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ORTHOTHECIUM LAPPONICUM: A DISJUNCTIVE CIRCUM-HOLARCTIC SPECIES

ORTHOTHECIUM LAPPONICUM: ДИЗЪЮНКТИВНЫЙ ЦИРКУМ-ГОЛАРКТИЧЕСКИЙ ВИД

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Abstract

Orthothecium lapponicum, considered by many authors as a mere infraspecific taxon of the widespread *O. chryseon*, was subsequently shown to be a morphologically distinct species. Initially known only from the mountains of Northern Sweden, subsequent investigations revealed its occurrence also in Spitsbergen. Here we document its further distribution on Ellesmere Island in Canada, and in the Verkhoyansk and Chersky Mountains of Yakutia. Molecular phylogenetic analysis of the nuclear ITS region showed that specimens of *Orthothecium lapponicum* from Europe, Asia and North America are fully identical and highly supported as a discrete clade in Bayesian and maximum parsimony analyses, supporting its status as a good species. Descriptions and illustrations are given in order to facilitate further discovery of the species, although the very restricted range of the species seems to be real, and not simply an artifact of undercollecting or lack of recognition.

Резюме

Orthothecium lapponicum еще недавно рассматривался многими авторами лишь как внутривидовой таксон широко распространенного *O. chryseon*, однако впоследствии было показано, что это хорошо отграниченный по морфологическим признакам вид. Он был изначально известен только из горных районов Северной Швеции, а затем найден также на Шпицбергене. В данной статье мы приводим находки этого вида на о. Элсмир в Канаде и в горных системах Верхоянья и Черского в Якутии. Молекулярно-филогенетический анализ последовательностей ДНК ядерного участка ITS показал, что образцы *Orthothecium lapponicum* из Европы, Азии и Северной Америки полностью идентичны по этому маркеру и образуют хорошо поддержанную кладу в деревьях, построенных по методу Байеса и максимальной парсимонии, что подтверждает самостоятельный статус этого вида. Приведены описание и иллюстрации вида для того, чтобы помочь выявить дополнительные образцы, хотя, по-видимому, редкость находок этого вида отражает его реальное распространение, а не является артефактом недостаточных сборов или нераспознанности.

KEYWORDS: Bryophytes, biogeography, phylogeny, taxonomy

INTRODUCTION

Orthothecium lapponicum (Schimp.) C. Hartm. was described from northern Sweden by Schimper (1860). Most subsequent authors treated it merely as a form of the highly polymorphous *Orthothecium chrsyeon* (Schwägr.) Schimp. (Limpricht, 1895; Roth, 1905; Brotherus, 1923; Jensen, 1939; Mårtensson 1956), or occasionally of *O. strictum* Lor. (Nyholm, 1965). In general it has been accepted as an infraspecific unit, or simply as a synonym, especially in literature from the second half of the 20th century (Corley *et al.,* 1981).

The species was thus ignored until Hedenäs (1988) resurrected it, clarifying its distribution in northern Scandinavia and highlighting its distinction from both *O. chryseon* and *O. strictum*. The main reason for the long neglect of *O. lapponicum* was probably its rarity. Hedenäs (1988) found only eight specimens of *O. lapponicum* out of 405 herbarium specimens of *Orthothecium* species deposited under *O. strictum, O. lapponicum, O. chryseon,* and *O. rufescens* (i.e. excluding only *O. intricatum*, which is unlikely to be confused with *O. lapponicum*). Since then, no fewer than 28 collections of this species were gathered (Stockholm herbarium database: http://herbarium.nrm.se/, accessed on 15 Nov 2019), all from four provinces in Northern Sweden: Torne Lappmark, Lule Lappmark, Pite Lappmark, and Lycksele

