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Oncophorus demetrii, a fifth Scandinavian species of *Oncophorus* (Musci) possible to recognize by morphology

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One of the three lineages found within *Oncophorus wahlenbergii* Brid. in a recent revision of Scandinavian *Oncophorus* is explored in detail. Consistent and well-supported nuclear ITS and plastid *trn*G and *rps*4 signals for a total of eight specimens belonging to this lineage, and the possibility to recognize its members by morphology, support recognition of *Oncophorus demetrii* (Renauld & Cardot) Hedenäs, *comb. nov*. (*Dicranum demetrii* Renauld & Cardot). This species differs from members of the other two *O. wahlenbergii* lineages by its more longly and narrowly acuminate leaves, projecting cell walls in the upper leaf margins, and the excurrent costa being rough from projecting cells or cell walls. Contrary to members of the other two *O. wahlenbergii* lineages, *O. demetrii* seems to prefer base-rich habitats. Outside Scandinavia, it is at present known from Labrador in Canada. *Oncophorus compactus* (Bruch & Schimp.) Kindb. is considered a synonym of *O. wahlenbergii* since *Dicranum homannii* Boeck, a synonym of *O. wahlenbergii*, was cited as a synonym of *Dicranum virens* var. *compactum* Bruch & Schimp. when the latter was described.

The predominantly northern temperate genus *Oncophorus* (Dicranales: Oncophoraceae; Frey and Stech 2009, Goffinet et al. 2008, Stech and Frey 2008) was until recently supposedly well-known (Frahm et al. 1998). However, as shown by Hedderson and Blockeel (2006) and Hedenäs (2005), and especially in a recent review of the genus in Scandinavia based on both molecular and morphological information (Hedenäs 2017), the genus has actually been poorly understood. Four Scandinavian species that can be distinguished by morphology were accepted by Hedenäs (2017), namely *O. elongatus* (I. Hagen) Hedenäs, *O. integerrimus* Hedenäs, *O. virens* (Hedw.) Brid. and *O. wahlenbergii* Brid. Beside the recognized species, Hedenäs (2017) found intraspecific variation with a phylogeographic signal in *O. elongatus* and *O. virens*, and identified three molecular *O. wahlenbergii* lineages that appear distinct at the species level and require further study.

The two most distantly related of the three *O. wahlenbergii* lineages could not be distinguished by morphological features, indicating truly cryptic species, whereas the third, called '*O. wahlenbergii* B', could potentially be distinguished by a few morphological characteristics (Fig. 1A, C; Hedenäs 2017). Only three *O. wahlenbergii* B specimens were, per chance, included in the sample of Hedenäs (2017) and further molecular data for such specimens are therefore required to decide how to treat them. As a follow-up to Hedenäs (2017), five specimens having a morphology similar to that of *O. wahlenbergii* B are here selected to test the idea that a fifth species could potentially be recognizable also by morphology. All the additional specimens turned out to belong to the same molecular lineage as *O. wahlenbergii* B of Hedenäs (2017), confirming that this lineage can be recognized by morphology and that it should be recognized as a fifth, morphologically recognizable Scandinavian *Oncophorus* species. Among the numerous old names existing for members of the Oncophoraceae and similar-looking Dicranaceae one species level taxon that is identical with *O. wahlenbergii* B, was discovered, *Dicranum demetrii* Renauld & Cardot. According to Van der Wijk et al. (1962), this taxon is a synonym of *O. wahlenbergii* Brid. (s.l.), but as it agrees with *Oncophorus wahlenbergii* B of Hedenäs (2017) the latter is from here on called *Oncophorus demetrii* (Renauld & Cardot) Hedenäs. This paper presents the results of the molecular evaluation, the species' morphological circumscription, and describes its Scandinavian distribution and habitat.

