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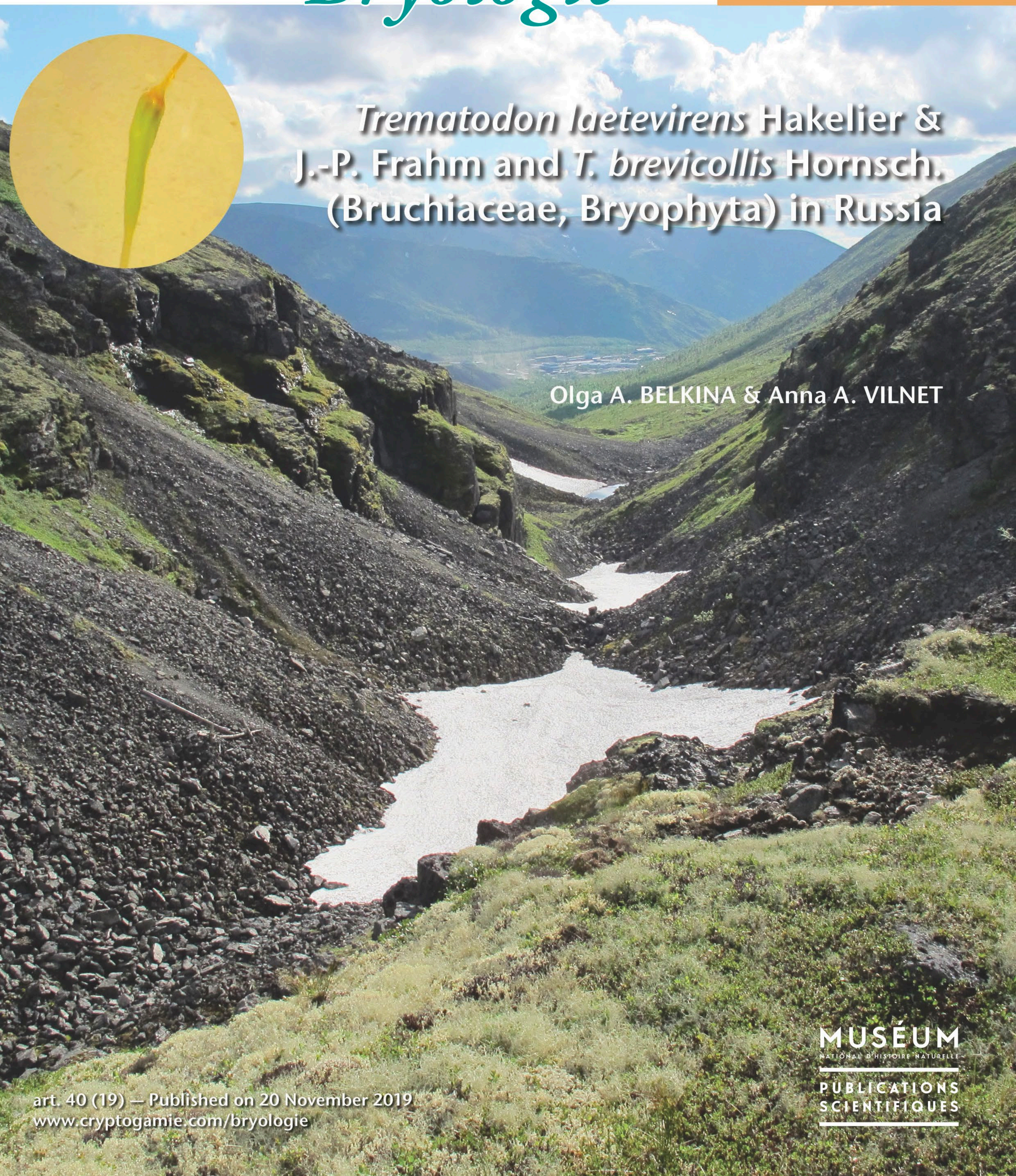

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Couverture / *Cover* :
Trematodon laetevirens - a capsule (above) and habitat on Yuksporrlak Pass in Khibiny Mountains (Russia)

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Trematodon laetevirens Hakelier & J.-P. Frahm and *T. brevicollis* Hornsch. (Bruchiaceae, Bryophyta) in Russia

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ABSTRACT
Trematodonl laetevirens Hakelier & J.-P. Frahm is here added to the Russian bryoflora based on records from the Khibiny Mts. (Murmansk Region, North-West Russia), Anadyr' River Basin (Chukotka Autonomous Region) and the Ushkovsky volcano (Kamchatka Peninsula). The Khibiny moss population, earlier defined as *T. brevicollis* Hornsch., is attributed to *T. laetevirens.* We reaffirmed that the East Sayan samples belong to *T. brevicollis,* so, currently only one locality of *T. brevicollis* is known in Russia. The revision of *T. longicollis* Michx. samples from the Kamchatka Peninsula, and Kunashir Island (the Kuril Islands) confirmed their affiliation to this species, despite some deviations in morphological features. The taxonomical concepts inferred from variation in morphological traits are supported by for the first molecular-phylogenetic analyses of the genus *Trematodon* based on the nucleotide sequence data of ITS2 nrDNA and *trn*L-F cpDNA. At present, four species of the genus *Trematodon* Michx. are known from Russia: *T. ambiguus* (Hedw.) Hornsch., *T. brevicollis, T. laetevirens* and *T. longicollis*. A key to Russian *Trematodon* species is provided.

KEY WORDS
Bryoflora,
Trematodon,
Khibiny Mts.,
Kamchatka,
Chukotka.

RÉSUMÉ
Trematodon laetevirens *Hakelier & J.-P. Frahm et* T. brevicollis *Hornsch. (Bruchiaceae, Bryophyta) en Russie.*
Récolté dans les Monts Khibiny (Région de Murmansk, Russie NW), dans le bassin de la rivière Anadyr (région autonome de Chukotka) et sur le volcan Ushkovsky (Péninsule de Kamchatka) *Trematodon laetevirens* Hakelier & J.-P. Frahm est nouveau pour la bryoflore russe. La population de mousse à Khibiny, définie auparavant comme *T. brevicollis* Hornsch., est attribuée à *T. laetevirens.* Nous réaffirmons que les échantillons de Sayans de l'Est appartiennent à *T. brevicollis,* ainsi *T. brevicollis* est connu en Russie d'une seule localité. La révision des spécimens de *T. longicollis* Michx. collectés dans la Péninsule de Kamachatka et dans l'île Kunashir (îles de Kuril) confirme leur appartenance à cette espèce, en dépit de quelques différences dans les caractères morphologiques. Les premières analyses en phylogénie moléculaire du genre *Trematodon* Michx. sur la base des données de la séquence d'ITS2 nrDNA and *trn*L-F cpDNA confirment les traits de variation morphologique. À présent, quatre espèces de *Trematodon* sont connues en Russie : *T. ambiguus* (Hedw.) Hornsch., *T. brevicollis, T. laetevirens* et *T. longicollis*. Une clé pour les espèces russes de *Trematodon* est donnée.