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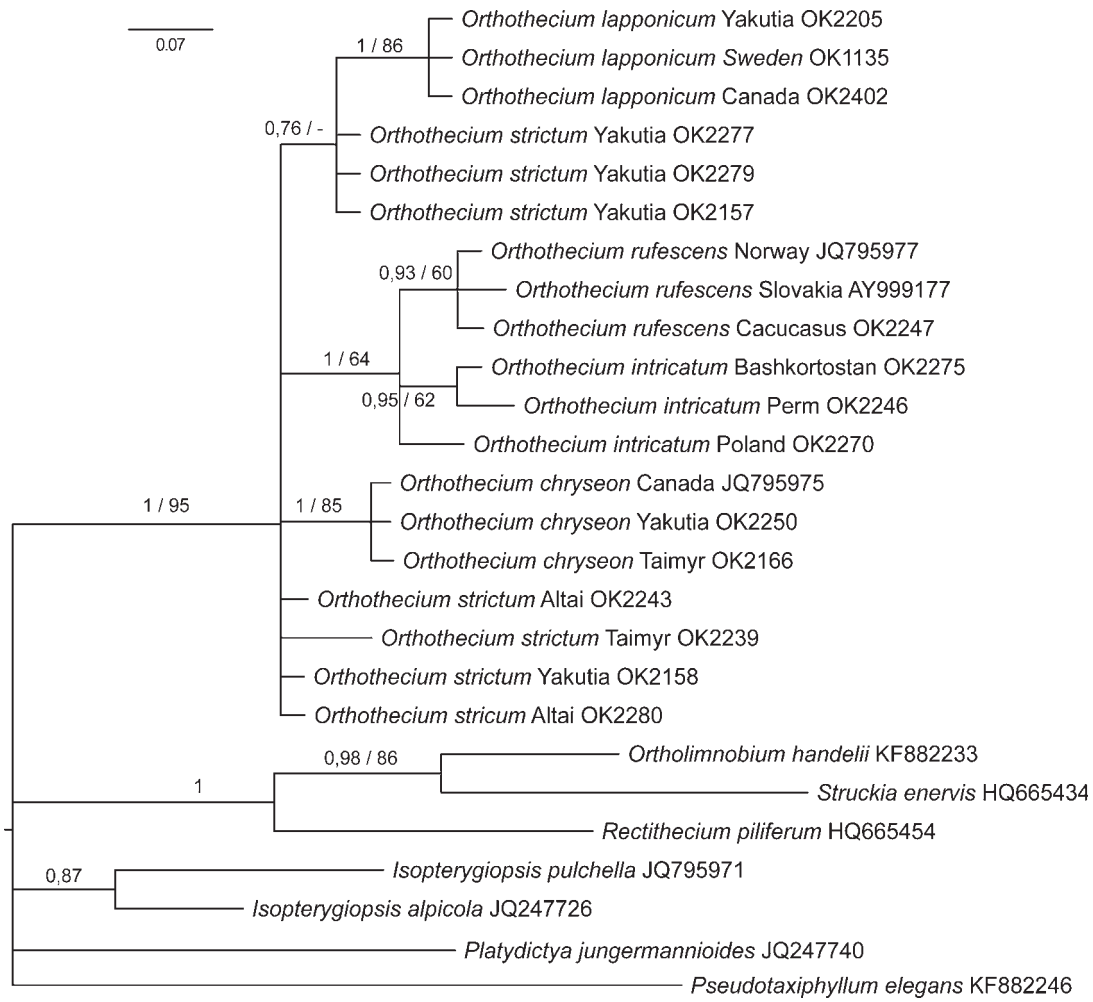

Fig. 1. Bayesian molecular phylogenetic tree inferred from the nrITS dataset. Posterior probabilities from Bayesian analysis (>70) and / bootstrap support from MP analysis (>60) are shown at nodes.

Lappmark. The map published by Hedenäs *et al.* (2014) therefore looks fairly similar to that published a quarter century ago, in Hedenäs (1988). Additional observations were reported at Artsdatabanken in Norway and Artportalen in Sweden (https://www.artsdatabanken.no; https://www.artportalen.se/; both accessed 20 November 2019), adding further Swedish localities and also several from northern Norway and Svalbard.

In the course of bryological explorations in recent years, and revisions of previously collected specimens, plants of a similar morphology were found in Yakutia (Eastern Siberia) and in the Canadian Arctic. Because these localities are so distant from the well-confirmed Scandinavian range, the specimens were additionally checked for their identity by molecular markers.

MATERIAL AND METHODS

Specimens of *O. lapponicum* from northern Sweden (near the "locus classicus"), Yakutia and Canada were sampled for DNA analysis. The nuclear ITS1-5.8S-ITS2 region was studied as it is one of the most informative markers for pleurocarpous mosses (cf. Huttunen *et al*., 2012). Attempts to add *trn*L-*trn*F and *rpl*16 were not successful, as these sequences displayed low variation and for many collections failed to amplify.

