*Journal of Bryology* (2006) **28:** 293–298

# Variation in *Dicranum majus* in central, western and northern Europe

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## Summary

We studied infraspecific morphological variation within European *Dicranum majus* Sm. A principal components analysis based on six leaf characters scored in 82 specimens revealed two distinct plant types. Plants with bistratose submarginal upper leaf lamina cells, numerous spine-like dorsal lamina projections, a costa that is dorsally rough far down and has two layers of guide cells in its basal part, and falcate or strongly falcate, long leaves are mainly of a relatively southern origin. Specimens with a unistratose, smooth upper leaf lamina, a costa that is dorsally rough only above and has one layer of guide cells, and with slightly curved to straight, short leaves were only collected in northern Europe. Even if most authors do not formally recognize variation within *D. majus*, our results suggest that the two kinds of plants should be recognized at least at the variety level. In view of the confusing nomenclature in *Dicranum* it is beyond the scope of this paper to find a name for the northern plant. Type material of *D. majus* var. *orthophyllum* A. Braun ex Milde, a name that was frequently used for northern North American plants, belongs to the southern phenotype.

KEYWORDS: *Dicranum majus*, morphological variation, principal components analysis.

## Introduction

During identification work for a biodiversity study in Switzerland in 2003 (Hintermann *et al.*, 2002), Norbert Schnyder and Niklaus Müller found two puzzling *Dicranum* specimens that resembled the drawings of *D. transsylvanicum* Lüth (Lüth, 2002). However, the specimens lacked the dorsal lamellae of the costa and the strong dorsal lamina spines found in the latter. After studies by Michael Lüth, Irene Bisang and Lars Hedenäs these were referred to *Dicranum majus* Sm. In Europe, *D. majus* is often treated as a relatively variable species, but without subspecific differentiation (e.g. Nyholm, 1954, 1987; Smith, 1978, 2004; Touw & Rubers, 1989; Frey *et al.*, 1995; Abramov & Volkova, 1998; Ignatov & Ignatova, 2003). However, Hagen (1899) had earlier noticed that arctic material usually has only one rather than two layers of guide cells in the leaf costa, although occasional guide cells may be divided into two. He later described such material as *Dicranum majus* var. *condensatum* (Hagen, 1915). Among later European authors, for example Brotherus (1923) distinguished this variety, with leaves secund or almost erect, relatively short, indistinctly dentate or entire, and with their costa relatively weakly dentate on its back. The variety *condensatum* was also recognized as an arctic or northern Russian taxon by Abramova, Savicz-Ljubitskaja & Smirnova (1961). In arctic North America, typical *D. majus* is rare (Steere, 1978). The taxon is commonly represented by a form which has usually been called var. *orthophyllum* A.Braun ex Milde. According to Steere (1978) this variety has straighter leaves than ordinary *D. majus*, with reduced lamellae on the dorsal costa. Crum & Anderson (1981) noted that this widespread arctic variety or form did not agree with their concept of *D. majus* in form, habitat or distribution. The variety *orthophyllum* was also mentioned by Limpricht (1886), even if he believed that *D. majus* is not a very variable species. Also, Mönkemeyer (1927) recognized *orthophyllum*, but only as a form with the upper leaves more or less erect.

Based on his floristic experience in Scandinavia, the senior author felt that the Swiss specimens were potentially something else than what is found in northern Europe. However, since *Dicranum majus* treatments are not consistent, we were unable to satisfyingly interpret the differences between the above-mentioned Swiss collections and material from northern Scandinavia. Four of us therefore decided to investigate the morphological and anatomical variation of this species in greater detail by studying material from central, western and northern and arctic Europe.