Material and methods

Study species and material

Five specimens of *Oncohorus demetrii* were selected based on morphological criteria used in the key to the Scandinavian *Oncophorus* species in the Taxonomy section. Sequences

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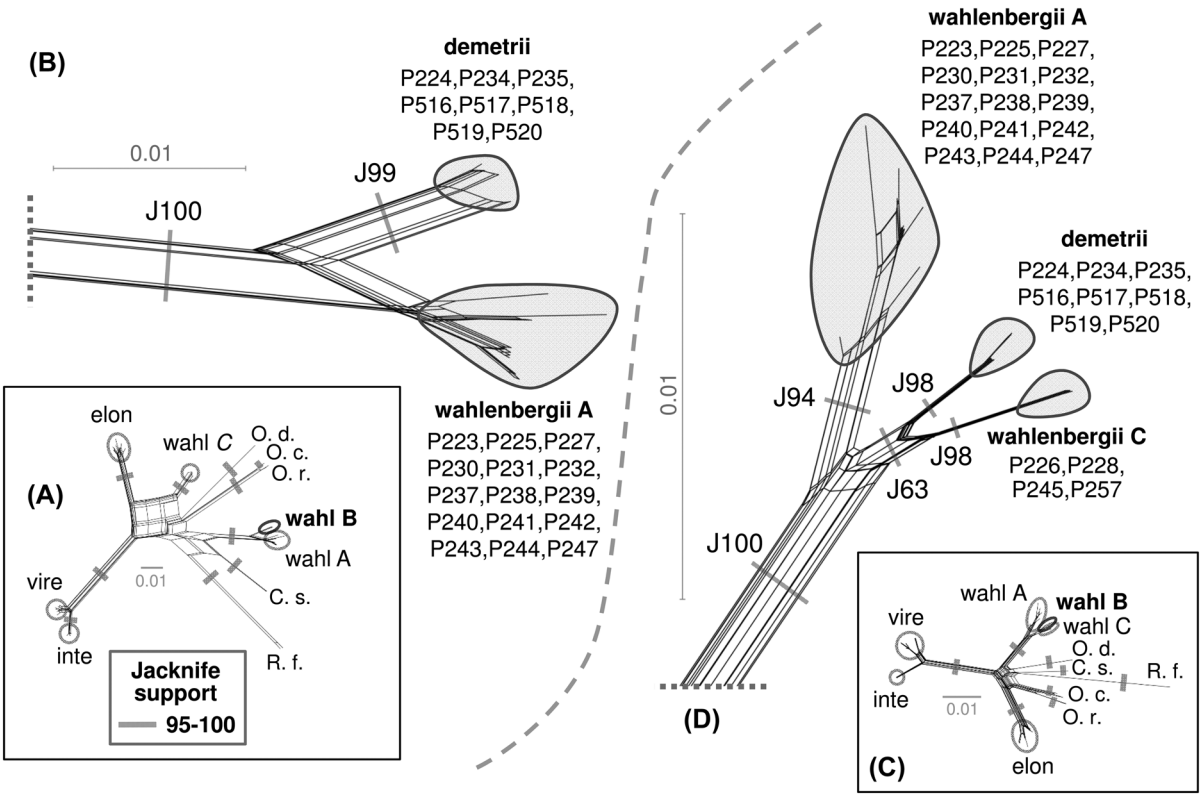


Figure 1. (A, C) Simplified NeighborNet split networks for *Oncophorus*, modified after Hedenäs (2017): *O. crispifolius* (*O.c.*, 2 specimens), *O. dendrophilus* (*O.d.*, 2), *O. elongatus* (24), *O. rauei* (*O.r.*, 2), *O. virens* (22), *O. wahlenbergii* s.l. (22), *O. integerrimus* (26), with outgroup (*C.s.* = *Cynodontium strumiferum*, 2; *R.f.* = *Rhabdoweisia fugax*, 2). Grey lines indicate Jacknife support values of 95–100. (B, D) Detailed portions of the split networks based on the current analysis with five additional specimens of *O. demetrii* ('*O. wahlenbergii* B' of Hedenäs 2017) included. Actual Jacknife support values are provided. (A, B) based on the nuclear ITS. (C, D) based on the plastid *trn*G and *rps*4. Locality information for specimens (P numbers) are provided in Hedenäs (2017) and Table 1.

generated for these specimens were added to those of the 100 *Oncophorus* specimens included in the earlier study (Hedenäs 2017), using *Cynodontium strumiferum* (Hedw.) Lindb. and *Rhabdoweisia fugax* (Hedw.) Bruch & Schimp. as outgroup based on their appearance in a clade sister to *Oncophorus* in Stech et al. (2012). The newly added specimens are listed in Table 1.