MOTS CLÉS
Bryoflore,
Trematodon,
Monts Khibiny,
Kamchatka,
Chukotka.

INTRODUCTION

The genus *Trematodon* Michx. includes approximately 80 species (Crosby *et al.* 1999) of which only 25 have good taxonomic characters (Zander 2007). In Russia, three species were recognized (Ignatov *et al.* 2006). *Trematodon ambiguus* (Hedw.) Hornsch. is widely distributed and occurs in European and Asian parts of Russia. A rarer species, *T. brevicollis* Hornsch., was known from East Sayan (Eastern Siberia; Bardunov 1969, 1974) and several localities in the Khibiny Mountains (Murmansk Region, North-West Russia; Schljakov 1961). *Trematodon longicollis* Michx. is reported from the Far East of Russia: in the upper reaches of the Bureya River in the Khabarovsk Territory (Ignatov *et al.* 2000), in the south of the Kamchatka Peninsula (Ignatova & Samkova 2006), Kunashir Island in the Kuril Islands (Bakalin *et al.* 2009; Ignatova *et al.* 2016), and from Moneron Island near Sakhalin Island (Kamimura 1939; Bakalin *et al.* 2012). The report of *T. longicollis* from Bering Island in the Commander Islands (Fedosov 2010) was subsequently revised and the specimens were assigned to *T. ambiguus* (Fedosov *et al.* 2012).

In 1976, *Trematodon laetevirens* Hakelier & J.-P. Frahm was described from two locations in Sweden and one (from three points) in Norway (Hakelier & Frahm 1976). Later, more localities were discovered in Scandinavia (Hallingbäck 2006) and the range expanded to Greenland (Mogensen 1980, 1983; Humle 1987; Zander 2007), western Canada (Yukon; Vitt *et al.* 1987), and adjacent Alaska (Stehn & Kofranek 2014). *Trematodon laetevirens* differs from *T. brevicollis* by a suite of characters (Hakelier & Frahm 1976): the gradually tapering leaves (vs. abruptly narrowed in the latter species), elongate-rectangular leaf cells with thin walls (vs. short rectangular cells with somewhat thickened walls), inner perichaetial leaf with a rounded apex, or with a short blunt apiculus, (vs a longer and sharp apiculus), a straight erect capsule (vs more or less curved and inclined), with gradual transition of the neck to the seta (vs a clearly visible, abrupt transition of the neck to the seta), rectangular-quadrate exothecial cells with slightly thickened walls (vs. elongate rectangular cells with strongly thickened walls), peristome teeth mostly perforated along the middle line and split at the top (vs. blunt, mostly whole, rarely split teeth), and smaller spores (i.e., 35-40 µm vs. 45-60 µm).

We first found *T. laetevirens* during a survey of nature sanctuary “*Encalypta* species of the Yuksporrlak Pass” in the Khibiny Mts. (Murmansk Region) in August of 2017 (Fig. 1). Schljakov (1961) reported *T. brevicollis* from the same locality, but the specimens are morphologically similar and likely belong also to *T. laetevirens*. This prompted an examination of other specimens identified as *T. brevicollis* from the Khibiny Mts. and East Sayan, and ultimately all specimens of *Trematodon* from Russian localities held in major Russia herbaria to assess the taxic diversity and species distribution on the Russian territory. The outcome of this morphology based revision of specimens is presented and complemented by the first inferences from sequence data for this genus.

MATERIAL AND METHODS

The focal area

The Khibiny Mountains are located in the Murmansk Region, 150 km north of the Arctic Circle and occupy an area of about 1300 sq. km. The mountains have plateau-shaped peaks with a maximum height of 1200 m above the sea level. The mountain range represents an intrusion of alkaline and ultrabasic rocks and nepheline syenites. The average annual temperature ranges from –0.5°C to –4.5°C, with averages of 7 to 12°C in June and –12 to –14°C in February. The total annual precipitation is between 1000 and 1200 mm (from May to October, 609 mm). The snow cover persists for 250 to 280 days (Scientific… 1988; Pozhilenko *et al.* 2002). The high-altitude zones include: the coniferous forest zone extending to 300-500 m a.s.l., followed by an open birch forest zone between 300 to 450 (-500) m, then the mountain tundra between 450-800 m and ultimately the cold stone deserts.

Taxon sampling

Specimen collected

Voucher specimen details for our sample are as follows: **Russia**. Murmansk Region, Khibiny Mts., northern spur of Rasvumchorr Mt., Yuksporrlak Pass, 67.66082°N, 33.84192°E, 606 m elev., mountain tundra zone, a W-exposed wet cliff, on soil over an inclined narrow ledge and shelves; fertile; with *Amphidium lapponicum* (Hedw.) Schimp., *Ditrichum heteromallum* (Hedw.) E.Britton, *Pogonatum urnigerum* (Hedw.) P.Beauv.; coll. 16.VIII.2017. O. A. Belkina, #657-6-17; KPABG (M) #122909.

Specimens examined

This specimen was compared with all the Schljakov’s samples gathered at three locations in the Khibiny (including the slope of Rasvumchorr Mt. on Yuksporrlak Pass) in 1948 and identified by him as *T. brevicollis* (Fig. 1). We also examined the *T. laetevirens* specimens collected by N. Hakelier in Sweden and Norway in 1974 and 1977 as well as two samples of *T. brevicollis* from the East Sayan (Irkutsk Region, Eastern Siberia). We compared these collections also to *T. brevicollis* samples from Mongolia (two samples), Arctic Alaska and West Greenland (Table 1, Appendix 1). All specimens had developed sporophytes. In order to discover other moss specimens belonging to these two species, we examined all specimens of *Trematodon* from Russia that are deposited in the largest Russian bryophyte herbaria (IRK, KPABG, LE, MHA, MW).

Two questionable samples from the Anadyr River Basin (Chukotka Autonomous Region, further – Chukotka) and Kamchatka Peninsula (Kamchatka Province, further – Kamchatka) identified as *T. ambiguus*, were revealed and re-evaluated. Along the way, four *Trematodon longicollis* samples, collected in the Russian Far East were verified, too (Table 1, Appendix 1). The samples from Moneron Island (Kamimura 1939; Bakalin *et al.* 2012) were not examined.