DOI: 10.1179/174328206X136296

Received 9 January 2006. Revision accepted 28 April 2006

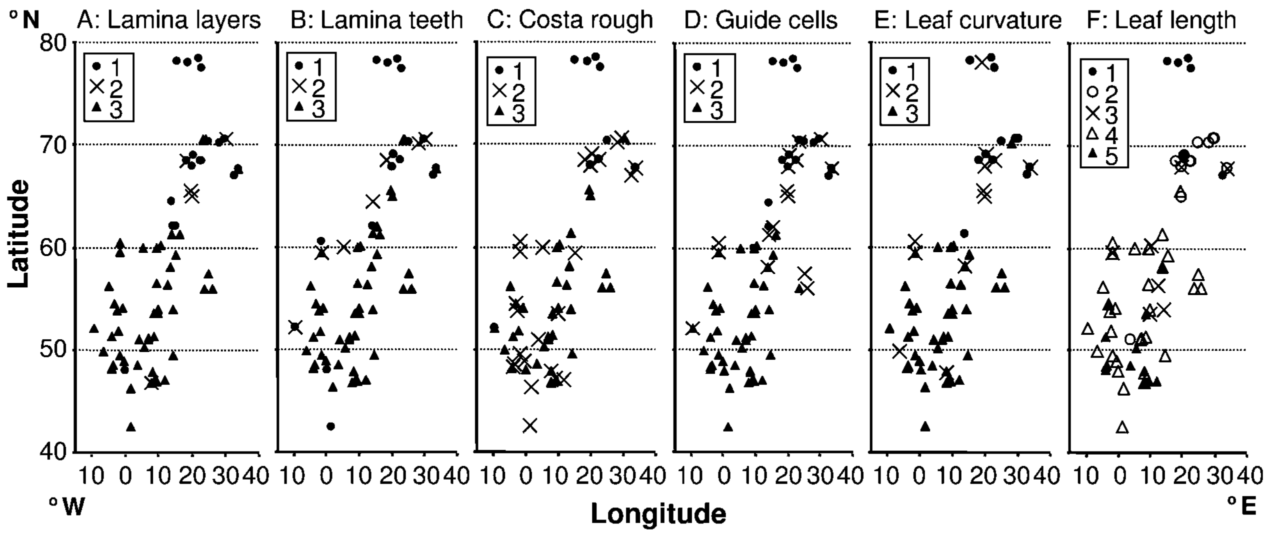


**Figure 1.** Latitudinal and longitudinal distribution of the states of the six characters scored in *Dicranum majus* ($n$=82 specimens studied). (A) Upper submarginal leaf lamina cells: 1, unistratose; 2, scattered cells bistratose; 3, bistratose in longitudinal band. (B) Upper dorsal leaf lamina cells: 1, smooth; 2, with scattered dorsally slightly projecting cell-ends; 3, with several to numerous dorsally strongly projecting, spine-like cell-ends. (C) Costa dorsally rough in upper: 1, 5–20%; 2, 21–40%; 3, 41–65%. (D) Guide cells in basal costa: 1, in one layer; 2, partly in one and partly in two layers; 3, in two layers. (E) Leaf curvature scored as: 1, 1 or 2 (straight or slightly falcate); 2, 3 (most leaves are slightly falcate); 3, 4 or 5 (falcate or strongly so). (F) Leaf length: 1, 4–5 mm; 2, 6–7 mm; 3, 8–9 mm; 4, 10–11 mm; 5, 12–13 mm. See Table 1 for further details.

## Materials and Methods

### *Plant material*

We studied 82 herbarium specimens from all over Europe (Appendix). For each specimen we scored the states of six characters that had either been suggested to differentiate the northern plant type from the southern (cf. above), or which we found to be variable during the course of our study (Table 1).

### *Data analysis*

We plotted characters against longitude and latitude of specimen origin. Altitude information was unfortunately too sparse to be included in the analyses. The data scored for all specimens were subjected to Principal Components Analysis (PCA) in order to identify directions of maximum variance. Latitude and longitude of the localities for the specimens were treated as supplementary values in the analysis. We calculated correlations among characters and between characters and latitude and longitude; since data were not normally distributed, Spearman Rank Order correlations were used. The statistical analyses were performed with the computer program STATISTICA (StatSoft, 2005).

