not included in the ML analysis. In a lack of elaborated phylogenies for *Crossidium* and closely related genera, the default root selection was not re-rooted. Also, we estimated between group distances in Mega11 (Tamura *et al.*, 2021). The number of base substitutions per site from averaging over all sequence pairs between groups were calculated using the Kimura 2-parameter model with nine sequences representing four groups, *C. squamiferum*, *C. aberrans*, two accessions of *C. crassinervium* (European specimens), and another two accessions of *C. crassinervium* (our Siberian specimens).

RESULTS

ITS sequences of the plants from Khakassia (isolate OK4602) and Buryatia (isolate BF275) were nearly identical and distinct from all other sequences in the alignment. Topologies of the trees inferred from the BA and ML were identical despite of absence the indel data in

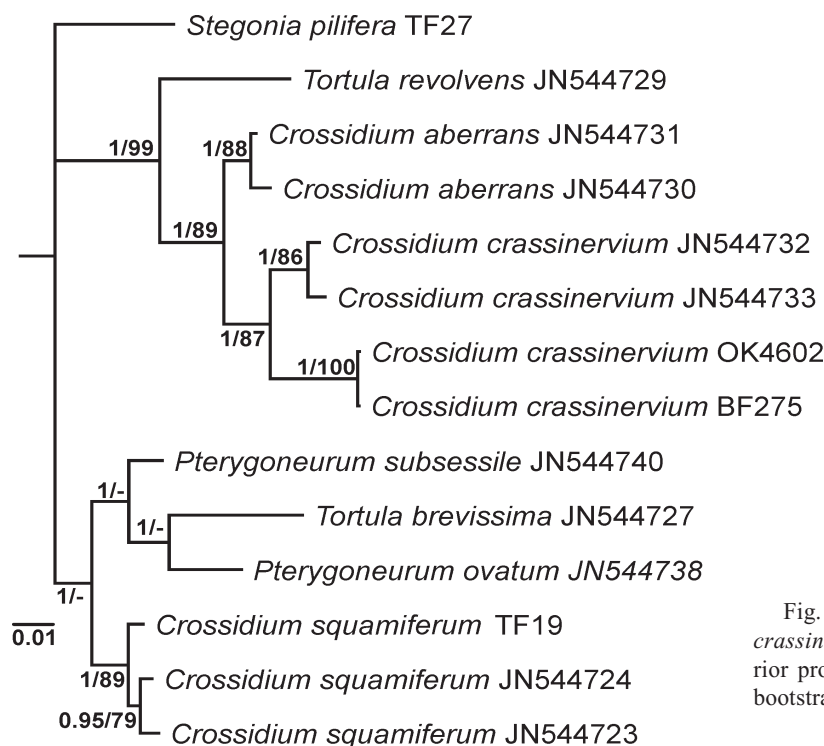


Fig. 1. Bayesian phylogenetic tree for *Crossidium crassinervium* and related species. Bayesian posterior probabilities (>90) and Maximum Likelihood bootstrap supports (>70) are shown at branches.

the ML analysis. Most accessions of Pottiaceae included in the analysis excepting *Stegonia pilifera* form two clades (Fig. 1). A weakly supported one, with the support from ML analysis below the 70 threshold includes a moderately supported clade with three accessions of *C. squamiferum* (PP = 1, BS = 89) and not supported clade with two accessions of *Pterygoneurum* and one of *Tortula brevissima*. All other accessions of *Crossidium* are found in the highly supported second clade (PP = 1, BS = 99), where they form a moderately supported clade (PP = 1, BS = 89) sister to a single accession of *Tortula revolvens*. Two Siberian accessions of *Crossidium crassinervium* form a maximally supported clade sister to the clade with two accessions of European *C. crassinervium*, so that their joint clade (PP = 1, BS = 87) is sister to *C. aberrans* clade.

Between group nucleotide distances were above 0.04 between *C. squamiferum* and three other *Crossidium* groups, 0.0265 between “European *C. crassinervium*” and “Siberian *C. crassinervium*”, 0.0215 between “European *C. crassinervium*” and *C. aberrans*, 0.0324 between “Siberian *C. crassinervium*” and *C. aberrans*.