In total, we studied 104 *Trematodon*-samples: 19 are mentioned above (*T. brevicollis*, *T. laetevirens* and *T. longicollis*), and

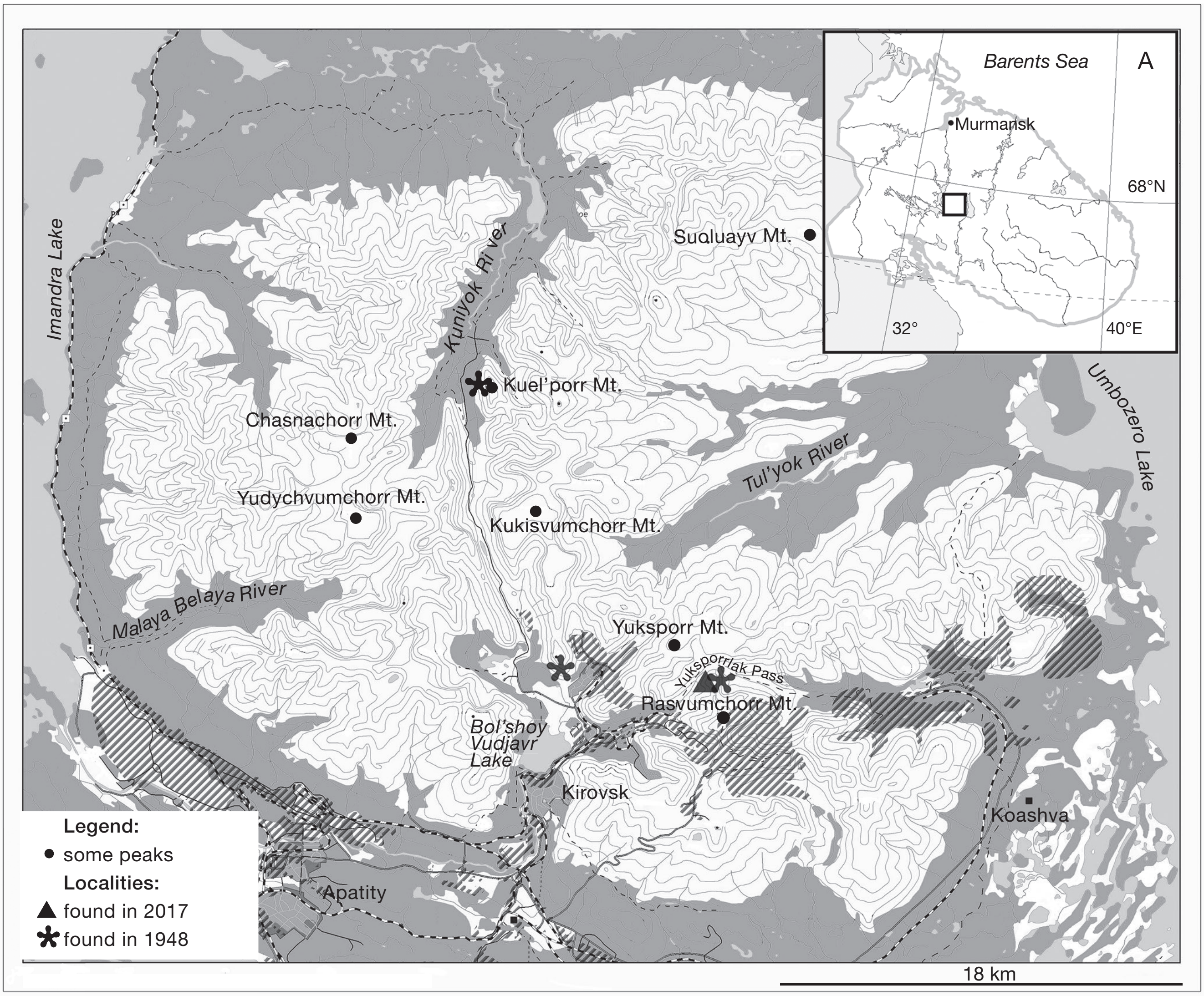

FIG. 1. — Localities of *T. laetevirens* Hakelier & J.-P. Frahm in the Khibiny Mountains (* and ▲): **A**, schemaric map of Murmansk Region and Khibiny Mts. location.

85 are specimens identified by different researchers as *Trematodon ambiguus* and collected in different regions of Russia.

The specimens stored in KPABG are included in "Cryptogamic Information System" (CRIS, http://kpabg.ru/m/), samples in MW are partially entered in "National Depository Bank of Live Systems, Moscow Digital Herbarium" in https://plant.depo.msu.ru/ (Seregin 2017). Most of KPABG, MHA, MW and LE specimens can also be found in the database of the "Moss Flora of Russia" at http://arctoa.ru/Flora/basa.php (Ivanov *et al.* 2017).

In addition to comparing anatomical and morphological features, we analyzed ITS2 nrDNA and *trn*L-F cpDNA nucleotide sequences newly obtained for 14 specimens of *T. laetevirens* and *T. brevicollis* samples, as well as for *T. ambiguus* from Russia (3), for *T. longicollis* from Russia (3) and Japan (1) and for single specimen of *T. boasii* W.B. Schofield from Canada. Additionally, the *trn*L-F sequence of *T. longicollis* from an unknown locality from study by La Farge *et al.* (2002) was included in the dataset. *Ceratodon purpureus* (Hedw.) Brid. was chosen as an outgroup based on La Farge *et al.* (2002), and representative ITS2 and *trn*L-F nucleotide sequences chosen from Nieto-Lugilde *et al.* (2018) (voucher: Spain, MUB Bryophyte 49538, ITS2: KP825881, *trn*L-F: KY229021). In total, nucleotide sequence data for 23 *Trematodon* specimens were included in the molecular analyses (Table 1).

Molecular analyses.

DNA isolation, amplification and sequencing. DNA was extracted from dried moss tissue using the NucleoSpin Plant Kit (Macherey-Nagel, Germany). The amplification and sequencing were performed using primers developed by White *et al.* (1990) for the ITS2 region, and by Taberlet *et al.* (1991) for the *trn*L-F region. PCR was carried out in 20 µL volumes with the following amplification cycles: 3 min at 94°C, 30 cycles (30 s 94°C, 40 s 56°C, 60 s 72°C) and 2 min of final extension time at 72°C. Amplified fragments were visualized

TABLE 1. — The list of studied *Trematodon* Michx. specimens, vouchers and GenBank accession numbers. The sequences downloaded from GenBank for *T. longicollis* Michx. and *Ceratodon purpureus* (Hedw.) Brid. are in **bold**.