**Table 1.** *Characters investigated for each specimen of* Dicranum majus. *For each specimen five young but mature leaves per shoot, from two shoots (i.e. 10 leaves) were examined*

| |
|---|
| (A) Upper submarginal leaf lamina cells: 1, unistratose; 2, scattered cells bistratose; 3, bistratose in longitudinal band. |
| (B) Upper dorsal leaf lamina cells: 1, smooth; 2, with scattered dorsally slightly projecting cell-ends; 3, with several to numerous dorsally strongly projecting, spine-like cell-ends. |
| (C) Upper dorsal costa roughness, scored in 10% categories of total leaf length (average of 10 leaves). |
| (D) Guide cell layers in lower third of costa: 1, one layer; 2, partly one and partly two layers; 3, two layers. |
| (E) Leaf curvature scored from entire specimen in five categories, where 1 means that all leaves are straight, 3 means that most leaves are slightly falcate and some are straight, and 5 means that all leaves are strongly falcate. |
| (F) Mean leaf length (mm) of the 10 leaves investigated. |

## Results

When the states of the different characters are plotted according to the origin of the specimens, a geographical component is evident (Fig. 1). Northern specimens tend to have a unistratose, smooth upper leaf lamina, a costa that is dorsally rough only in its upper part and has one layer of guide cells, and slightly curved to straight, relatively short leaves (Fig. 2B). Southern phenotypes have a band of bistratose, submarginal cells, many upper lamina cells with spine-like dorsal projections, a costa that is dorsally rough down to mid-leaf and has two layers of guide cells, and falcate or strongly falcate, long leaves (Fig. 2A). However, this simple plotting of the states as to the origin of the material suggests that geographical overlap exists between different states of several of the characters (Fig. 1).

The results of the PCA provide a different picture (Fig. 3). They suggest that there are two readily distinguishable morphological types within European *Dicranum majus*. The eigenvalues reveal that the first axis (factor) represents the major part of the variation occurring in the samples, whereas the other axes are of much less significance (Table 2). All the six characters studied are correlated with the first axis, and also the supplementary parameters are correlated with this

