Sciuro-hypnum dovrense (Limpr.) Draper et Hedenäs comb. nov., a distinct Eurasian alpine species

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Abstract – Morphological and molecular evidence confirm that *Sciuro-hypnum dovrense*, nowadays considered conspecific with *S. glaciale*, is actually a distinct species that can be distinguished from related species by gametophytic characters, such as plant size and colour, branch shape, stem leaf shape and orientation, and costa length. An amended description of this moss is presented and its diagnostic characters are discussed. Finally, the known distribution of the species is extended with several localities from mountainous areas of Scandinavia, and its habitat preferences are inferred mainly based on specimen label information.

Sciuro-hypnum reflexum / Sciuro-hypnum glaciale / Brachytheciaceae / Bryopsida / taxonomy

INTRODUCTION

In 1896, Limpricht (1895-1904) described Brachythecium glaciale var. dovrense Limpr., a new variety of the species nowadays called Sciuro-hypnum glaciale (Schimp.) Ignatov et Huttunen. He based the description on specimens collected in 1885 by E. Adlerz and C. Kaurin in Norway (Knudshö, Dovre), and stated that the morphological characteristics of these specimens were so different from the type variety that he had previously considered the two taxa as distinct species. He pointed out as diagnostic characters the smaller size and more graceful form of the new variety, and also described differences, especially the colour of the wefts (shining in *glaciale* and not in *dovrense*), stem leaf shape (longer than wide in *glaciale* and as long as wide in *dovrense*), decurrency (shortly decurrent in glaciale and longly so in *dovrense*) and roughness (clearly plicate in *glaciale* and smooth in *dovrense*), stem leaf median lamina cell shape (5-8(10) times longer than wide in glaciale and 4-5 times longer than wide in dovrense), branch leaf length (1.1-1.5 mm long in the middle of the branches in *glaciale* and 0.6-0.9 mm long in *dovrense*), capsule constriction below mouth (not or slightly constricted when dry and empty in *glaciale* and strongly constricted in *dovrense*), and spore size (12-16 µm in glaciale and 15-20 µm in dovrense).

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In 1907, H. Möller combined the taxon as *Hypnum glaciale* var. *dovrense* (Limpr.) H. Möller, although his suggestion had little impact since most authors kept *Brachythecium* as a separate genus. Based on the small size of *dovrense*, the looser tufts, the decurrent stem leaves with a long costa, and the slightly papillose seta, Loeske (1909, 1910) considered that this taxon is more closely related to *Sciuro-hypnum reflexum* (Starke) Ignatov & Huttunen and *S. tromsoeense* (Kaurin *et* Arnell) Draper *et* Hedenäs, than to *S. glaciale*. In fact he considered *S. reflexum*, *B. glaciale* var. *dovrense*, and *S. tromsoeense* to belong to a single species (*S. reflexum*), and that the morphological variation described is induced by different environmental and climatic conditions, *dovrense* being an alpine and boreal form of *reflexum*. Consequently, he named it *Brachythecium reflexum* var. *dovrense* (Limpr.) Loeske. His suggestion was followed by authors such as Röll (1915), Jensen (1939), and Podpěra (1954), although others kept treating this taxon as a variety of *glaciale*, in line with Limpricht's original description (e.g. Brotherus, 1923; Nyholm, 1965).

Amann (1918) was the first to combine this taxon at the species level in Brachythecium, as B. dovrense. However, he annotated it as "B. III dovrense". The "III" indicates that he thought it is a species of the third order and that its status is lower than that of first or secondary order species (cf. Amann, 1888). Amann (1888) also writes that other authors may prefer to treat second and third order species at levels below the species. Also Schljakov (1952) superficially appeared to treat this taxon as a distinct species by redundantly making the combination ('comb. n.') in Brachythecium. However, in his comment he states that the combination is not well founded, and that despite clear differences from S. reflexum it could be referred to the latter based on both gametophytic and sporophytic characters. Ignatov (1998) believed that S. dovrense could be a distinct species because of the differences in distribution between this taxon and S. glaciale. When he, together with Huttunen (Ignatov & Huttunen, 2002), studied the circumscription of taxa within the family Brachytheciaceae, they suggested that this taxon belongs to the newly segregated genus *Sciuro-hypnum* Hampe. However, they didn't include specimens of this taxon in their molecular studies, and its status therefore remained to be confirmed. Only Ochyra et al. (2003) combined it as Sciuro-hypnum glaciale var. dovrense (Limpr.) Ochyra et Zarnowiec based on studies of type or other material. Despite all the stated differences and the considerations of these authors, Brachythecium dovrense and B. glaciale var. dovrense were considered as synonyms of S. glaciale in the last checklist of the mosses of Europe (Hill et al., 2006).