DISCUSSION

Identification of Siberian specimens of *Crossidium* was not straightforward. First, using the key to identification in Pócs *et al.* (2004), we supposed that specimens from Buryatia may belong to *C. laxefilamentosum* Frey & Kürschner due to a high proportion of filaments with smooth, conic upper cell. However, spore size did not fit the description of this species: they were highly variable, 8–11 µm in one capsule and 11–19 µm in another

one from the same population. It agrees with the opinion of Cano (2006) who commented a high variability of morphological characters in this group in Iberian Peninsula, so that within one population and even one plant characters of *C. crassinervium* and *C. laxefilamentosum* may be observed. As a result, the latter name was added into synonymy of highly variable *C. crassinervium*.

Crossidium laevipilum Thér. & Trab., described from Sahara in Algeria, is accepted either as a species (Cano, 2006) or a variety, *C. crassinervium* var. *laevipilum* (Thér. & Trab.) Delgadillo (Heyn & Hermsstadt, 2004). The latter authors separate them solely by gametophytic characters: var. *crassinervium* has ‘leaves ovate-lanceolate to lingulate, often twisted when dry, apex obtuse to acute, upper leaves with hair-point at least as long as lamina’ vs. in var. *laevipilum* ‘leaves wide-ovate or ovate-lanceolate, not twisted when dry, apex round-obtuse or emarginate, upper leaves with hair-point usually shorter than lamina’ (Heyn & Hermsstadt, 2004, p. 211). Contrary to that treatment, Cano (2006) provides mainly sporophytic characters for separating these two taxa: length of peristome (300–812 µm in *C. crassinervium* vs. 105–350 µm in *C. laevipilum*) and spore size (7.5–15 µm vs. 15–20 µm, respectively). For leaves, only shape of their apices is given in the key: obtuse and not cucullate in *C. crassinervium* vs. rounded and cucullate in *C. laevipilum*. However, illustrations of their leaves are contrastingly different, and in the descriptions leaf length is given as 0.4–1.3 mm for *C. crassinervium* and 0.3–0.7(–0.9) mm for *C. laevipilum*, and the length of hair-points is 0.1–1.0(–1.5) mm vs. 0.05–0.2(–0.8) mm, respective-