The subsequent morphological analysis was based on the eight specimens of *O. demetrii* that were included in the molecular analysis, whereas the geographical distribution of this species was mapped based on the Scandinavian material present in the Swedish Museum of Natural History (S).

Table 1. Specimen data and GenBank accession numbers for the newly generated sequences of *Oncophorus demetrii*. Data format: Sample no. (in bold), Locality, Coll. Year, *Collector* [*collector's no.*]; S herbarium registration no.; GenBank accession numbers for ITS, *trn*G, *rps*4.

P516: Sweden. Jämtland, Frostviken, Mt. Brakkfjället; 2009, *L. Hedenäs*; B163785; MF124875, MF124885, MF124880.
P517: Sweden. Härjedalen, Tännäs, Mt. Kliehpie; 2014, *L. Hedenäs*; B207474; MF124876, MF124886, MF124881.
P518: Sweden. Pite Lappmark, Arjeplog, Mávasjávrre; 2015, *L. Hedenäs et al.*; B226164; MF124877, MF124887, MF124882.
P519: Sweden. Lycksele lappmark, Tärna, Mt. Raavriedenjuenie; 2016, *L. Hedenäs*; B237838; MF124878, MF124888, MF124883.
P520: Sweden. Härjedalen, Hamrafjället; 1981, *T. Hallingbäck 1904*; B182827; MF124879, MF124889, MF124884.

Detailed label information for these specimens is available at <http://herbarium.nrm.se/>.

Molecular methods

The molecular methods employed to generate sequences of the nuclear internal transcribed spacers 1 and 2 (ITS) and the plastid *trn*G_{UCC} G2 intron (*trn*G) and *rps*4 gene + *trn*S-*rps*4 spacer (*rps*4) are the same as in Hedenäs (2017), and the reader is referred to that paper for further information.

Sequence editing and analysis of molecular data

Nucleotide sequence fragments were edited and assembled for each DNA region using PhyDE 0.9971 (<www.phyde.de/index.html>). The assembled sequences were manually aligned in PhyDE. Regions of partially incomplete data in the beginning and end of the sequences were identified and excluded from subsequent analyses. Gaps were coded as informative by simple indel coding (Simmons and Ochoterena 2000), using SeqState (Müller 2005). The sequence alignments used in the analyses are available on request. European Nucleotide Archive (EMBL-ENA) accession numbers for the earlier sequences are found in Hedenäs (2017) and GenBank accession numbers for the newly generated ones are listed in Table 1.

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Paralogous ITS haplotypes are occasionally encountered in bryophytes (but see Košnar et al. 2012). However, the ITS chromatograms generated in this study did not show 'messy' patterns or noise that could suggest paralogy, and the 5.8S gene was invariable among the samples (cf. Shaw et al. 2002, Feliner and Rosselló 2007). Therefore, the revealed ITS variation is interpreted as being among homologous haplotypes.

The program TCS (Clement et al. 2000) was used to evaluate relationships among specimens in a haplotype context. Reticulation was revealed in the haplotype networks based on either ITS or chloroplast data. Because reticulation occurs, a split network was computed with the NeighborNet (NN) method as implemented in SplitsTree ver. 4.12.6 (Huson and Bryant 2006) to visualise similarities or relationships among samples. A Jacknife analysis (1000 replications) was performed with the program TNT (Goloboff et al. 2003) to test whether supported lineages exist among the studied *Oncophorus* species in a phylogenetic tree context. ITS and chloroplast data were analysed separately, since Hedenäs (2017) found the two data sets to be incongruent.