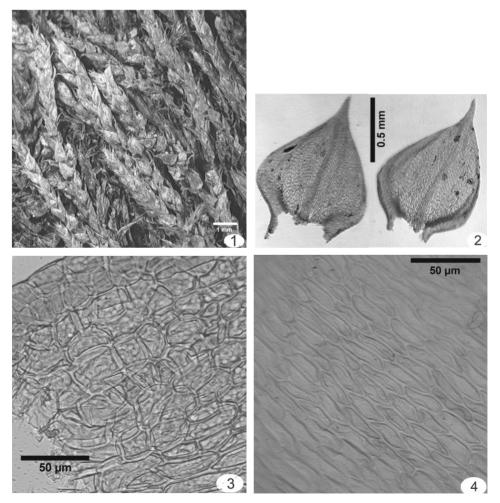
In our molecular studies for the circumscription of problematic European taxa within the Sciuro-hypnum reflexum complex, we included two specimens having morphological character states of S. glaciale var. dovrense, as well as ten specimens of S. glaciale and eight of S. reflexum. The specimens of S. glaciale var. dovrense appeared as a clearly separate clade in the molecular analysis, segregated both from S. glaciale and from S. reflexum, based on markers from both the chloroplast (rpl16 and trnG; Jacknife and Bootstrap support for the S. glaciale var. dovrense clade = 97) and the nucleus (ITS; Jacknife and Bootstrap support for this clade = 63). Details on the molecular studies performed, as well as the obtained trees, can be found in Draper & Hedenäs (2009), and support the validity of this taxon as a separate species belonging to *Sciuro-hypnum*, S. dovrense (Limpr.) Draper et Hedenäs. In addition to the molecular evidence, there are morphological characters that support the differentiation of this moss from related taxa. In this paper we amend the description of this species, provide morphological characters to distinguish it, and discuss its habitat preferences and known distribution area.

DESCRIPTION

Sciuro-hypnum dovrense (Limpr.) Draper et Hedenäs, comb. nov.

Figs 1-4

Brachythecium glaciale var. dovrense Limpr., Laubm. Deutschl. 3: 112. 1896. Hypnum glaciale var. dovrense (Limpr.) H. Möller, Bot. Not.: 144. 1907. Brachythecium reflexum var. dovrense (Limpr.) Loeske, Stud. Morph. Syst. Laubm. 182. 1910. Brachythecium dovrense (Limpr.) J.J. Amann, Fl. Mouss. Suisse 2: 308. 1918. Sciuro-hypnum glaciale var. dovrense (Limpr.) Ochyra et Zarnowiec, Biodiv. Poland 3: 174. 2003. **Type**: NORWAY, Dovre: Knudshö: p. australi ad rivulum. Aug. 1885. Chr. Kaurin (BG-M-14538; **lectotype** selected by Draper & Hedenäs, 2009; BG-M-14536; syntype); NORWAY, Dovre, Knudshö, Sprenbäcken, VII[sic!].1885, E. Adlerz (BG-M-14541, S-B125943, and TRH-58812; possible syntypes).



Figs 1-4. *Sciuro-hypnum dovrense* (Limpr.) Draper *et* Hedenäs (Sweden, S-B100723). **1**. Plant habit. **2**. Stem leaves shape. **3**. Alar cells (Sweden, S-B5244). **4**. Areolation of lamina in mid-leaf.