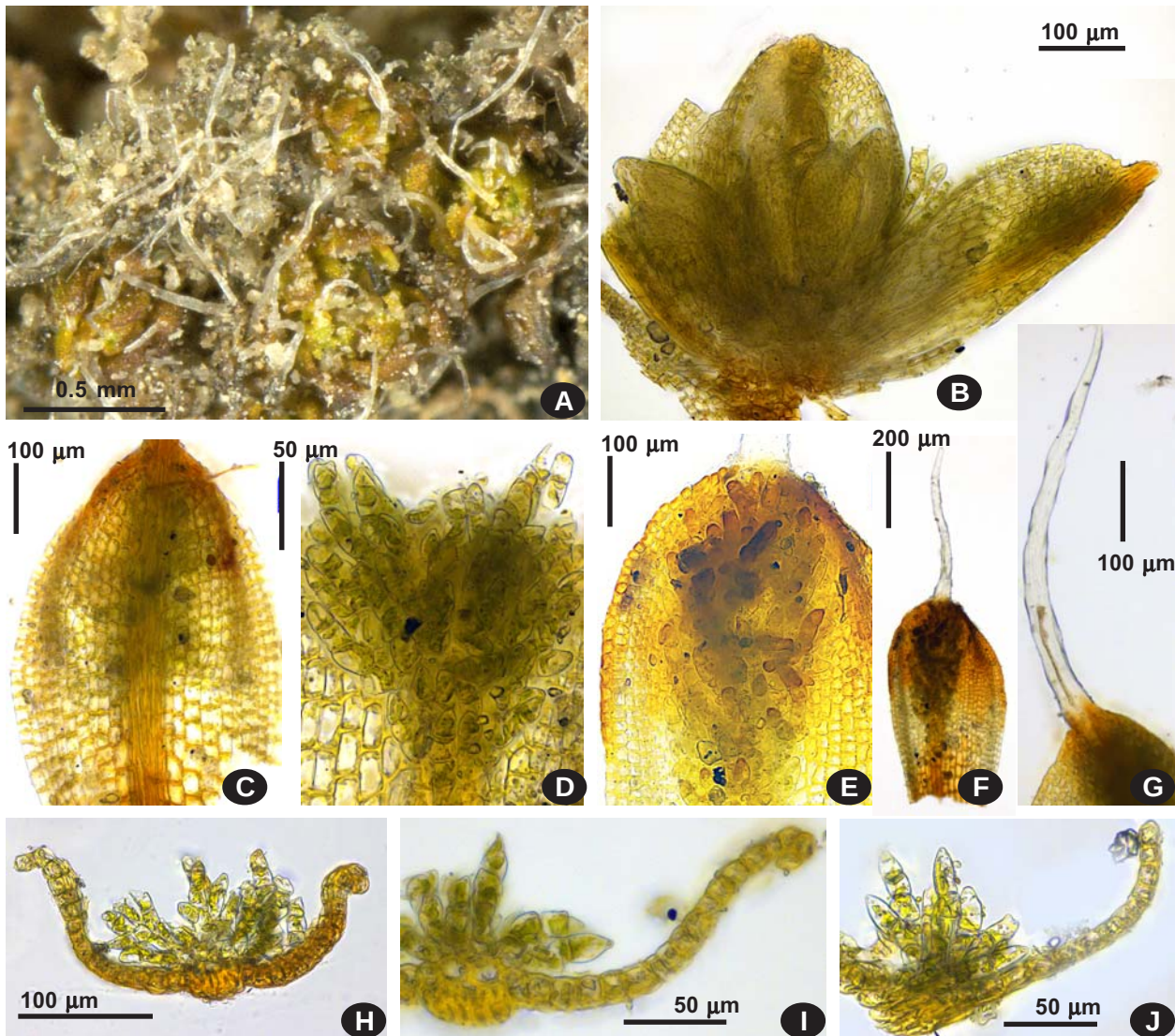


Fig. 2. *Crossidium crassinervium* (A–J: from Khakassia, Ignatov & Spirina 11-5172a, MHA9132216). A: habit; B: upper part of male plant, showing antheridia, paraphyses and perigonal leaves lacking hyaline awn; C: leaf dorsal view, showing elongate cells of dorsal epidermis of the costa; D–F, M: leaf ventral views, showing costal filaments; G: leaf hyaline awn, note its entire margin; H–J: leaf transverse sections, showing branched filaments.

ly. The specimen from Khakassia lacks sporophytes, its leaves are 0.4–0.5 mm long, ovate in shape, rounded at apex and not twisted but appressed when dry, which fits var. *laevipilum*. However, hair-points of its leaves are as long as lamina or longer, 0.5–0.7 mm long, which agrees with var. *crassinervium*. Actually, the Khakassian plants are most similar to the illustrations of *C. crassinervium* in the Moss Flora of Mexico (Delgadillo, 1994), where, however, female plants with sporophytes are shown, while the Khakassian plants are male (probably all of them). Specimens from Buryatia are similar to the Khakassian plants in leaf shape, length of hair-points and predominantly smooth, conic upper cells of costal filaments, though few obtuse cells with 2–3 papillae were also seen in both localities. Peristome teeth in specimen MW9131505 were partially broken, so they hardly exceeded 200 µm (Fig. 2K) where-

as in specimen from NSK they varied from 300–400 to 560 µm.

Summing up, the Siberian specimens agree with the circumscription of *C. crassinervium* in the essential morphological characters but possess a different variability in leaf shape than the European plants.

According to the topology of the tree inferred from nr ITS data, *Crossidium crassinervium* and *C. aberrans* do not form a clade with *C. squamiferum*, the type species of the genus *Crossidium*. Also, these species differ from *C. squamiferum* in the absence of thick-walled hyaline cells in upper part of leaf margin. Further studies based on wider selection of taxa and extensive set of more conservative markers are needed to resolve a phylogeny of the extremely diverse group currently classified in the genus *Tortula* s.l. and a suite of genera close to it, and to revise its genus level taxonomy.