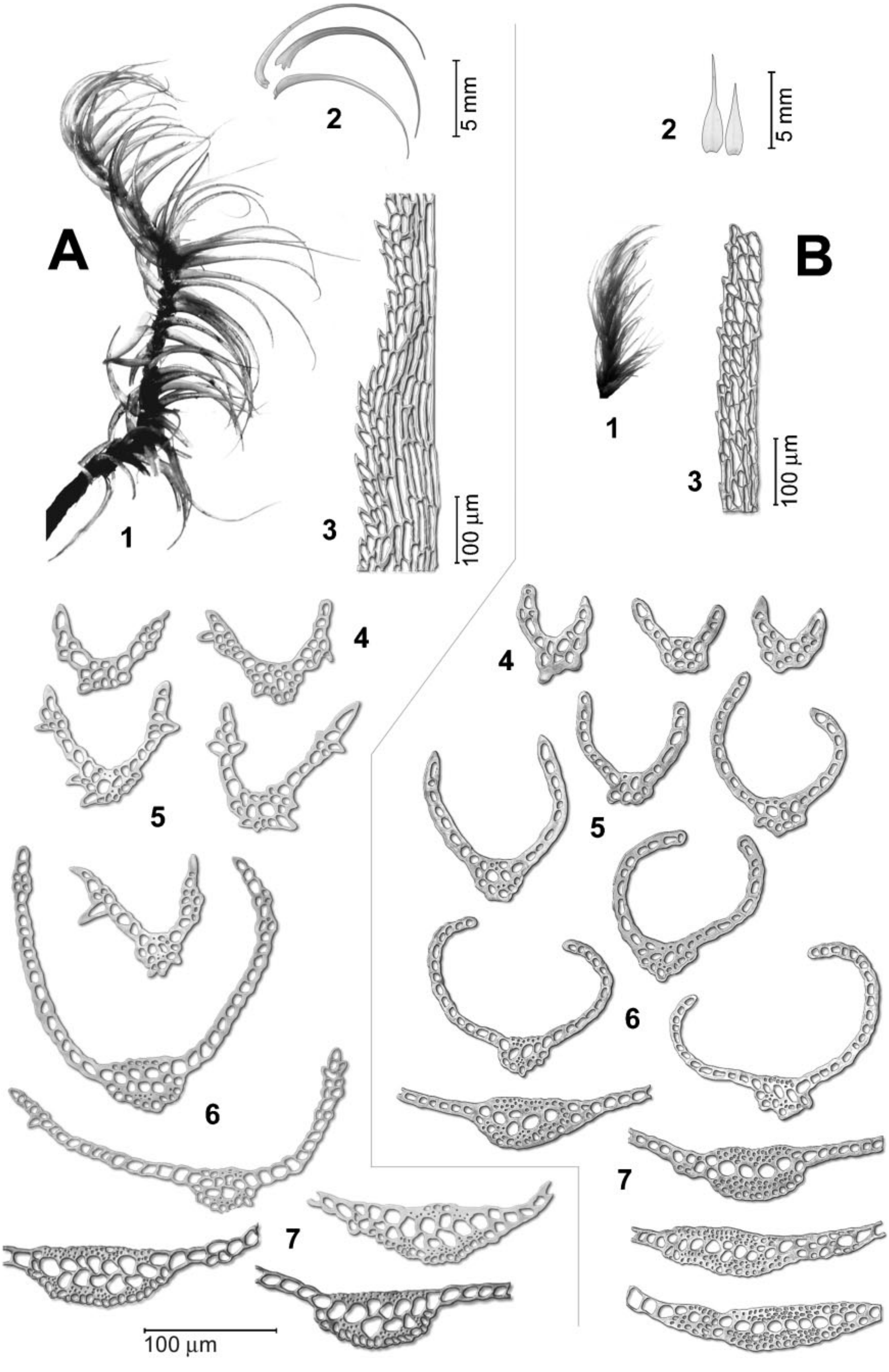


**Figure 2.** Characters differentiating the southern (A) and northern (B) phenotype of *Dicranum majus.* 1, Shoot; 2, leaves; 3, leaf margin in upper quarter of leaf; 4–7, transverse sections of leaf, from upper to lower portions of leaf. (A) Switzerland. Canton Schwyz, Unteriberg, 11 December 2003, N. Schnyder, in herb. Schnyder. (B) Sween. Torne Lappmark, Karesuando, N.W. of Mt Pältsan, 30 June 1980, L. Hedenäs, in S. Illustration by M. Lüth.