Total genomic DNA was extracted from dry plants using the Nucleospin Plant Extraction Kit (Macherey-Nagel, Germany). The laboratory protocol was essentially the same as used in previous moss studies, described in detail by, *e.g.,* Gardiner *et al.* (2005).

Sequences were aligned by Clustal and modified manually using BioEdit 7.0 (Hall, 1999). Bayesian analysis of the ITS dataset was conducted in MrBayes (Huelsenbeck & Ronquist, 2001) using the GTR+G model. Analyses were run on the Cipres Science Gateway (http://www.phylo.org/portal2) on XSEDE for 50,000,000 generations, with sampling every 1000 generations, with 20,000,000 generations; the chain temperature was set at 0.02. The first 25% of sampled trees was discarded as the burn-in. Supplementary maximum parsimony (MP) analysis was performed in Nona (Goloboff, 1994) run under a Winclada shell (Nixon, 1999), with bootstrap calculation for 2000 replications (N searches 100, starting trees per rep 100, max trees 100, do max).

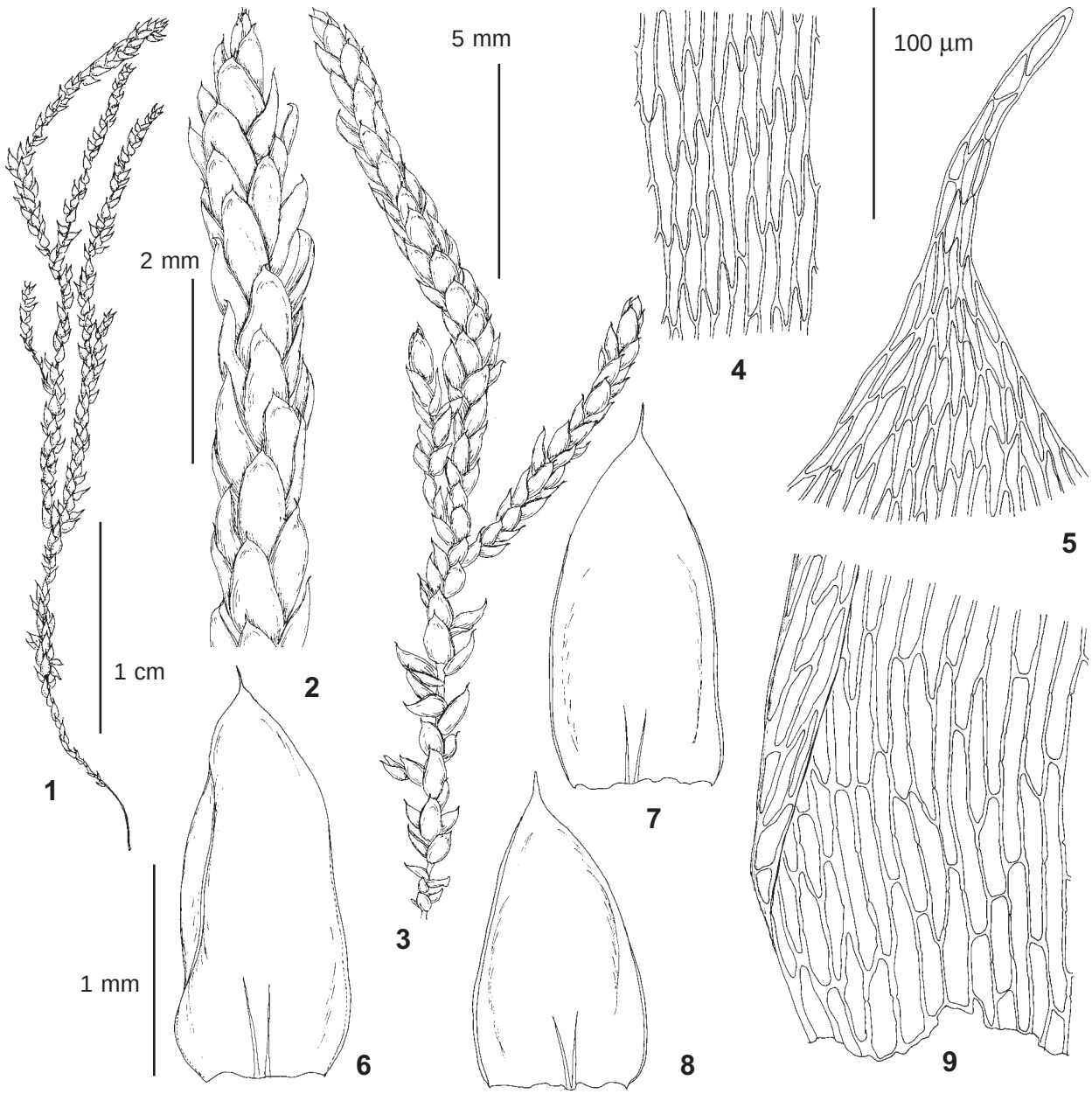

Fig. 2. *Orthothecium lapponicum* (Russia, Yakutia, Suntar-Khayata Mt. Range, 8.VII.2005, *Nikolin*, MHA): 1–3 – habit, dry; 4 – median laminal cells; 5 – upper laminal cells; 6–8 – leaves; 9 – basal laminal cells. Scale bars: 1 cm for 1, 5 mm for 3, 2 mm for 2; 1 mm for 6–8; 100 µm for 4–5, 9.

Results