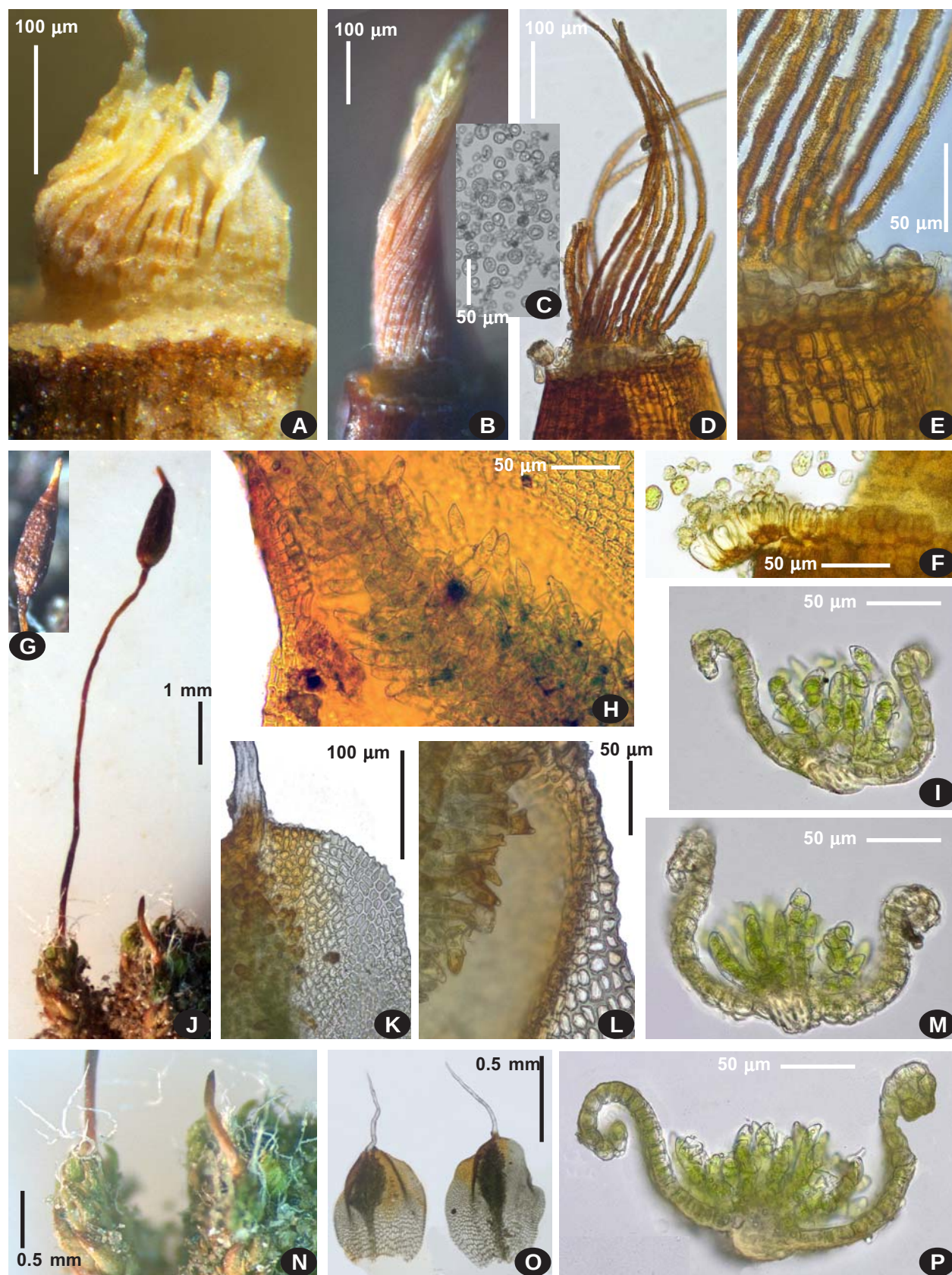


Fig. 3. *Crossidium crassinervium* (A: from Buryatia, Fedosov 23-0156, MW9131505; B–N: from Buryatia, Pisarenko s.n., NSK). A–B & D–E: peristome; C: spores; F: annulus; G: capsule; H, K, L: leaf ventral views, showing costal filaments; I, M, P: leaf transverse sections, showing branched filaments; J, N: habit; O: leaves.

TAXONOMY

Crossidium crassinervium (De Not.) Jur., Laubm.-Fl. Oesterr.-Ung. 128. 1882. — *Tortula crassinervia* De Not., Mem. Reale Accad. Sci. Torino 40: 303. 1838. Fig. 2.

Type: [Italy, Sardinia, Cagliari] “ad vias Calaim” (RO). Not seen.