Plants small to medium-sized, in yellowish to greenish wefts; shoots prostrate, with leaves 0.25-0.75 mm in diameter when dry, irregularly pinnate or unbranched; branches generally long and secondarily branched, creeping straight and parallel to principal stem, short curved branches and narrow flagelliform branches occasionally present. Stem round in transverse section, with poorly to clearly defined central strand, large-celled basic tissue, and 2-3 stratose cortex of small and incrassate cells. *Rhizoids* scattered in creeping stems, more frequent in basal parts, irregularly branched, dark brown, smooth. Paraphyllia absent. Pseudoparaphyllia foliose, rounded, sometimes with short apiculus. Axillary hairs 0-1, strictly axillary or inserted on stem shortly above leaf axil, with one longly rectangular hyaline upper cell, 8-12 µm wide, and 1-2 shortly rectangular brownish basal cells. Stem leaves $0.7-1.5 \times 0.5-1.0$ mm, erect to loosely imbricate with erect to patent and rarely crisped apex when dry, erect to patent when moist, stem generally visible between leaves except in youngest parts, both when dry and moist, leaves broadly ovate, abruptly or rarely gradually narrowed in upper fifth to acute or shortly acuminate apex (acumen up to 300 µm long), base sometimes cordate; lamina strongly concave; margin plane above and slightly recurved near base, slightly denticulate throughout to almost entire, marginal cells similar to cells further in; *costa* single or rarely branched in basal half, ending shortly below acumen to percurrent, smooth, sometimes becoming reddish in old leaves, stout and (30)45-75 µm wide near base, in mid-leaf 2-3 stratose and consisting of incrassate homogeneous cells, surface cells on both ad- and abaxial sides linear and similar to adjoining lamina cells; *basal cells* broadly linear to rectangular, $20-40 \times 10-18 \mu m$, slightly to moderately incrassate, not or hardly porose; *alar cells* irregularly isodiametric to oblong, slightly to moderately incrassate, not or hardly porose, irregularly arranged in a poorly delimited, moderately to strongly excavate, rarely almost plane, quadrate to triangular group, transition to other basal cells gradual, shortly ascending along margin and extending from margin to half distance to costa, up to nine rows of alar cells usually shortly decurrent, rarely to leaf below; *median lamina cells* oblong to broadly linear, with shortly tapering ends, $16-57 \times 4-13 \mu m$, slightly to moderately incrassate, not or hardly porose, smooth; apical cells oblong, slightly to moderately incrassate, not or hardly porose. Branch leaves generally smaller but similar to stem leaves in shape, ovate, abruptly or gradually narrowed into acute to shortly acuminate apex: lamina moderately to strongly concave; *margin* plane or slightly recurved near base, slightly denticulate throughout to almost entire; *costa* generally single and well defined, ending in upper half of leaf to percurrent, smooth or (rarely) ending in a spine on back above, very rarely with prorate distal cells ends. Specialized vegetative reproductive organs not observed.

Autoicous. Perigonia laterally inserted on stem; perigonial leaves round to ovate, with round to acute apex; margins not bordered or with a row of pale cells parallel with margin, entire or slightly denticulate towards apex; *antheridia* well developed, with few paraphyses of 4-6 hyaline cells. Perichaetia laterally inserted on stem; inner perichaetial leaves smooth, straight and erect, with oblong basal part (1/2-2/3 of lamina), gradually or abruptly narrowed into acumen; margins unbordered or with a row of pale cells parallel with margin, entire throughout to denticulate in acumen, without costa; lower lamina cells rectangular to broadly linear, slightly to moderately incrassate, eporose and smooth, upper cells oblong to linear, slightly incrassate, eporose and smooth; axillary hairs 4-6, strictly axillary, with 1-2 longly rectangular upper cell and 1-2 shortly rectangular basal cells; archegonia well developed, with numerous paraphyses of 3-4 brownish quadrate basal cells and 5-6 hyaline oblong thinwalled cells. *Calyptra* cucullate, 4-5 stratose, of homogeneous cells, smooth, naked. *Vaginula* upper epidermis cells longly rectangular, thin-walled, eporose.

Sporophytes usually scarce. Seta up to 10 mm long, with central strand and 2-3 stratose cortex of small incrassate cells, orange to dark red, slightly or moderately mammillose throughout, dextrorse when dry. Capsule exerted, orthogonal, ellipsoidal, not furrowed, not or hardly constricted below mouth when dry, dark brown when mature. Exothecial cells in mid-capsule irregularly quadrate or rectangular, $14-24 \times 24-30$ µm, incrassate, smooth; below mouth 1-4 rows of small, approximately isodiametric, incrassate cells; stomatal pore ovate, surrounded by radial cells. Peristome double, with teeth curved inwards when dry, but leaving an open aperture; exostome teeth orange, with lower outside transversely striate and upper outside papillose, not furrowed, margins entire, border gradually narrowed upwards; endostome basal membrane 40-50% of endostome height, processes pale yellow, papillose throughout, slightly to moderately perforate (perforations to 10 µm wide), cilia 3-4, half as long as processes, with upper portions appendiculate. Annulus of 1-2 separating cell rows. Operculum conic, with basal cells radial, slightly incrassate. Spores round, moderately papillose, 12-14 µm, mature in summer.