NN	Species	Region of the world, field and/or herbarium number of the specimen, herbarium acronym	GenBank accession number ITS2 nrDNA	GenBank accession number trnL-F cpDNA
1.	*Ceratodon purpureus*	Spain, Bryophyte 49538 (MUB)	**KP825881**	**KY229021**
2.	*Trematodon ambiguus* (Hedw.) Hornsch.	Russia, Murmansk Region, Khibiny Mts., Bol'shoy Vudjavr Lake, R.N.Schljakov, #1073; KPABG (M) #9381	MK010990	MK012202
3.	*T. ambiguus*	Russia, Murmansk Region, Lavna-tundra Mts., O.A.Belkina, #329-87; KPABG (M) #9380	MK010991	MK012203
4.	*T. ambiguus*	Russia, Irkutsk Region, Vitim Nature State Reserve, L.V.Bardunov; IRK	MK010992	MK012204
5.	*T. boasii* W.B. Schofield	Canada, British Columbia, Garibaldi Lake, W.B.Schofield, #32990; LE	MK129545	MK135789
6.	*T. brevicollis* Hornsch.	Russia, Irkutsk Region, East Sayan Mts., L.V.Bardunov (1); IRK	MK010987	MK012198
7.	*T. brevicollis*	Russia, Irkutsk Region, East Sayan Mts., L.V.Bardunov (2); IRK	No data	MK012199
8.	*T. brevicollis*	Mongolia, Mongolian Altai Mts., Ts.Tsegmed, #4612; LE	No data	MK012197
9.	*T. brevicollis*	Mongolia, Gobi-Altai Mts., M.S.Ignatov, #01-328; MHA	No data	MK012196
10.	*T. brevicollis*	USA, Arctic Alaska, De Long Mts., W.C.Steere, #16666; LE	MK010988	MK012200
11.	*T. brevicollis*	Denmark, West Greenland, K.Holmen, #13.501; LE	MK010989	MK012201
12.	*T. laetevirens* Hakelier & J.-P. Frahm	Russia, Murmansk Region, Khibiny Mts., Yuksporrlak Pass, O.A.Belkina, #Б57-6-17; KPABG (M) #122909)	MK010986	MK012195
13.	*T. laetevirens* (indentified as *T. brevicollis*)	Russia, Murmansk Region, Khibiny Mts., Yuksporrlak Pass, R.N.Schljakov, #2047; LE	No data	MK012193
14.	*T. laetevirens* (as *T. brevicollis*)	Russia, Murmansk Region, Khibiny Mts., Kukisvumchorr Mt. R.N.Schljakov, #1814; LE	MK010984	MK012192
15.	*T. laetevirens* (as *T. brevicollis)*	Russia, Murmansk Region, Khibiny Mts., Kuel'porr Mt., R.N.Schljakov, #2307; KPABG (M) #9382	MK010985	MK012194
16.	*T. laetevirens* (as *T. ambiguus)*	Russia, Chukotka Autonomous Region, Anadyr' River basin, O.M.Afonina; LE	MK129543	MK135787
17.	*T. laetevirens* (as *T. ambiguus*)	Russia, Kamchatka Peninsula, Ushkovsky volcano, I.V.Chernyadjeva, #45; LE	MK129542	MK135786
18.	*T. laetevirens*	Norway, Oppland, Vågå, N.Hakelier; KPABG (M) #123522	MK010983	MK012191
19.	*T. laetevirens*	Sweden, Jämtland, Åre, Åreskutan, N.Hakelier; LE	MK129544	MK135788
20.	*T. longicollis*	Russia, Khabarovsk Territory, Bureya River, M.S.Ignatov, #97-1124; MHA	No data	MK307895
21.	*T. longicollis*	Russia, Kuril Islands, Kunashir Island, Tyatya Volcano, M.S.Ignatov, #06-1812 (MHA)	No data	MK307893
22.	*T. longicollis*	Russia, Kuril Islands, Kunashir Island, Zmeiniy stream, T.I.Koroteeva, #15-6/1-3, (MHA)	No data	MK307894
23.	*T. longicollis*	Russia, Kamchatka Peninsula, Pauzhetka River, T.Yu.Samkova #3-2; MW #9068429	No data	No data
24.	*T. longicollis*	Japan, Shikoku Island, H.Ando; LE	MK010993	MK012205
25.	*T. longicollis*	Risk 10853 (DUKE)	No data	**AF435352**

on 1% agarose TAE gels by Ethidium bromide staining, purified using the GFX PCR DNA and Gel Band Purification Kit (Amersham Biosciences, United States), and then used as a template in sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, United States) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, United States).

Phylogenetic analyses. The ITS2 and *trn*L-F nucleotide datasets were automatically aligned in BioEdit 7.0.1 (Hall 1999) with ClustalW option and then manually corrected. The preliminary phylogenetic analyses revealed a topology congruence between both datasets and they were then combined. All positions of the final alignment were included in the phylogenetic analysis; absent data at the ends of regions and unsequenced loci were coded as missing. The infrageneric and infraspecific variability of ITS2 and *trn*L-F for *Trematodon* species was estimated as the value of the *p*-distances calculated in Mega 5.1 (Tamura *et al.* 2011) using the pairwise deletion option for counting gaps.

The combined alignment ITS2+*trn*L-F was analyzed under the criteria of maximum parsimony (MP) with TNT v. 1.5 (Goloboff & Catalano 2016) and maximum likelihood (ML) with PhyML v. 3.0 (Guindon *et al.* 2010). The parsimony analysis with TNT involved a New Technology Search with a search for the minimal length tree by five iterations and 1000 bootstrap pseudoreplicates, the default settings were used for other parameters, gaps were treated as missing. The GTR+I+Γ model was selected in the ML analysis as the best-fit evolutionary model of nucleotide substitutions for alignment using the ModelGenerator software (Keane *et al.* 2006), with default settings. Bootstrap support (BS) for individual nodes was assessed using a resampling procedure with 500 pseudoreplicates. According to the stopping frequency criterion (FC) for the bootstrapping procedure (Pattengale *et al.* 2010), 350 replicates were enough for reaching BS convergence with Pearson average ρ100 = 0.994433 as estimated by RAxML v. 7.2.6 (Stamatakis 2006).

RESULTS

Our study of anatomical and morphological features reveals a similarity of specimens from Khibiny, Norway, Sweden, Chukotka and Ushkovsky volcano (Kamchatka) and their correspondence to *Trematodon laetevirens*. General characteristics of plants from these samples and some differences are given in the following description.

Trematodon laetevirens Hakelier & J.-P. Frahm

Lindbergia 3: 223 (1976).

Description

Gametophytes
2-3 mm in height;

Leaves
1.0-1.8 mm long and 0.3-0.6 mm wide, erect spreading or contorted (in Chukotka specimen – leaves slightly falcate and concave), oblong-lanceolate, gradually tapering or on some shoots (in Norwegian, Swedish, Rasvumchorr specimens) rather suddenly narrowed in upper part; leaf margins flat and unistratose, cells in lower part of leaf thin walled, elongate or short-rectangular, 20-60 μm × 12-17 μm, becoming longer and narrower on margins (to 80-100 μm in length) and shorter and quadrate towards the apex (15-35 μm).

Costa
About 100 μm wide (in Norwegian sample – 150 μm, in Kuel'porr – up to 175 μm), occupying ⅓ of leaf lamina base (in Rasvumchorr sample – some wider, in Chukotka' – much wider, about ½ of leaf width), ending in and completely filling the apex, without stereids, in cross section with ventral (adaxial) row of large cells, smaller cells on abaxial side and with equal or just smaller "central" cells with curved or even tortuous walls (like after pressing).