The ITS alignment of *Orthothecium* (without outgroups) includes 15 substitutions (10 parsimony informative) and five indels (four parsimony informative). Of these, three parsimony informative substitutions are unique to *O. lapponicum*. The molecular phylogenetic tree resolved *Orthothecium* in a clade with maximal support in Bayesian analysis and high support in MP (BS=96). The *Orthothecium* clade is composed of a polytomy of individual *O. strictum* specimens plus three clades: 1) a highly supported clade of *O. chryseon* (PP=1, BS=87); 2) a clade of *O. rufescens+O. intricatum* (PP=1, BS=64), including a clade of three *O. rufescens* (PP=0.93, BS=60), two specimens of *O. intricatum* from the Urals (PP=0.95, BS=64), and a Central European *O. intricatum*, and 3) a poorly supported clade (PP=0.76, BS<50) with *O. strictum* specimens forming a basal grade, within which a highly supported (PP=1, BS=85) clade of *O. lapponicum* is resolved.

Discussion

The three geographically disparate specimens of *Orthothecium lapponicum* were recovered as a clade with support nearly as high as for *Orthothecium chryseon*, and higher than the other three species of the genus. The three unique parsimony informative substitutions found for *O. lapponicum* are also unique in the broader alignment of the region for 200 samples used in various previous stud-

Fig. 3. Habit of dry herbarium specimens of three species of *Orthothecium* from specimens used for DNA study, see Appendix for more details. **A:** *O. stricum* (Altai, isolate OK2280); **B:** *O. lapponicum* (Canada, isolate OK2402); **C:** *O. chryseon* (Russia, Yakutia, isolate OK2250), **D–E:** *O. lapponicum* (Yakutia, isolate OK2205); **B:** *O. lapponicum* (Sweden, isolate OK1135). Scale bars is 1 mm for all three species.