DISCUSSION

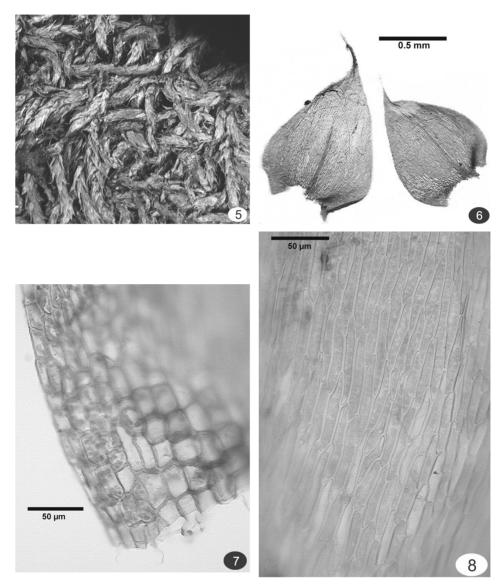
Sciuro-hypnum dovrense belongs to the S. reflexum-S. glaciale complex, a group of species that are extremely plastic in some of their morphological characters. Because of their morphological plasticity, this complex has been considered as one of the most problematic in Europe regarding the species circumscriptions. As mentioned above, S. dovrense has been treated as a distinct species in the complex, as well as a variety of S. glaciale or S. reflexum, and even considered conspecific with S. glaciale. Molecular data indicate that the closest taxon to S. dovrense is S. reflexum (Draper & Hedenäs, 2009), although morphologically it is more similar to S. glaciale except in its long costa. In order to find the diagnostic characters to differentiate S. dovrense from the related species, numerous specimens from well separated geographical areas, as well as type material of the three mentioned species was studied. The studied type material of S. glaciale and S. dovrense is listed in Draper & Hedenäs (2009). For S. reflexum, a neotype was selected by Draper & Hedenäs (2008).

According to our experience, the most reliable characters to distinguish the three species are found in the stem leaves (orientation when dry, shape, costa, mid-leaf areolation). Additionally, plant size, colour, and habit can be useful to separate the species in the field, as well as alar group appearance and decurrency (Table 1). On the contrary, the differences between some morphological characters of the sporophytes that were suggested to be diagnostic by previous authors, such as the constriction below the capsule mouth, the spore size, and the mamillosity of the seta, are too variable and do not clearly separate the three taxa. Table 1. Comparison of diagnostic characters, European distributions, and habitats of *Sciuro-hypnum dovrense* (Limpr.) Draper *et* Hedenäs, *S. reflexum* (Starke) Ignatov *et* Huttunen, and *S. glaciale* (Schimp.) Ignatov *et* Huttunen. Leaf characters refer to stem leaves.

	S. dovrense	S. glaciale	S. reflexum
Plant size (diameter with leaves)	Small (0.25-0.75 mm when dry)	Medium sized (0.5-1.0 mm when dry)	Small (0.25-0.75 mm when dry)
Plant habit	Prostrate stem; branches usually creeping	Prostrate stem; branches variable	Prostrate stem; branches usually short and curved
Plant colour	Yellowish to greenish, not shining	Yellowish, shining	Greenish, shining
Leaf orientation when dry	Erect to loosely imbricate, spreading from stem in the lowermost part, so stem usually visible	Erect to imbricate, appressed to the leaves above, so stem usually not visible	Erect to imbricate, appressed to the stem in the lower part, stem visible or not
Leaf shape	Base cordate to broadly ovate, abruptly or (rarely) gradually narrowed in upper fifth to acute or shortly acuminate apex (acumen (100)150- 250(300) µm long)	Base cordate, triangular to ovate, abruptly (rarely gradually) narrowed in upper fifth to shortly acuminate apex (acumen (100)300-500(800) µm long)	Base cordate to ovate, abruptly narrowed in mid leaf to longly acuminate apex (acumen (300)450- 650(750) µm long)
Costa	Ending in the acumen	Ending below the acumen	Ending in the acumen
Decurrence	Up to nine rows of alar cells usually shortly decurrent, rarely to leaf below	Up to six rows of cells shortly to longly decurrent (down to the leaf below)	Up to eight rows of cells usually longly decurrent (down to the leaf below)
Alar cells	Irregularly isodiametric to oblong, irregularly arranged in a poorly delimited quadrate to triangular group, moderately to strongly excavate, rarely almost plane, shortly ascending up along the margins	Regularly quadrate to shortly rectangular, arranged in regular rows in a poorly delimited triangular group, generally not excavated, shortly ascending up along the margins	Regularly quadrate to shortly rectangular, irregularly arranged in a moderately well delimited triangular group, generally not excavated, ascending up along the margins
Median lamina cells	Oblong	Oblong to linear	Oblong to linear
Distribution and habitat preferences	Boreal or alpine at high altitude terri-saxicolous, typically in late snow-beds	Alpine terri-saxicolous, typically in late snow-beds	Lowlands to montane humicolous or terri- saxicolous