Perichaetial leaves
Larger than others, convolute-sheathing, various in shape and size: one of the inner perichaetial leaves conspicuous – much larger and wider (1.8-2.2 mm long × 0.66-0.8 mm wide), straight, oval (or sometimes almost spathulate), rounded off abruptly at the apex (Khibiny, Kamchatka specimens) or with very short obtuse (angle more than 90°) apiculus (Norwegian and Chukotka specimens); one-two other perichaetial leaves also wide, but smaller, with more or less sharp and long apiculus.

Seta
6-7 mm long (to 9-11 mm in Kukisvumchorr and Kuel'porr and 3.5-6.5 mm in Kamchatka and Chukotka).

Capsule
Erect (in Kukisvumchorr specimen slightly inclined), straight (in Swedish sample slightly curved with angle about 160-170°); capsule neck about equal to the urn in length, about 1.3-1.4 mm long, not strumose, gradually turning into the seta (in Chukotka and Kamchatka specimens the ratio urn – neck is from 1:1.5 to 1:1.7 in some sporophytes).

Exothecial cells
Rectangular, quadrate or irregular shaped, in indistinct rows (in Kuel'porr arranged in more or less clear rows), with slightly thickened walls (in Norwegian and Swedish specimens – with more thickened walls)

Peristome teeth
All or part of them perforated along the midline (sometimes also on sides) and split at the apex (in Kukisvumchorr and Norwegian specimens – slightly perforated or split).

Annulus
Often partly remaining on the urn mouth, double.

Spores
35-38 μm (in Kukisvumchorr 40-45 μm and in Norwegian sample 40-42 (-45) μm), in Khibiny Mts. maturing in September.

Trematodon brevicollis Hornsch.

Flora 2: 88 (1819).

Description

The specimens from East Sayan differ significantly from those of Khibiny and are similar to *Trematodon brevicollis* samples from Mongolia, Alaska and West Greenland. Their characteristics are listed in description below.

Gametophytes
2-4 mm in height,

Leaves
Appressed or slightly contorted, 0.7-1.3 mm long and 0.4-0.6 mm wide, oblong or ovate suddenly or gradually narrowed into more or less long lanceolate upper part (apiculus), leaf margins flat, unistratose, leaf cells rectangular and short-rectangular (30-5 × 5 μm × 10-20 μm) in lower part and the same or shorter (16-40 μm long) in upper part of lamina, often irregular, thin walled.

Costa
100-175 μm wide, occupying about ⅓ of leaf width and filling the uppermost leaf apex, without stereids, in cross

Table 2. — The value of infrageneric and infraspecific *p*-distances for the genus *Trematodon*, n/c – non calculated value due to single specimen only.

Taxon	Within species, ITS2/trnL-F, %	Between species, ITS2/trnL-F, %				
		T. laetevirens	*T. brevicollis*	*T. ambiguus*	*T. longicollis*	*T. boasii*
T. laetevirens Hakelier & J.-P. Frahm	0/0	–	–	–	–	–
T. brevicollis Hornsch.	0.8/0.1	6.8/1.0	–	–	–	–
T. ambiguus (Hedw.) Hornsch.	0.2/0.1	15.2/6.3	13.7/6.0	–	–	–
T. longicollis Michx.	n/c/1.3	14.4/4.0	12.6/3.7	6.5/5.0	–	–
T. boasii W.B. Schofield	n/c/n/c	13.5/5.0	12.3/4.7	3.8/3.3	5.6/3.8	–

section with ventral (adaxial) row of large cells, smaller cells on abaxial side and with equal or just smaller, central cells often with curved walls.

Perichaetial leaves
Differentiated: the largest one – obovate or almost spathulate, with distinct more or less long sharp apiculus (angle less than 90°), 1 or 2 innermost leaves linear-lanceolate and acute, other perichaetial leaves from wide-obovate or obovate base suddenly constricted into rather long subula.

Seta
4-5 mm in East Sayan and Mongolian Altai specimens, 5.5-6 mm in West Greenland, 6-8 mm in Gobi-Altai and Alaska.

Capsule
Curved (when dry at 90-120°, when moist at 120-150°), inclined or rarely almost erect, the capsule neck to urn ratio about 1:1, neck about 1 mm long, not strumose.

Exothecial cells
Thick walled, rectangular or near the mouth quadrate, on convex side of urn (i.e. on upper side of incline capsule) longer and more thick-walled than on concave.

Peristome teeth
Blunt, neither perforated nor split.

Annulus
Sometimes partly remaining, 1-2-rowed.

Spores
(30-) 40-50 (-55) μm in East Sayan specimen, 40-45 μm in others.

Notes on *T. longicollis* specimens from Russia
Four *Trematodon longicollis* specimens from Russian Far East are represented by few plants and have only single or few mature sporophytes. In addition, two samples are in a poor condition – plants (especially capsules) dead, or partially destroyed, or covered with black cyanobacteria and fungi. The plants from the Kunashir (Tyatya volcano)/ Kunashir (Zmeiniy stream)/ Kamchatka Peninsula (Table 1, Appendix 1) have the following features (based on one sporophyte only for the Kunashir and the Kamchatka specimens): seta 8.5/ 8-19/ 11 mm, capsule neck 1.8/ 2.5-3.25/ 2.5 mm, urn 1.3/ 1.0-1.5/ 1.5 mm long, respectively. The length ratios of urn to capsule neck are 1:1.2/ 1:2 - 1:3/ 1:7. In all specimens, the leaf margins are more or less revolute or incurved above (at least on one side) and bistratose in the subula (one cell row along edge). Costa does not entirely fill the subula, and has a ventral (adaxial) row of large thin-walled cells, an abaxial row of smaller cells and well distinguishable stereids in the center. At some site, the large cells of the ventral row are replaced by 2-4 smaller cells with thickened walls, and at the point of transition, 2 or 3 large cells, resembling guide cells, occur below in a second row (under ventral). In Kunashir sample (Zmeiniy stream) having capsule in good mature condition, spores are 22-24 μm, peristome teeth are forked or perforated along middle line.

The specimen from Khabarovsk Territory is difficult to identify: it contains few plants and combines the features both *T. longicollis* and *T. ambiguus* in morphology. The neck to urn length ratio varies between 1:1.2 and 1:2, and in some leaves the costa fills the entire width of the subula width, and in others it completely occupies only the uppermost part of acumen. The latter leaves also have a margin that is bistratose above (in width of one row of cells).

Molecular relationships
The combined nucleotide sequence alignment of ITS2 (516 sites) and *trn*L-F (452 sites) generated for 24 specimens consists of 968 character sites. The numbers of invariable sites in ITS2 and *trn*L-F are 369 (71.51%) and 397 (87.83%), respectively. The matrix comprises 126 (24.42%) and 53 (11.73%) variable ITS2 and *trn*L-F positions, of which 85 (16.47%) and 33 (7.30%) are parsimony informative.