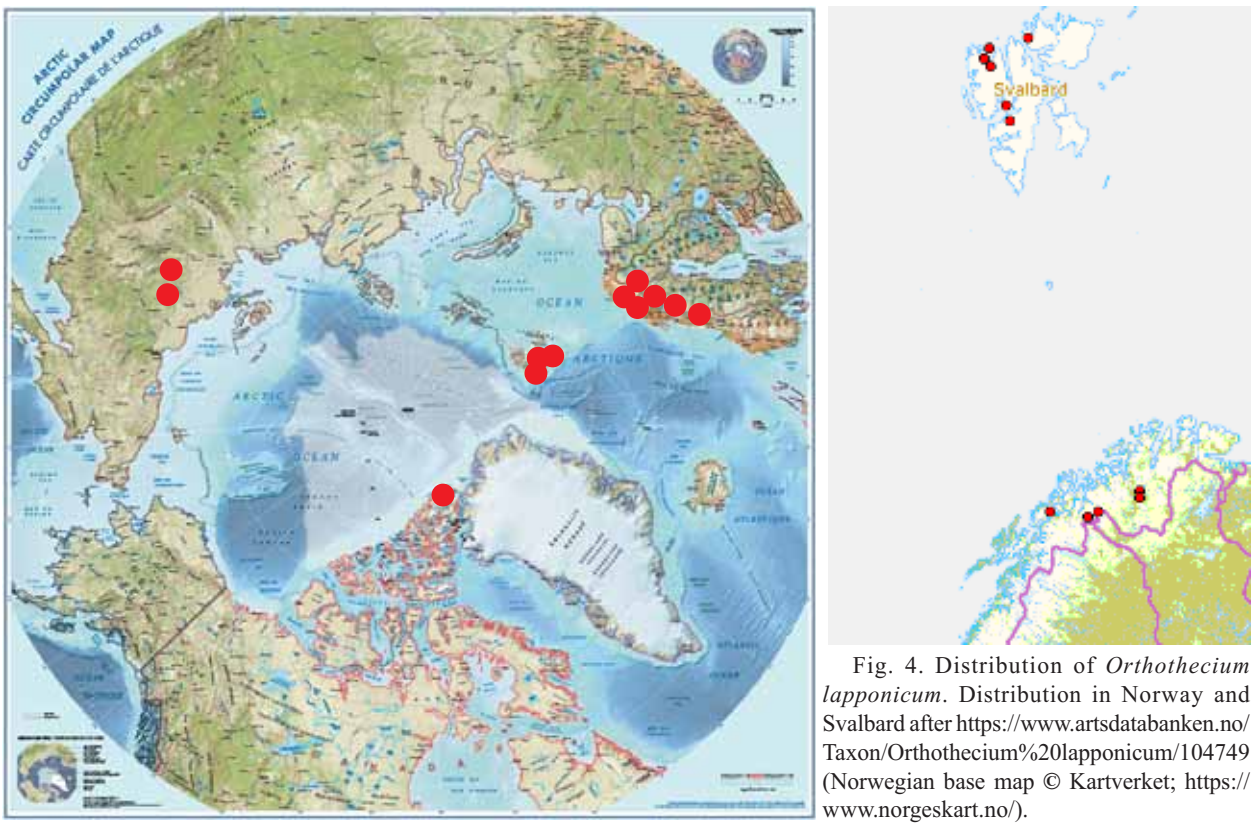

Fig. 4. Distribution of *Orthothecium lapponicum*. Distribution in Norway and Svalbard after https://www.artsdatabanken.no/Taxon/Orthothecium%20lapponicum/104749 (Norwegian base map © Kartverket; https://www.norgeskart.no/).

ies of the Plagiotheciaceae (Huttunen *et al.*, 2013; Wynns *et al.*, 2016; Li *et al.*, 2015; Ignatova *et al.*, 2019).

Thus, the evidence for the monophyly of *O. lapponicum* is strong, and its segregation as a good species is fully confirmed. Here we provide an updated description and add illustrations based on our now wider geographic sample in order to facilitate further searches for this interesting species.

Orthothecium lapponicum (Schimp.) C. Hartm., Handb. Skand. Fl. ed. 10, 2:29. 1871. — *Brachythecium lapponicum* Schimp., Syn. Muse. Eur. 697. 1860. — *Ortholhecium chryseon* var. *lapponicum* (Schimp.) Lindb. in G. Roth, Eur. Laubm. 2:397. 1905. Holotype in BM!, isotypes in UPS!, H-SOL! (see Hedenäs, 1988).

Plants in loose tufts, rather soft, golden yellow to yellow-brown to bright red, moderately lustrous. Stems ± julaceous, to 5 cm long, simple or occasionally irregularly branched, branches similar to stems, easily detached, usually rhizoid-bearing at their base and forming an acute angle with the stem; central strand present; hyalodermis absent, outer cortical cells thick-walled in 2–3 layers; rhizoids axillary, purple to purplish brown, granular-papillose when young; dormant branch initials not surrounded by any foliose structures; axillary hairs sparse, about 5–11µm wide, their upper part 1–4-celled, the basal cell pale brown. Stem leaves imbricate to slightly spreading, ovate, not or hardly decurrent, rather suddenly narrowed to acute or acuminate and mostly recurved apex, strongly concave and not or hardly plicate, 1.0-2.3 mm long and 0.5-0.9 mm wide; leaf margins narrowly recurved from base nearly to apex, entire or finely denticulate just below leaf apex; costa short and double, rarely single; median leaf cells 40–95 µm long and 5–10 µm wide, epapillose, slightly to strongly incrassate and porose; the basal-most cells shorter, wider, more strongly incrassate and strongly porose, usually orange or reddish; alar cells not differentiated. Branch leaves similar to the stem leaves. Dioicous. Only male plants seen [Swedish, Canadian and Siberian plants are sterile]. Inner perichaetial leaves of unfertilized perichaetia lanceolate, long-acuminate, entirely or partly orange-brown; margins irregularly dentate or denticulate, unbordered; nerve short and double or absent. Sporophytes unknown.