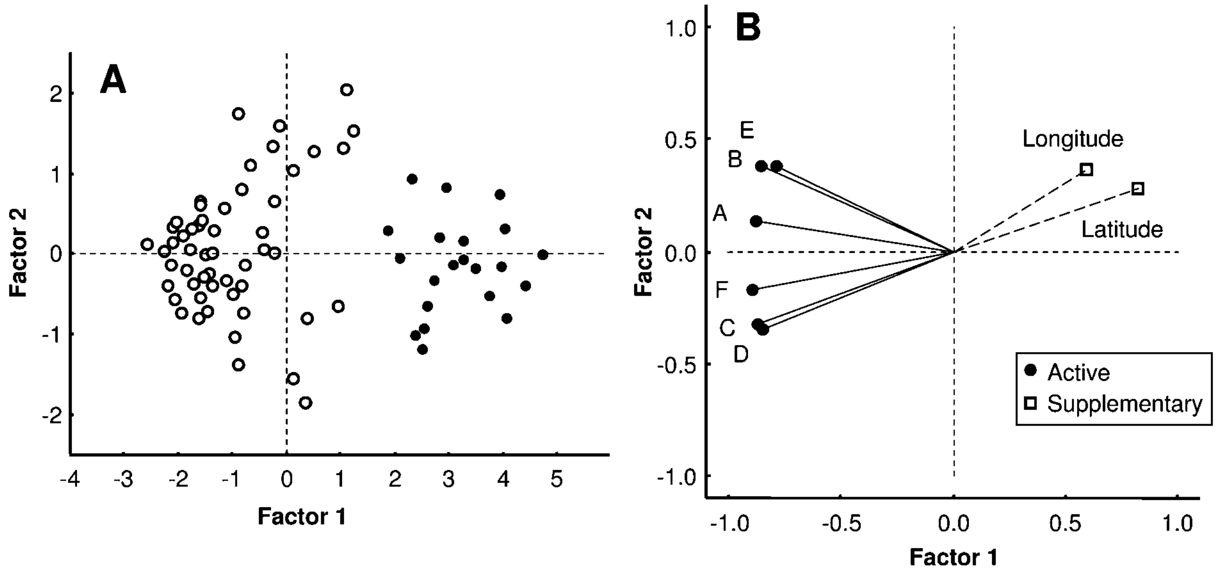


**Figure 3.** Ordination diagrams based on Principal Components Analysis (PCA) of the six characters scored for 82 samples of *Dicranum majus* s.l. (A) Specimen scores along the first two factors. Filled symbols=northern type of *D. majus* (samples 1–16, 60–62, 68–69; cf. Appendix); open symbols=southern type of *D. majus* (remaining samples). (B) Character scores along the first two factors. Letters indicate: A, presence of submarginal bistratose band in upper lamina; B, presence of teeth/spines on upper dorsal lamina; C, number of layers of guide cells in basal costa; D, degree of 'secundness' of leaves; E, percentage of costa that is dorsally rough; F, leaf length.

factor (Fig. 3). In addition, all characters are correlated with each other and all except one (% of costa dorsally rough versus longitude) are correlated with the two geographical parameters (Table 3).

## Discussion

Our data give evidence of a considerable morphological and anatomical variation within European *Dicranum majus*, and of a distinct geographic pattern in the variation found. The characters studied vary significantly with latitude, and to a lesser extent also with longitude. Although the co-variation of individual characters with latitude is gradual, the total variation in these characters is clearly discontinuous as shown by the PCA. Two kinds of plants with different morphological and anatomical characteristics apparently occur, one northern and one southern. Our results therefore support the treatments which formally recognize the infraspecific variation, such as by Hagen (1899), Brotherus (1923), Abramova *et al.* (1961) and Steere (1978), rather than the majority of authors who suggested that no differentiation worth naming occurs in this species. In this context it should of course be noted that some authors did not cover geographical areas where more than one of the plant types could be expected (e.g. Touw & Rubers, 1989; Smith, 2004).

The distinct, geographically related variation motivates the recognition of two different taxa. However, we are at present hesitating regarding the taxonomic level at which to treat them. We believe that molecular studies including

**Table 2.** *Eigenvalues and percentage variance accounted for by the six factors in the Principal Components Analysis of six characters in* Dicranum majus

| Factor | Eigenvalue | % of total variance |
|---|---|---|
| 1 | 4.388 | 73.1 |
| 2 | 0.561 | 9.4 |
| 3 | 0.451 | 7.5 |
| 4 | 0.236 | 3.9 |
| 5 | 0.223 | 3.7 |
| 6 | 0.141 | 2.4 |

**Table 3.** *Statistically significant correlations among characters, and between characters and geographical parameters in* Dicranum majus *(Spearman Rank Order correlations; significant at* $P<0.00179$*, corresponding to a Bonferroni-corrected* $P<0.05$*)*

| | B | C | D | E | F | G | H[1] |
|---|---|---|---|---|---|---|---|
| A: Upper submarginal leaf lamina | 0.78 | 0.55 | 0.73 | 0.59 | 0.72 | −0.59 | −0.65 |
| B: Upper lamina cell prorateness | – | 0.67 | 0.63 | 0.57 | 0.65 | −0.37 | −0.56 |
| C: % of costa dorsally rough | – | – | 0.52 | 0.59 | 0.57 | n.s. | −0.43 |
| D: Guide cells in basal costa; no. of cell layers | – | – | – | 0.76 | 0.74 | −0.66 | −0.81 |
| E: Leaf curvature | – | – | – | – | 0.72 | −0.54 | −0.70 |
| F: Leaf length (mm) | – | – | – | – | – | −0.67 | −0.80 |
| G: Longitude (decimal system) | – | – | – | – | – | – | 0.73 |

n.s., Not significant.

[1]H: Latitude (decimal system).

several specimens of each phenotype, as well as species closely related to *D. majus*, will provide critical information for a final decision regarding taxonomic level. Until then, the northern plant type needs to have a name in order to be recognized in future investigations. The southern plant with strongly falcate leaves is clearly the one described under *D. majus* by Smith (1804), and described and illustrated as *D. majus* in the almost parallel publication by Turner (1804). The nomenclature in *Dicranum* is confusing because of numerous names that exist, and we do not want to add more uncertainty by selecting a name that may become redundant after a number of years. We therefore intend to look for potential names for the northern plant in a separate investigation. Initial studies, however, have revealed that type material of the name *Dicranum majus* var. *orthophyllum* A. Braun ex Milde (Buchwälder bei Sassnitz an Hohlwegen, September 1866, Herb. J. Milde [Ex herb. A. Braun], S; bei Sassnitz. September 1866, A. Braun, S) belongs to the southern phenotype, although the very distal leaves in some shoots are relatively straight. Based on the literature description (Steere, 1978), it also seems unlikely that arctic North American material belongs to *Dicranum majus* var. *orthophyllum*.