The MP analysis with TNT yielded a single most parsimonious tree of 236 steps, with CI = 0.923729 and RI = 0.958998 and the ML analysis a single tree with a Log likelihood of -2548.072205. The tree topologies recovered under the two criteria are identical (Fig. 2). The 23 *Trematodon* specimens compose two main clades with four subclades. The first subclade (BS = 85% in MP, BS = 99% in ML, or 85/99) contains three specimens from the Murmansk Region identified by R.N. Schljakov as *T. brevicollis*, two specimens of *T. laetevirens* by N. Hakelier from Norway and Sweden, the specimen recently gathered by the senior author from Murmansk Region, and the two specimens from the Kamchatka Peninsula and Chukotka Autonomous Region morphologically somewhat similar to *T. laetevirens*.

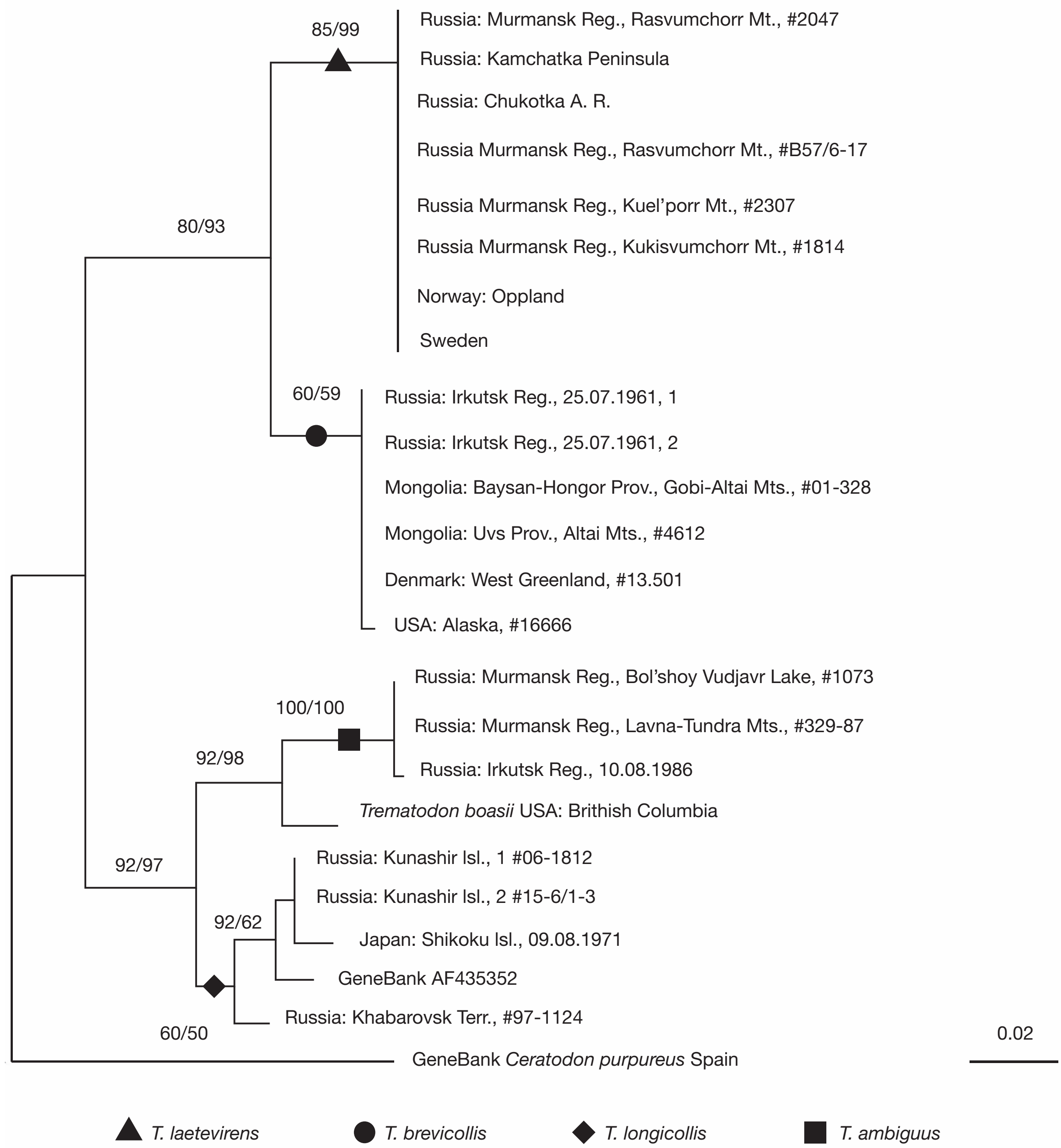

FIG. 2. — Most likely phylogeny inferred from concatenated ITS2 and *trn*L-F data for species of *Trematodon* reported from Russia. Bootstrap support values of maximum parsimony and maximum likelihood analyses (MP/ML) higher than 50% are indicated. Scale: substitution per site.

The second subclade (60/59) consisted of six specimens of *T. brevicollis* from Irkutsk Region, Mongolia, USA and Denmark. The sister group relationships between *T. laetevirens* and *T. brevicollis* is moderately to well supported (i.e., 80/93). Three specimens of *T. ambiguus* from the Murmansk and Irkutsk Regions were located in the third subclade (100/100), *T. boasii* was placed in the sister relation to it (92/98). Five specimens of *T. longicollis* composed the fourth subclade (60/50). The clade of *T. ambiguus*, *T. boasii* and *T. longicollis* had support 92/97.

The variability of ITS2 and *trn*L-F for *Trematodon* species differed within the obtained subclades. Thus, specimens from the first subclade identified as *T. brevicollis* or *T. laetevirens* did not reveal variability in *p*-distances in either locus (ITS2: 0%, *trn*L-F: 0%, or 0/0%; Table 2), but specimens from the Kamchatka Peninsula and Chukotka A.R. differed from others by one repeat of "GCC" motif in the ITS2. The samples of *T. brevicollis* share identical sequences except for the specimen from Alaska, which accounts for the slight variation (i.e., 0.8/0.1%) within the subclade (Table 2).

Within the *T. longicollis* subclade, *trn*L-F sequences differed by 1.3 %, and the two specimens from Kunashir Island shared identical sequences. Unfortunately, we were not able to obtain nucleotide sequence data for *T. longicollis* specimen from Kamchatka Peninsula (#3-2) possibly due to low preservation of DNA in the plants. The level of sequence divergence among the *T. ambiguus* specimens amounts to 0.2/0.1%. As expected, distances between clades are larger, ranging from 5.6 to 15.2% in ITS2 and from 1.0 to 6.3% in *trn*L-F.