Morphological study and analysis of measurements

The morphology of the five newly added *O. demetrii* specimens was studied as described by Hedenäs (2017), including standard comparisons of qualitative and quantitative characters and the quantification of vegetative leaf size, and leaf cell size and shape. For each specimen, three vegetative leaves were sampled from two shoots (two leaves from one stem and one from the other). For each leaf, length and maximal width were measured, and the length, width, and length to width ratio of 20 cells in the upper acumen, 20 in the lower acumen, and 20 in the sheathing basal lamina were recorded. Temporary images of the leaves were taken through an Olympus BX43 microscope using an Olympus SC50 digital camera and the Olympus cellSens Standard ver. 1.13 software (Olympus Corporation) for automatic and continuous image stacking. Measurements were made from these leaf and cell images, using the Olympus cellSens Standard ver. 1.13 software. In this way, measurements of all eight specimens of molecularly confirmed *O. demetrii* are now available.

Comparisons among *O. elongatus*, '*O. wahlenbergii* A plus C' (two morphologically indistinguishable lineages), and *O. demetrii* (cf. Hedenäs 2017) are based on two approaches. First, the cell measurements were compared. Shapiro Wilks W-test (normality) and Levenes test (homogeneity of variance) were both statistically significant, and inspection of the distributions of residuals in preliminary Anovas showed that the data do not meet the criteria of normality and homogeneity of variance. Thus, the nonparametric Kruskal–Wallis test was employed to compare the cell measurements among the three. Second, the measurements of the individual leaves (length, width, and the mean cell length, cell width, and cell length to width ratio, at each of the three positions in the leaf; in total 11 parameters) were subjected to a principal component analysis (PCA) to see whether the combined information corresponds with *O. elongatus*, *O. wahlenbergii* (A plus C), and *O. demetrii*. In the PCA, measurements of three leaves from the isotype of *Dicranum demetrii* Renauld & Cardot were also included to make sure that this agrees with what is here called *O. demetrii*. All statistical calculations were made in STATISTICA 13 (<http://statistica.io/>; accessed 28 April 2017).

Results

Relationships among *Oncophorus wahlenbergii* s.l. specimens

The five newly sequenced specimens of *Oncophorus demetrii* group with the three that had been studied earlier, both based on ITS and plastid data (Fig. 1B, D). In the ITS analysis they form a clade with a Jacknife support of 99, sister to *O. wahlenbergii* A, in a clade with Jacknife support of 100 (Fig. 1B). ITS data place *O. wahlenbergii* C in a different branch (cf. Fig. 1A). In the plastid analysis all three *O. wahlenbergii* entities are found together (Jacknife support: 100), but the three form three separate and well-supported lineages (Jacknife support: 94, 98, 98), and within this main lineage *O. demetrii* and *O. wahlenbergii* C are weakly supported as sister groups (Jacknife support: 63) (Fig. 1D). No *O. wahlenbergii* s.l. (including *O. demetrii*) specimens appear in positions intermediate between the three lineages.

Statistical comparison of the measurements

Oncophorus elongatus, *O. demetrii* and *O. wahlenbergii* (A plus C) differ from each other in five of the nine measured parameters. In the remaining parameters two of the species differ from each other or one species is different from both the other ones (Table 2). According to the PCA, there is only limited overlap between *O. elongatus* and *O. wahlenbergii* (A plus C) (Fig. 2A). *Oncophorus demetrii* and *O. wahlenbergii* are likewise only slightly overlapping, whereas *O. demetrii*, including the isotype of *Dicranum demetrii*, overlaps strongly with *O. elongatus*. The separation of the species occurs mainly along a gradient from the upper left to the lower right in the diagram, and suggests that leaf length and width, and width of the apical and middle lamina cells are

Table 2. Means plus standard errors for cell measurements in the acumen (20 cells per leaf), in mid-leaf (20), and in the sheathing base (20) from three leaves in each of 18 specimens of *Oncophorus elongatus*, 8 of *O. demetrii*, and 14 of *O. wahlenbergii* (A plus C; *wahl.* AC). Lengths and widths are in µm, and the number of cells measured at each position, n, is indicated after the species names. Significant pair-wise differences revealed by the Kruskal–Wallis test are indicated by letters appended after the values in the columns, for the Bonferroni corrected p-values corresponding with $p < 0.05$.