Sciuro-hypnum dovrense is generally smaller than S. glaciale. Its creeping stems are sometimes unbranched, or have long, prostrate branches that creep parallel to the principal stem, and its stem leaves are dull yellowish to greenish, distantly inserted, and spreading from the stem in their lowermost part, so the stem is generally visible between them (Fig. 1). The stems of Sciuro-hypnum glaciale are also prostrate, but are more often branched. Its branches are sometimes short and curved upwards, and it has shining yellowish, imbricate stem leaves, that are appressed to the leaves above, so the stem is rarely visible between them (Fig. 5). In addition, microscopical characters help separating the two. In S. dovrense, the stem leaves are broadly ovate, sometimes almost orbicular (0.9-1.5(2.0) times longer than wide), abruptly narrowed in the upper fifth to an acute or shortly acuminate apex, and the acumen may be up to 300 µm long (Fig. 2). The stem leaves of S. glaciale are usually longer (1.1-2.5 times longer than wide), triangular to ovate and abruptly (rarely gradually) narrowed in their upper fifth to an acuminate apex, and the acumen can be up to 550 µm long (Fig. 6). Together with the stem leaf shape, the length of the costa is a good character to distinguish these species, since it ends far up in the acumen in most leaves of S. dovrense, whereas it usually does not reach the acumen in S. glaciale. The alar cells and decurrency of the leaves frequently differs between the species, the alar cells of S. dovrense being irregular and arranged in an often excavate group (Fig. 3), whereas they are generally quadrate and regularly arranged in rows in a frequently plane group in S. glaciale (Fig. 7). However, this is a more variable character that should be used in combination with other characters. The stem leaves of S. dovrense are generally shortly decurrent and rarely reach the leaf below, whereas the decurrencies of S. glaciale more often reach the leaf below. Finally, the areolation of the mid-leaf cells can be useful to separate the two species: S. dovrense has predominantly oblong mid-leaf cells with a ratio "median value" of cell length / median value of leaf length" between 25 and 39 (Fig. 4), whereas S. glaciale has more variable cells, from oblong to linear, and with a ratio between 30 and 77 (Fig. 8). Given the variability of some of the mentioned characters, such as the length of the cells in S. glaciale, specimens should be referred to S. dovrense based on a combination of the mentioned morphological characters.

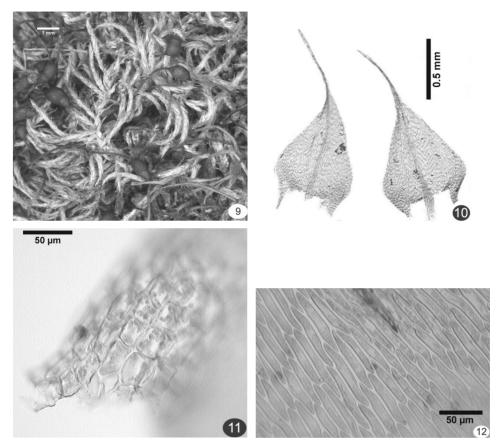
Although molecularly closer, S. dovrense is more easily distinguished from S. reflexum than from S. glaciale. These species normally occur in different environments, since S. dovrense is a boreal moss that is found scattered at high elevations in the mountains (see below), whereas S. reflexum mostly grows from the lowlands to the montane belt (Table 1). In addition, they are easily differentiated by their branching pattern, since S. reflexum branches are short, ascending, and curved (Fig. 9), instead of long and creeping like those of S. dovrense. Under the microscope, S. reflexum has stem leaves with an ovate or cordate basal part that abruptly narrows around mid-leaf into a longly acuminate apex, and the acumen can be up to 650 µm long (Fig. 10), whereas the leaves of S. dovrense are only narrowed in the upper fifth into an acute or shortly acuminate apex. Finally, the decurrency of the stem leaves is usually longer in S. reflexum, often reaching the leaf below, the alar group has more regularly arranged cells and is usually plane (Fig. 11), and the mid-leaf cells are oblong to linear and similar to those of S. glaciale (Fig. 12), whereas in S. dovrense the leaf decurrency is usually short, the alar group is more often excavate, and the mid-leaf cells are predominantly oblong.