DISCUSSION

Specimens of *Trematodon laetevirens* from Khibiny, Norway and Sweden are very similar. Small differences appear in peristome teeth structure, size of spores, capsule position. The leaves of *T. laetevirens* tend to gradually narrow, but an abrupt narrowing in the lower third or half is not uncommon. Although some deviations from typical characters were observed, comparison of the nucleotide sequence data reveals that all the Khibiny specimens are identical to each other and to the *T. laetevirens* samples from Norway and Sweden (Fig. 2).

Trematodon laetevirens samples from Russian Far East differ from European ones by a shorter seta, and capsule neck, which is 1.5-1.7 times as long as the urn. Furthermore, the samples from Chukotka have perichaetial leaves with a well-pronounced blunt apiculus and their vegetative leaves on sterile shoots have a wide strong costa (about ½ of leaf base width). In addition, the nucleotide sequences of Far Eastern plants possess a deletion of three base pairs in the ITS2 compared with Europeans samples. These minor differences may indicate the beginning of an evolutionary process toward isolation the western and eastern populations. But taking into account the phylogenetic position and the level of nucleotide sequence variability we treat the specimens from Murmansk Region, Kamchatka and Chukotka as belonging to a single species, namely *T. laetevirens*.

The stable diagnostic characteristics for *T. laetevirens* can be recognized: 1) the shape of one of the inner perichaetial leaf, making it conspicuous in field work, being bigger and wider than other perichaetial leaves, straight and rounded at the apex or have a short blunt apiculus (other perichaetial leaves consist of an elongated, lanceolate or oval base and abruptly taper to the long subula or sharp apiculus); 2) rectangular-quadrate exothecial cells with slightly thickened walls; 3) an erect, straight capsule on most sporophytes and the lack of a struma; and 4) perforated and cleaved teeth of the peristome. The size of the spores varies among samples, but 35-40 µm spores prevail. In *T. brevicollis*, the transition of the neck to the seta can be abrupt or gradual, but in *T. laetevirens* it is always gradual, difficult to discern. The length ratio of capsule neck to urn varies among samples of different geographic regions: 1/1 in European samples, 1/1-1/1.5 (in a few sporophytes) in samples from the Pacific Region. The annulus is often not preserved or remains partially and incompletely attached, so we could not evaluate its significance for species identification. *Trematodon laetevirens* occurs mostly in mountains, above treeline and is currently known from northern Europe, Asia and North America, and exhibit a disjunctive distribution.

Specimens of *T. brevicollis* from the East Sayan differ clearly from those from Khininy in a number of characteristics – shape of the inner perichaetial leaves, exothecial cells, curved capsule, blunt whole peristome teeth, size of spores and are identical to the other examined *T. brevicollis* samples from Arctic Alaska, West Greenland and Mongolia. The most variable feature is the length of the seta – from 0.4 mm in specimens from Mongolian Altai and in one of two specimens from East Sayan to 8 mm in Alaska.

Trematodon brevicollis occurs on bare soil enriched humus or on sandy soil, in tundra or on rock shelves and crevices, in the Arctic and in mountain alpine zone (included the East

Key to Russian species of *Trematodon* Michx.

1. Costa in cross section with stereids; capsule neck strumose on most of mature sporophytes; neck equal of urn or much longer 2
— Costa in cross section without stereids; capsule neck not strumose on mature sporophytes; length of neck almost equal of urn or, in Far East, sometimes longer 3

2. Capsule neck about 1.3 time the length of urn or much longer; costa not filling the entire width of the linear-subulate acumen; leaf more or less gradually narrowed to upper part; leaf margins bistratose in subula .... *T. longicollis* Michx.
— Capsule neck about the length of urn; costa filling the entire width of the subula; leaf from obovate or oblong base suddenly narrowed to long subula .... *T. ambiguus* (Hedw.) Hornsch.

3. The largest perichaetial leaf straight, oblong or spathulate, rounded on the apex or with very short obtuse apiculus; capsule straight, erect on most plants; transition of the neck to the seta gradual and difficult to discern; exothecial cells rectangular to quadrate, with slightly thickened walls; peristome teeth perforated along tooth length and split above; on sterile plants stem leaves from obovate or elongate-obovate base gradually narrowed to long upper part. .... *T. laetevirens* Hakelier & J.-P. Frahm
— Largest perichaetial leaf with acute more or less long apiculus; capsule mostly incurved, more or less inclined; transition of the neck to seta gradual, but clearly visible; exothecial cells narrow, thick walled; peristome teeth usually whole, blunt; on sterile plants stem leaves suddenly or more gradually narrowed to long upper part ... . *T. brevicollis* Hornsch.