## Acknowledgements

We thank Niklaus Müller for valuable contributions and the curators of FB, KR, STU and Z for the loan of specimens.

Taxonomic Additions and Changes: Nil.

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## Appendix

Specimens of *Dicranum majus* Sm. studied. Latitude and longitude of the collecting localities are indicated in decimal system after the specimen data. Bold numbers in parentheses are the numbers given to the specimens by the authors.

**Austria. (25)** Tirol, Erzherzog-Johann-Klause, September 1858, P. Reinsch (KR); 47.0°N, 12.0°E. **Belgium. (58)** Ardennen, 1800–1865, A. Libert, plant. Crypt. Ard. 305 (KR); 50.2°N, 5.6°E. **(77)** Bois de Juslenville, 1910, Cornet (S); 51.0°N, 4.0°E. **Czech Republic. (55)** Böhmen, Isergeleg, 6 August 1898, V. Schiffner (KR); 49.5°N, 14.5°E. **Denmark. (50)** Hald Ege at Viborg, 5 September 1965, E. Warncke (KR); 56.5°N, 9.5°E. **Estonia. (51)** Tallin Distr., Lahema Ntl. Park, 22 September 1989, Å. Strid (S); 57.4°N, 25.0°E. **Finland. (4)** Lapponia enontekiensis, Karesuvanto, 22 July 1966, H. Roivainen (STU); 68.5°N, 22.5°E. **(8)** Lapponia enontekiensis, Kaunäeno, 13 July 1934, Roivainen (Z); 68.5°N, 22.8°E. **France. (73)** Ariège, Montareign près Salun, 7 September 1923, P. Culmann (Z); 42.5°N, 1.5°E. **(52)** Bretagne, Quimper, Valle de Odet, 4 October 1992, Düll (STU); 48.1°N, 4.0°W. **(32)** Bretagne. Loqueffret, St. Herbot, 28 March 2003, M. Lüth 4066 (priv. herb.); 48.3°N, 3.8°W. **(75)** Cherbourg, 25 July 1889, L. Corbière (Z); 49.5°N, 1.5°W. **(83)** Creuse-Bussieres-Dunoise, April 1932, C. Sarrassat (S); 46.3°N, 1.8°E. **(74)** Finistère, St. Herbot, 12 June 1878, Cramer (?) (Z); 48.5°N, 3.5°W. **(43)** Finistère, Huelgoat, 20 July 1971, H. Huber (Z); 48.5°N, 3.8°E. **(79)** Falaise (Calvados), July, Husnot, Musci Galliae (S); 48.9°N, 0.2°W. **(71)** Le Mans, taillis De Douce Aune, October 1894, Monguillier (S); 48.0°N, 0.2°E. **Germany. (39)** Oberbaden, Feldberg, August 1865, Sickenberger (FB); 47.8°N, 8.1°E. **(33)** Flora der Rheinlande, Remscheid, 1862, Doring (FB); 51.2°N, 7.2°E. **(34)** Flora der Rheinprovinz, Enpen, September 1875, Römer (FB); 51.0°N, 7.0°E. **(24)** Hamburg, Hirschfelder Holz, December, W. Sonder (FB); 53.5°N, 10.0°E. **(54)** Ostfriesland (FB); 53.5°N, 8.5°E. **(44)**