Figs 5-8. *Sciuro-hypnum glaciale* (Schimp.) Ignatov *et* Huttunen (Sweden, S-B115296). **5**. Plant habit. **6**. Stem leaves shape. **7**. Alar cells. **8**. Areolation of lamina in mid-leaf.

Distribution and habitat preferences

Sciuro-hypnum dovrense has been reported from scattered localities in the northern and central parts of Eurasia. Most of the authors that included *S. dovrense* in their floras, such as Limpricht (1895-1904), Podpěra (1954) and Brotherus (1923), only referred to the type locality in the mountains of Dovre



Figs 9-12. *Sciuro-hypnum reflexum* (Starke) Ignatov *et* Huttunen (Sweden, S-B116941). 9. Plant habit. 10. Stem leaves shape. 11. Alar cells. 12. Areolation of lamina in mid-leaf

(Norway). Nevertheless, Amann (1918) provided a locality from Central Europe in Valais (Switzerland). In addition, Nyholm (1965) stated that she had seen specimens with the morphological characteristics of this taxon from Torne Lappmark in Sweden, although she didn't indicate locality details. For Russia it has been reported from the Beringian Chukotka (Afonina & Czernyadjeva, 1995; Afonina, 2004) and from the Kola Peninsula (Ignatov, 1998). Finally, it has been found in the Altai Mountains, in central Asia (Ignatov, 1998).

In addition to the type material, for this study we revised all the material of *S. dovrense*, *S. glaciale* and *S. reflexum* kept in S. We found specimens of *S. dovrense* from Norway (Finmarken, Troms and Dovre), Sweden (Lule Lappmark, Pite Lappmark, Lycksele Lappmark and Jämtland), and Finland (Lapponia enontekiensis) previously identified either as *S. dovrense* or as *S. glaciale*. Central European material of *S. glaciale* sometimes approaches *S. dovrense* in appearance, but we have found no specimens that we would place in *S. dovrense* with full confidence. The report of *S. dovrense* by Amann (1918) should thus be confirmed to assure its occurrence in C Europe.

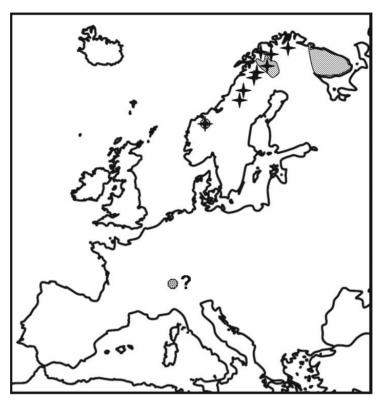


Fig. 13. Known distribution of *Sciurohypnum dovrense* (Limpr.) Draper *et* Hedenäs in Europe. Rounded dotted areas (reported localities) and irregular hatched areas (without locality details) indicate reports previous to this paper. Stars indicate localities newly reported in this paper. The question mark indicates reported localities that should be confirmed (see text).

The currently known populations of *S. dovrense* suggest that this is a relatively rare mountain species that occurs in the alpine zone (Fig. 13). For some old collections there are no data regarding the habitat where the species was found, but the available data indicate that all the collections in Scandinavia where made in late snow beds. In the Altai Mountains, *S. dovrense* grew on a wet clayish bank, also in the alpine belt. These data suggest that this moss is preferably terricolous on moist soil.

REPRESENTATIVE S. DOVRENSE SPECIMENS EXAMINED

Norway. Finmarken, Rastekaisen [Rásttigáisá], R. Hult (S-B118294). Troms, Lyngen, L. Hedenäs (S-B83043). Dovre, Knudshö, C. Kaurin (TRH-58806; TRH-58811), Dovre, Knudshö, N. Bryhn (S-B118295). Sweden. Lule Lappmark, Virijaurtrakten, E. Nyman (S-B118276). Lule Lappmark, Gällivare, T. G. Halle (S-B118290). Pite Lappmark, Arjeplog, G. Een (S-B79191). Lycksele Lappmark, Tärna, A. Hülphers (S-B5243; S-B118085) & C. M. Norrman (S-B5244). Jämtland, Frostviken, L. Hedenäs (S-B100723). Finland. Lapponia enontekiensis, Kahperus, H. Roivainen (S-B118328).

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