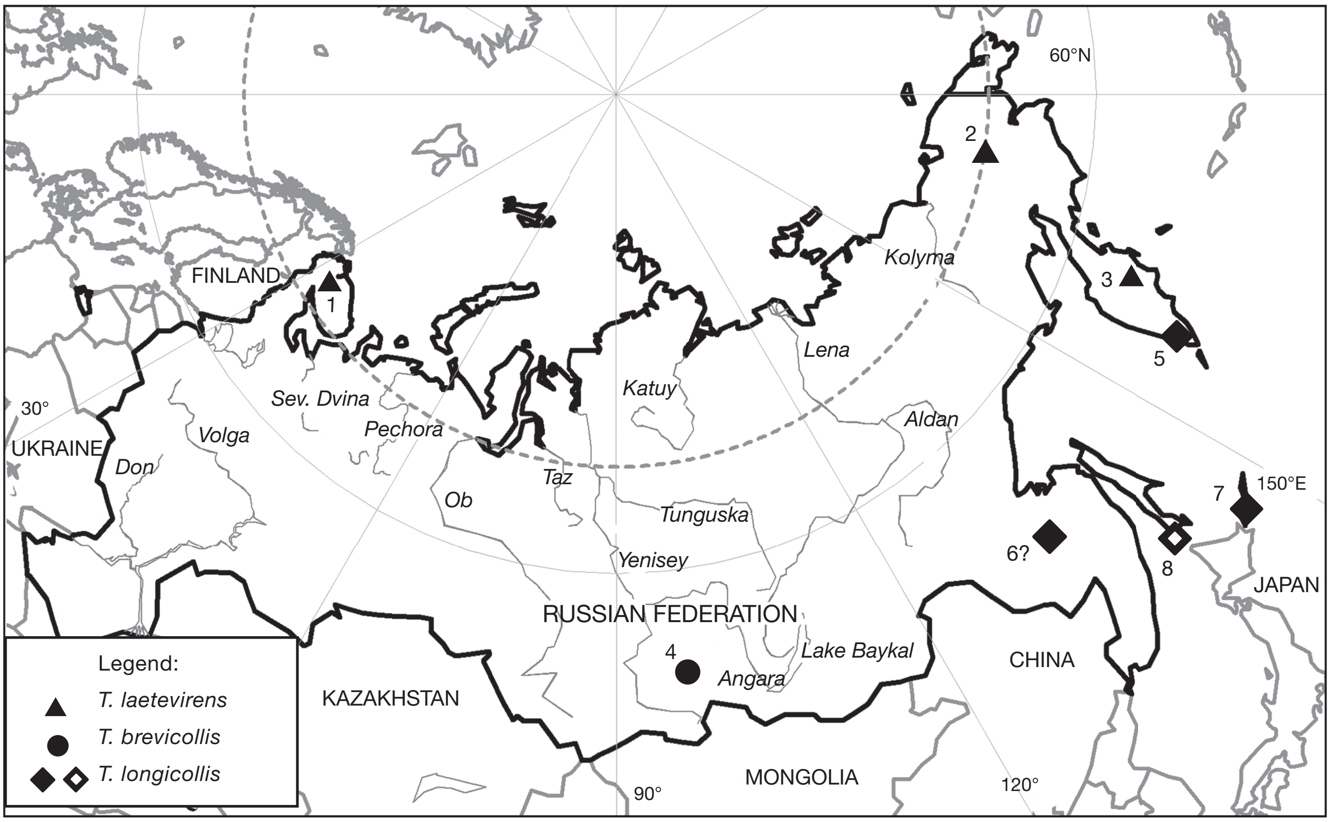

Fig. 3. — Distribution of *T. laetevirens* Hakelier & J.-P. Frahm (1-3), *T. brevicollis* Hornsch. (4) and *T. longicollis* Michx. (5-8) in the Russian Federation (8 – open symbol – samples not examined)

Sayan population of this species) in northern Europe, central Asia, eastern Siberia (east Sayan), Alaska and Greenland (Savicz-Ljubitzkaja & Smirnova 1970; Hallingbäck 2006; Zander 2007).

Plant parameters in specimens from Kunashir Island (Tyatya Volcano and Zmeiniy stream) and Kamchatka (Pauzhetka River) presented above corresponded to the range of characteristics given for *T. longicollis* (Cao & Gao 1988; Crum 1994; Duarte Bello 1997; Gao *et al.* 1999; Ramsay *et al.* 2018). They are, however, intermediate to those given for *Trematodon* species in Japan (Iwatsuki & Suzuki 2006) – the length of urn, capsule neck and their ratio as well as size of seta. The sporophytes of *T. longicollis* from the Russian Far East are smaller in size and have a shorter capsule neck compared to Japanese specimens. The taxonomic status of plants from Khabarovsk Territory (Bureya River) is not clarified exactly now and need further investigation and more materials. Nevertheless, the molecular genetic analysis confirmed that samples from the Khabarovsk Territory, Kunashir Island and Japan belong to a single clade. Considering morphological and molecular variability of *T. longicollis* in the Far East, further study is needed to describe existing diversity and verify the taxonomic identity.

At present, four species of the genus *Trematodon* are confirmed for Russia: *T. ambiguus, T. brevicollis, T. laetevirens* and *T. longicollis*. The first species is widespread, but not frequent. It occurs from the Arctic to the Caucasus and from the European part of Russia to Siberia and Far East, including Kamchatka Peninsula. The other three species are rare in Russia, their distribution is shown in Fig. 3.

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APPENDIX 1. — The list of vauchers for the studied specimens of *Trematodon brevicollis* Hornsch., *T. laetevirens* Hakelier & J.-P. Frahm and *T. longicollis* Michx. from Russia (square brackets – approximate coordinates based on data in the labels). *Numbers correspond to Table 1.**golets – bald peak, mountain cold rocky desert in upper part of mountains in Russian Asia (Siberia, Far East).

N N*	Species	Vaucher of the specimens, herbarium acronym
6	*Trematodon brevicollis*	Russia, Irkutsk Region, East Sayan Mts.,Uda River basin, upper reaches of Bol'shoy Khangorok Creek, golets**, [53.4111°N, 97.6689°E], 2050 m elev., bank of the stream; on bare soil. 25.07.1961, L.V.Bardunov (1), IRK
7	*T. brevicollis*	loc. cit., Dryas-tundra. 25.07.1961, L.V.Bardunov (2), IRK
12	*T. laetevirens*	Russia, Murmansk Region, Khibiny Mts., northern spur of Rasvumchorr Mt. on Yuksporrlak Pass, 67.66082°N, 33.84192°E, 606 m elev., mountain tundra zone, west exposed wet cliff, narrow ledges, on soil; 16.08.2017. O.A.Belkina, #Б57-6-17, KPABG (M) #122909
13	*T. laetevirens*	loc.cit., northern spur of Rasvumchorr Mt. on Yuksporrlak Pass, in crevice of cliff. 08.08.1948, R.N.Schljakov, #204, LE
14	*T. laetevirens*	loc.cit., southern spur of Kukisvumchorr Mt. [67.6608°N, 33.6922°E], middle part of southern slope, 16.08.1948, R.N.Schljakov, #1814, LE
15	*T. laetevirens*	loc.cit., Kuel'porr Mt., upper part of western slope, [67.7736°N, 33.6131°E], mountain tundra zone, cliff shelf, 6.09.1948, R.N.Schljakov, #2307, KPABG (M) #9382
16	*T. laetevirens*	Russia, Chukotka Autonomous Region, Anadyr' River basin, upper reaches of Belaya River, Enmyvaam Creek, 66.40°N, 173.29°E, upper part of a hill, *Dryas-Carex*-moss-dominated tundra. 09.07.1980, O.M.Afonina, LE
17	*T. laetevirens*	Russia, Kamchatka Province, Kamchatka Peninsula, Klyuchevskaya group of volcanoes, Ushkovsky volcano, western slope, 58.2500°N, 160.2500°E, 1260 m elev., rocks, in a crevice, 20.08.2005, I.V.Chernyadjeva, #45, LE
20	*T. longicollis*	Russia, Khabarovsk Territory, Verkhne-Bureinsky District, right bank of Bureya River, Tastakh Creek mouth, 51.5833°N, 133.6833°E, 430 m elev., old road, on soil, 29.08.1997, M.S.Ignatov, #97-1124, MHA
21	*T. longicollis*	Russia, Kuril Islands, Kunashir Island, main conus of Tyatya Volcano, 44.3333°N, 146.2667°E, 1800 m elev., crater mouth, 14.09.2006, M.S.Ignatov, #06-1812, MHA
22	*T. longicollis*	Russia, Kuril Islands, Kunashir Island, Okhotsk Sea shore, Zmeiniy stream, 1 km from away sea shore, Stolbovskie thermal springs, 44.0069°N, 145.6833°E, 6-10 m elev., on hot soil, 06.08.2015, T.I.Koroteeva, #15-6/1-3, MHA
23	*T. longicollis*	Russia, Kamchatka Peninsula, Ust-Bolsheretzk District, upper terrace on right side of Pauzhetka River, 51.4667°N, 156.8167°E upper thermal field, 170 m elev., on hot substrate, 01.18.2006, Samkova T.Yu. #3-2, MW #9068429