Distinction: *Orthothecium lapponicum* differs from *O. strictum* in having larger plants with concave and ovate leaves that are abruptly tapered to a short acumen, versus moderately concave, ovate-lanceolate leaves that are gradually tapered to a rather long acumen. *Orthothecium chryseon* usually has a gradually tapered leaf, although there are morphotypes with overall leaf shape more or less similar to *O. lapponicum*; in the latter case, strong leaf plication and hooked leaf apices in many leaves (cf. Figs. 3 B and C) are the most reliable characters for plant recognition in the field. Usually *O. chryseon* is a tall plant, often reaching decimetres in length, and in Arctic fens even over two decimetres, and thus is generally larger than *O. lapponicum*. Furthermore, the strongly concave leaves of the latter make its shoots tumid and sometimes wider that those of the appressed-leaved *O. chryseon* (Fig. 3). Another good character is found in

Fig. 5. *Orthothecium lapponicum* growing at the margin of a small brook (Mt. Raavriedenjuenie, Lycksele Lappmark, Sweden). Habitat (above) and habit (below). Photo by L. Hedenäs.

the mid-leaf cells; these are elongate, with a length to width ratio of 5–10:1 in *O. lapponicum* versus linear, and mostly 10–20:1 in *O. chryseon.*

Distribution and ecology. At the time of the first modern paper on the species (Hedenäs, 1988) there were few data on species habitats in Sweden. According to more recent database data (http://herbarium.nrm.se/, accessed 14 Nov. 2019), *Orthothecium lapponicum* is mostly found at elevations between 700 and 1240 m, with the lowest locality at 460 m. It most commonly grows in close proximity to late snow-beds, on slopes below these on wet soil or rocks, often with trickling meltwater, or sometimes at the margins of small brooklets.

In Yakutia, *Orthothecium lapponicum* was found two times. One locality in the mountain range Ulakhan Chistai (whatershed of Kolyma and Indigirka Rivers), at 1000 m alt., is in a marble mountain, a habitat of *Andraeobryum*; this area is described and illustrated by Ignatov *et al.* (2018). Another Yakutian locality, ca. 500 km from the first, is at 533 m alt., at the edge of the calcareous area, near one of *Andraeobryum* locality. In both places, *O. lapponicus* grew on wet moderately shaded rocks.

In the only known Canadian locality the species was abundant on the margins of a meltwater stream ca 3 km downstream of a glacier, on soils derived from thin-bedded shales. Colonies were bright red, and nearly overlooked as the very abundant and common *Bryum cryophilum* Mårtensson. Despite extensive collections in the area, the species was only found once.

Since its resurrection at the end of the 1980ies, *Orthothecium lapponicum* has been found at numerous localities in the Scandinavian mountains, as well as at a handful of sites in Svalbard (Fig. 4). This shows that once the species and its habitat are known it is likely to be found at new places. Even if the species is globally rare, it is clear that it is only moderately rare in northern Scandinavia. The finds from North-Western Europe and

Svalbard, as well as the new finds from Ellesmere Island and East Yakutia, are all from cold or very cold areas. Even if we can now expect further finds from other areas with similar climates, we believe that, overall, *O. lapponicus* is not a common species and that the warming climate will cause shrinking of areas with potentially suitable habitats.