Schleswig-Holstein, Fechtenhagen, 5 January 1962, Mechmesshausen (Z); 54.0°N, 10.0°E. **(31)** Schwarzwald, Herzogenhorn, 7 July 2002, M. Lüth 3838 (priv. herb.); 47.9°N, 8.1°E. **(45)** Westfalen, bei Handorf, August, H. Müller (FB); 51.3°N, 8.5°E. **Ireland. (42)** Killarney, 22–26 June 1865, W. P. Schimper (STU); 52.1°N, 9.5°W. **(21)** Killarney, Glena, 22 July 1873, S. O. Lindberg (S); 52.1°N, 9.5°W. **Latvia. (49)** Prov. Zemgale, distr. Jeigava, 28 April 1940, H. & K. Starcs 1035 (STU); 56.0°N, 23.5°E. **(38)** Prov. Vidzeme, Vestiene, 21 July 1942, K. Starcs 2194 (STU); 56.0°N, 26.0°E. **Norway. (36)** Buskerud Fylke, Sigdal, 16 August 1998, I. Holz IH98190 (STU); 60.0°N, 9.5°E. **(56)** Buskerud Fylke, Sigdal, 16 August 1998, I. Holz IH98189 (STU); 60.0°N, 9.5°E. **(63)** Finmark, Båtsfjord, Vesterelva, 16 June 1980, L. Hedenäs (S); 70.6°N, 29.7°E. **(19)** Finmark, Båtsfjord, Ytre Syltefjord, 14 June 1980, L. Hedenäs (S); 70.6°N, 30.3°E. **(62)** Finmark, Porsanger, Ytre Billefjord, 20 June 1980, L. Hedenäs (S); 70.3°N, 25.1°E. **(61)** Finmark, Tana, Tana bru, 12 June 1980, L. Hedenäs (S); 70.2°N, 28.2°E. **(66)** Finnmark, Söröysund, Seiland (Siev'jo), Stuorajurvag'gi, L. Övervatnet, 22 July 2001, L. Hedenäs (S; reg. no. B63137); 70.5°N, 23.4°E. **(67)** Finnmark, Söröysund, Seiland (Siev'jo), Stuorajurvag'gi, S end, 23 July 2001, L. Hedenäs (S; reg. no. B63133); 70.4°N, 23.4°E. **(28)** Hordaland, Fitjar, Levag, 17 June 1990, M. Ahrens (KR); 60.0°N, 5.3°E. **(65)** Kvalsund, Myrland, Ledunvarre, 15 July 1968, M. Haapasaari 8219 (S); 70.5°N, 24.0°E. **(48)** Oppland, Jevnaker, River Svenåa, 22 July 1980, L. Hedenäs (S); 60.2°N, 10.5°N. **Poland. (35)** Swinemünde, 1885, R. Ruthe (KR); 53.9°N, 14.2°E. **Russia. (6, 23)** Chibiny Massif, Vudjavrcorr Mt, 18 September 1975, R.N.Schljakov, Bryophyta Murmanica Exsiccata (STU; 2 specimens); 67.7°N, 33.8°E. **(11)** Lapponia orientalis, inter Kanda & Knjäscha, August 1872, V. F. Brotherus (FB); 67.0°N, 32.8°E. **(9)** Murmansk, reg. Chibiny Mts Vudyavrchorr Mt, 18 October 1975, Schljakov (Z); 67.7°N, 33.8°E. **Svalbard. (3)** Spitzbergen, Stor-Fjord, 1967, G. Philippi (KR); 78.0°N, 19.0°E. **(1)** Südost-Spitzbergen, Barents-Insel, 1967, G. Philippi (KR); 78.4°N, 22.0°E. **(2)** Südost-Spitzbergen, Edge-Insel, 1967, G. Philippi (KR); 77.5°N, 23.0°E. **(5)** West-Spitzbergen, Longyearbyen, 1967, G. Philippi (KR); 78.2°N, 15.5°E. **Sweden. (60)** Dalarna, Älvdalen, Hykjeberg, 18 July 1981, L. Hedenäs (S); 61.3°N, 14.0°E. **(64)** Hälsingland, Hanebo, Nannsjön, 23 June 1941, T. G. Halle (S); 61.2°N, 16.4°E. Hälsingland, **(68)** Kårböle, 26 June 1935, C. Malmström (S); 62.0°N, 15.3°E. **(69)** Härjedalen, Sveg, Lake N. Tävremstjärnen, 11 July 1989, L. Hedenäs HD89-9 (S); 62.0°N, 