Plants minute, bud-like, usually immersed into substrate, so only leaf tips and hyaline awns are visible, yellowish-green or brownish-green, whitish due to long hyaline hair-points, in small groups on soil or forming clusters ca. 2 cm in diameter. *Stems* 0.5–1 mm long, not branched. *Leaves* ovate, 0.4–0.75×0.3–0.6 mm, with length/width ratio 1.4–1.7, concave, obtuse to rounded at apex, weakly cucullate; margins recurved in the middle 2/3; costa ca. 50 µm wide at base, excurrent into flexuose, almost smooth hair-point 0.5–1.0 mm long, in transverse section with one layer of guide cells and 2–3 layers of dorsal stereids, on ventral surface in distal half with 5–7 rows of filaments 4–7 cells high, simple or branched, their distal cells conic or bifid, smooth or with 1–2 round papillae; lamina unistratose, smooth; upper laminal cells subquadrate to short rectangular, 9–14×8–10 µm, in midleaf 14–17×12 µm, firm-walled, chlorophyllose; basal laminal cells short rectangular to rectangular, thinner-walled, 16–55×(9–)14–20 µm, basal marginal cells not differentiated or shorter. *Dioicous*. Perigonia terminal, perigonal leaves similar to vegetative leaves but lacking hair-points, with costa excurrent into short brownish mucro. Perichaetia terminal, perichaetial leaves smaller than vegetative leaves, with very short hair point, ca. 0.1 mm. *Seta* 3–5 mm, yellowish to brownish. *Capsules* short cylindric to ovate-cylindric, 1.1–1.3×0.4–0.5 mm, brownish. *Opercula* high conic, ca. 0.5 mm long. *Peristome* ca. 270–560 µm, orange, later whitish, on basal membrane ca. 70–100 µm, teeth oblique to twisted, strongly papillose. *Spores* 8–15(–19) µm. *Calyptrae* cucullate, ca. 1.3 mm long.

Distinction. *Crossidium crassinervium* is readily distinguished from *C. squamiferum* in having dioicous sexual condition and firm-walled distal cells not differing contrastingly from other laminal cells. In contrast, *C. squamiferum* is gonioautoicous and has leaves with distal cells very thick-walled, with obliterated lumens, often hyaline. These two species also differ in leaf shape: leaves are ovate, rounded at apex in *C. crassinervium* and deltoid, acute at apex in *C. squamiferum*.

Specimens examined (with GenBank accession numbers): RUSSIA: **Republic of Khakassia**, Altaysky District, near village Letnik, left bank of Yenisey River, 53°30'23"N, 91°38'34"E, 300 m alt. Steppe site, W-faced slope, on soil. 21 Aug 2011, coll. Ignatov & Spirina 11-5172a, det. A. Bezgodov {MHA9132216}. Isolate OK 4602. ITS: PZ741027. **Republic of Buryatia**: Tunkinskij Distr., Mondy Settl., 51.679722°N, 100.95444°E, 1300 m alt., near border service office, edge of gravel road, on sandy ground, 14 Sept 2017, Pisarenko

{NSK2006763}; Okinskij Distr., East Sayan Mountains, Belyj Irkut River valley close to border outpost on the Mondy-Orlik road, 51.76805°N – 100.71004°E, 1400 m alt., on ledge of a limestone rock, 15 July 2023, Fedosov 23-0156 {MW9131505}. Isolate BF275. ITS: PZ741028.

Other sequenced specimens: *Stegonia pilifera*, Russia: Krasnoyarsk Territory, Taimyr Distr., coll. 07 Aug 2011, Fedosov 11-648 {MW9021753}. Isolate TF27. ITS: PZ741025. *Crossidium squamiferum*, Russia: Republic of Dagestan, coll. 18 May 2009, Ignatov & Ignatova 09-121 {MW9030065}. Isolate TF19. ITS: PZ741026.

Specimens from Buryatia were previously published under the name *C. squamiferum* (Sandanov & Pisarenko, 2018; Fedosov *et al.*, 2025).

Both territories hosting the listed localities are characterized by sharply continental climate: large annual and daily temperature fluctuations are combined with low precipitation; summers are hot; winters are cold, long and snowless; the average annual temperature is slightly negative. True steppe and exposed forest-steppe form the background of the vegetation cover of the regions (Alisov, 1956).

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