Selected specimens studied: **Sweden.** Lycksele Lappmark, Tärna, Mt. Raavriedenjuenie, 2016, *L. Hedenäs*, S; reg. no. B237312. Pite Lappmark, Arjeplog, Merkenes, 1918, *H. Möller*, S; reg. no. B113367. Pite Lappmark, Arjeplog, N of Mávasjávrre, Mt. Lulep Guhkavárddo, 2015, *L. Hedenäs et al*., S; reg. no. B223770. Pite Lappmark, Arjeplog, N of Mávasjávrre, Mt. Ákháris, 2015, *L. Hedenäs et al.*, S; reg. no. B227608. Pite Lappmark, Arjeplog, Mt. Skärrim, 2017, *L. Hedenäs et al.*, S; reg. no. B258086. Pite Lappmark, Arjeplog, Mt. Tjápkávárddo, 2017, *L. Hedenäs et al.*, S; reg. no. B259665. Lule Lappmark, Jokkmokk, Kasakpoulta, 2005, *T. Hallingbäck* TH 43401, S; reg. no. B217031. Lule Lappmark, Jokkmokk, Kierkevare, 2002, *H. Weibull* TH 38402, S; reg. no. B217026. Lule Lappmark, Jokkmokk, KÍbrek, 2005, *T. Hallingbäck* TH 43277, S; reg. no. B217029. Lule Lappmark, Jokkmokk, Unna Titer (Dijdder), Padjelanta, 2007, *T. Hallingbäck* TH 45261, S; reg. no. B217033. Torne Lappmark, Jukkasjärvi, Abisko nat. p., Kårsajåkka, 1990, *L. Hedenäs*, S; reg. no. B236586. Torne lappmark, Jukkasjärvi, Garddecohkka, 2014, *N. Lönnell* 3784, S; reg. no. B218787. Torne Lappmark, Jukkasjärvi, Björkliden, Rákkasorda, 2017, *L. Hedenäs*, S; reg. no. B263400. Torne Lappmark, Jukkasjärvi, Vassijaure, Vássečohka, 2017, *L. Hedenäs*, S; reg. no. B263253. Torne Lappmark, Karesuando, Pältsa, 2011, *T. Hallingbäck 5567*, S; reg. no. B188876. **Russia**: Yakutia, Momsky Distr., Mramornaya Mt., *Ignatov & Ignatova 18-1535*, MHA. Yakutia, Tomponsky Distr., 63°03'38"N, 137° 51'15"E, 533 m elev., *N.B. Ermakov, E.I. Troeva, E.G. Nikolin,* 8 Jul 2005 (MHA, SASY). **Canada**. Nunavut, Ellesmere Island, coll. *Hedderson* 8 Aug 1988 (NFLD).

Acknowledgements

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APPENDIX. *Orthothecium* speciemens used for sequencing and their Genbank accession numbers

O. lapponicum Yakutia (Russia, Yakutia, Momsky Distr., Mramornaya Mt., coll. Ignatov & Ignatova 18-1535 (MHA); isolate OK 2205) MN794384

O. lapponicum Sweden (Sweden, Pite Lapmark, coll. Hedenäs 9 Aug 2015 (S-B227367); isolate OK 1335) MN794385

O. lapponicum Canada (Canada, Nunavut, Ellesmere Island, coll. Hedderson 8 Aug 1988 (NFLD); isolate OK 2402) MN794386

O. chryseon Yakutia (Russia, Yakutia, Orulgan Range, coll. Ignatov 11-3974 (MHA); isolate OK 2250) MN794387

O. chryseon Taimyr (Russia, Taimyr, Anabar, coll. Fedosov, 08-54 (MHA); isolate OK 2166) MN794388

O. strictum Altai (Russia, Altai, Tokpak, coll. Ignatov 36/42 (MHA); isolate OK 2243) MN794389

O. strictum Taimyr (Russia, Taimyr, Anabar, coll. Fedosov 05-133 (MHA); isolate OK 2239) MN794390

O. strictum Yakutia (Russia, Yakutia, Lenskie Stolby, coll. Ignatov & Ignatova, 16-487 (MHA 9021376); isolate OK 2158) MN794391
O. stricum Altai (Russia, Altai, coll. Ignatov 0/1020 (MHA); isolate OK 2280) MN794392
O. strictum Yakutia (Yakutia, Saakhtaany, coll. Pisarenko 01053 (MHA); isolate OK 2277) MN794393
O. strictum Yakutia (Russia, Yakutia, Orulgan Range, coll. Ignatov 11-4526 (MHA); isolate OK 2279) MN794394
O. strictum Yakutia (Russia, Yakutia, Tomponsky Distr., Sakkyryr, coll. Ignatov & Ignatova, 17-635 (MHA 9025425) (isolate OK 2157) MN794395
O. rufescens Caucasus (Russia, Krannodar Territory, Fisht Mt., coll. Ignatov 19 Aug 1999, s.n. (MHA); isolate OK 2247) MN794396
O. intricatum Bashkortostan (Russia, Bashkortostan, coll. Baisheva 135-07 (MHA ex UFA); isolate OK 2275) MN794397
O. intricatum Perm (Russia, Perm Province, coll. Bezgodov, 17 Aug 2014 #477 (MHA); isolate OK 2246) MN794398
O. intricatum Poland (Poland, coll. Ignatov & Ochyra, 10 March 1985, s.n. (MHA); isolate OK 2270) MN794399