14.2°E. **(70)** Jämtland, Frostviken, Vallån, 11 August 1988, L. Hedenäs J88-311 (S; reg. no. B6146); 64.4°N, 14.0°E. **(29)** Närke, Tysslinge, Filipshyttan, 19 August 1989, M. Ahrens (KR); 59.3°N, 15.3°E. **(20)** Pite Lappmark, N of Abborrträsk railway station, 28 July 1981, L. Hedenäs (S); 65.5°N, 19.5°E. **(47)** Skåne, Svanshall, 7 March 1980, L. Hedenäs (S); 56.3°N, 12.6°E. **(15)** Torne Lappmark, Jukkasjärvi, N.W. of Kiruna, 13 July 1980, L. Hedenäs (S); 67.9°N, 20.0°E. **(7)** Torne Lappmark, Jukkasjärvi, 2 km S.E. of Krokvik, 12 July 1980, L. Hedenäs (S); 67.9°N, 20.0°E. **(12)** Torne Lappmark, Jukkasjärvi, E of Lake Pajep Njuorajaure, 10 August 1983, L. Hedenäs (S); 68.5°N, 18.3°E. **(16)** Torne Lappmark, Jukkasjärvi, W of Lake Pajep Njuorajaure, 13 August 1983, L. Hedenäs (S); 68.5°N, 18.3°E. **(10, 14)** Torne Lappmark, Karesuando, N.W. of Mt Pältsan, 30 June 1980, L. Hedenäs (S; 2 specimens); 69.0°N, 20.5°E. **(13)** Torne Lappmark, Karesuando, S of Mt Pältsan, 2 July 1980, L. Hedenäs (S); 69.0°N, 20.5°E. **(17)** Västerbotten, S of Jörn, 10 August 1981, L. Hedenäs (S); 65.0°N, 20.0°E. **(57)** Västergötland, 1951, Carl Stenholm (STU); 58.1°N, 13.6°E. **(41)** Västergötland, Valstad, Gorserna, 1 August 1974, Düll (STU); 58.1°N, 13.6°E. **Switzerland. (53)** Ct. Graubünden, Rhätische Alpen, Ganeythal ob Sewis, 29 September 1867, W. Pfeffer (S); 46.9°N, 9.6°E. **(46)** Ct. Luzern, Sörenberg, Salwiden, 5 July 1970, H. Huber (Z); 46.8°N, 8.0° E. **(18)** Ct. Luzern, Sörenberg, Schönisei-Schwarzenegg, 17 July 1970, H. Huber (Z); 46.8°N, 8.0°E. **(30)** Ct. Sankt Gallen, Kaltbrunn, Vorderwengi, 5 July 2003, N. Schnyder (priv. herb.); 47.2°N, 9.1°E. **United Kingdom. (81)** Anglia, Slingebymoor, Spruce (S); 54.1°N, 0.9°W. **(72)** England, Devon, Watersmeet, Lynmouth, 12 July 1978, H. Huber (Z); 51.2°N, 3.8°W. **(82)** England, Dolphinholme, Lancs, 1911, Wheldon (S); 53.8°N, 2.5°W. **(80)** England, Westmorland, 1873, P. Dreesen (S); 54.5°N, 3.0°W. **(78)** England, Buckstone, Stanton, Glos., 23 October 1912, H. H. Knight (S); 51.8°N, 2.0°W. **(76)** England, Westmorland, Lingmoor, May 1908, J. A. Wheldon (Z); 54.5°N, 3.0°W. **(40)** Isles of Scilly, St Mary's, Watermill Cove, 14 June 1996, D. T. Holyoak 96-222 (herb. Holyoak); 49.9°N, 6.3°W. **(27)** Scotland, Shetland, Fair Isle, Gill o' Finniquoy, 19 June 1963, G. Een UK 525 (S; reg. no. B70209); 59.5°N, 1.6°W. **(26)** Scotland, Shetland, Fair Isle, Johnny's Peats, 22 June 1963, G. Een UK 511 (S; reg. no. B71937); 59.5°N, 1.6°W. **(22)** Scotland, Shetland, mainland, Ronas Hill, 8 August 1954, P. A. H. Arnell (S); 60.5°N, 1.5°W. **(37)** Scotland, Stirlingshire, Loch Lomond, 11 August 1898, R. Kidston (S); 56.2°N, 4.7°W.

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