Position; measurement	*elongatus* (1080)	*demetrii* (480)	*wahl.* AC (840)
Acumen; length (AL)	14.6 (0.1) a	15.5 (0.2) b	17.3 (0.2) c
Acumen; width (AW)	10.8 (0.1) a	10.9 (0.1) a	12.3 (0.1) b
Acumen; AL/AW ratio (AR)	1.40 (0.02) a	1.45 (0.02) b	1.45 (0.02) ab
Mid-leaf; length (ML)	17.4 (0.2) a	19.8 (0.3) b	19.4 (0.2) b
Mid-leaf; width (MW)	10.4 (0.0) a	10.1 (0.1) b	11.5 (0.1) c
Mid-leaf; ML/MW ratio (MR)	1.72 (0.02) a	2.03 (0.04) b	1.74 (0.02) a
Base; length (BL)	51.1 (0.5) a	62.3 (0.8) b	47.5 (0.5) c
Base; width (BW)	10.2 (0.1) a	9.4 (0.1) b	10.0 (0.1) c
Base; BL/BW ratio (BR)	5.20 (0.06) a	6.92 (0.12) b	4.87 (0.06) c

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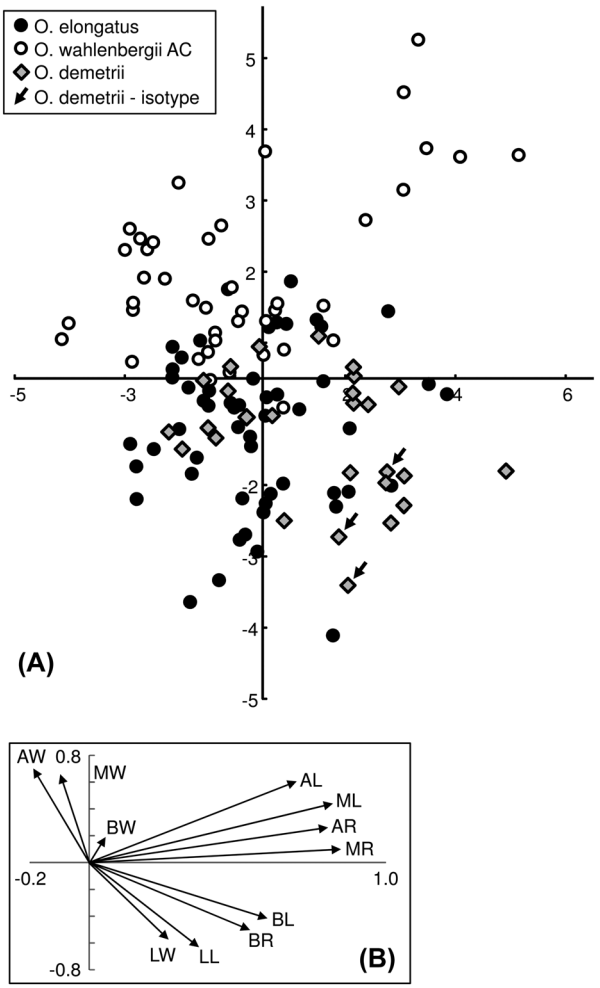


Figure 2. (A) The positions of three leaves from each of eighteen molecularly identified specimens of *O. elongatus,* fourteen of *O. wahlenbergii* A plus C (AC), eight of *O. demetrii* (Fig. 1), and the studied isotype of *Dicranum demetrii* Renauld & Cardot (S, reg. no. B249252) along the first two axes in a PCA. The PCA is based on each leaf's length (LL), width (LW), and leaf lamina cell length, width, and length/width ratio in the apical (AL, AW, AR), middle (ML, MW, MR), and sheathing basal (BL, BW, BR) lamina. Cell measurements are the mean values of 20 cells per position in each leaf. Axes 1 and 2 explain 30.81% and 25.12% of the variation. (B) Explanatory factors in the plane of axes 1 and 2.

important explanatory factors (Fig. 2B). Even if there are differences between some or all species and we find a relatively clear separation in the PCA, the species overlap considerably in all the measured characters (Fig. 3).

Taxonomy

Key to Scandinavian Oncophorus species

Note: Check the upper portions of numerous, relatively young leaves to correctly judge the states of *O. wahlenbergii* and *O. demetrii*. Descriptions and nomenclature of *O. elongatus*, *O. integerrimus*, *O. virens* and *O. wahlenbergii* are provided by Hedenäs (2017).

1. Stem leaf margin plane throughout; alar cells not or weakly differentiated from other basal cells 2
–. Stem leaf margin at least partly distinctly recurved in lower leaf; alar cells well differentiated 4
2. Lamina of basal, sheathing leaf portion in its middle and lower portions with long and narrow cells along margin; margin and often back of costa in upper (10)25–35(50)% of many leaves denticulate or dentate, often sharply so, rarely with only a few leaves having scattered obtuse teeth above. Vegetative leaves 2.5–6.4 × 0.4–1.2 mm *O. elongatus*
–. Lamina of basal, sheathing leaf portion with quadrate to elongate-rectangular cells extending down along margin (from spreading lamina); margin and back of costa smooth or with one or a few indistinct and mostly obtuse teeth, especially close to apex, or with projecting cell walls along upper margin and costa rough on back from projecting cells or cell walls. Vegetative leaves 1.4–4.8 × 0.3–0.8 mm 3
3. Leaf margin entire or with an occasional indistinct denticle near apex, if cell walls slightly projecting as obtuse denticles in upper margin, then excurrent costa smooth on back; leaf apex obtuse to narrowly acuminate *O. wahlenbergii*
–. Leaf margin above often with one or a few indistinct and mostly obtuse teeth, especially close to apex, in many or all leaves cell walls distinctly projecting in upper 5-25% of leaf margin, and excurrent costa rough from projecting cells or cell walls; leaf apex narrowly acuminate or occasionally acuminate *O. demetrii*
4. Leaf margin in acumen and often down to mid-leaf regularly to irregularly dentate or coarsely denticulate with mostly sharp and often some double teeth, strong teeth often directed forwards, occasional leaves less distinctly dentate. Dry leaves with acumen from above sheathing base erect and tightly incurved to spreading, above strongly twisted *O. virens*
–. Leaf margin in acumen entire or indistinctly and obtusely denticulate, occasionally distinctly denticulate close to leaf apex. Dry leaves with acumen from above sheathing base erect-patent to spreading and loosely incurved or curved upwards, upper acumen loosely but relatively strongly twisted *O. integerrimus*

Oncophorus demetrii (Renauld & Cardot) Hedenäs, comb. nov. Fig. 4, 5

Basionym: *Dicranum demetrii* Renauld & Cardot, Bot. Gaz. 22: 48. 3A. 1896. Type: [Canada] 'Herb. J. CARDOT. "Dicranum demetrii Ren. Et Card." (e specim. origin.) = *Oncophorus virens* Brid. var.! Amer. sept., Labrador, Leg. Rev. Waghorne, 1892', (S, reg. no. B249252!; isotype).

Plants from a few mm to several cm high, in loose tufts or dense cushions, green or yellow-green. *Stem* with large central strand, a cortex plus epidermis of 12 layers of incrassate cells, epidermis not differentiated as a hyalodermis; axillary hairs with 27(8)-celled, hyaline upper portion, 69 μm wide, basal 12 cells rectangular or elongate-rectangular, hyaline or pale brown; rhizoids strongly branched, red-brown, smooth, in leaf axils or shortly above. *Leaves* 2.6–4.8 × 0.4–0.8 mm, when moist from sheathing base almost erect to patent or sometimes spreading and straight or slightly curved, when dry with middle leaf spreading and gradually curved upwards-inwards and more or less curled, from oblong or slightly oblong-obovate sheathing portion (often narrowed

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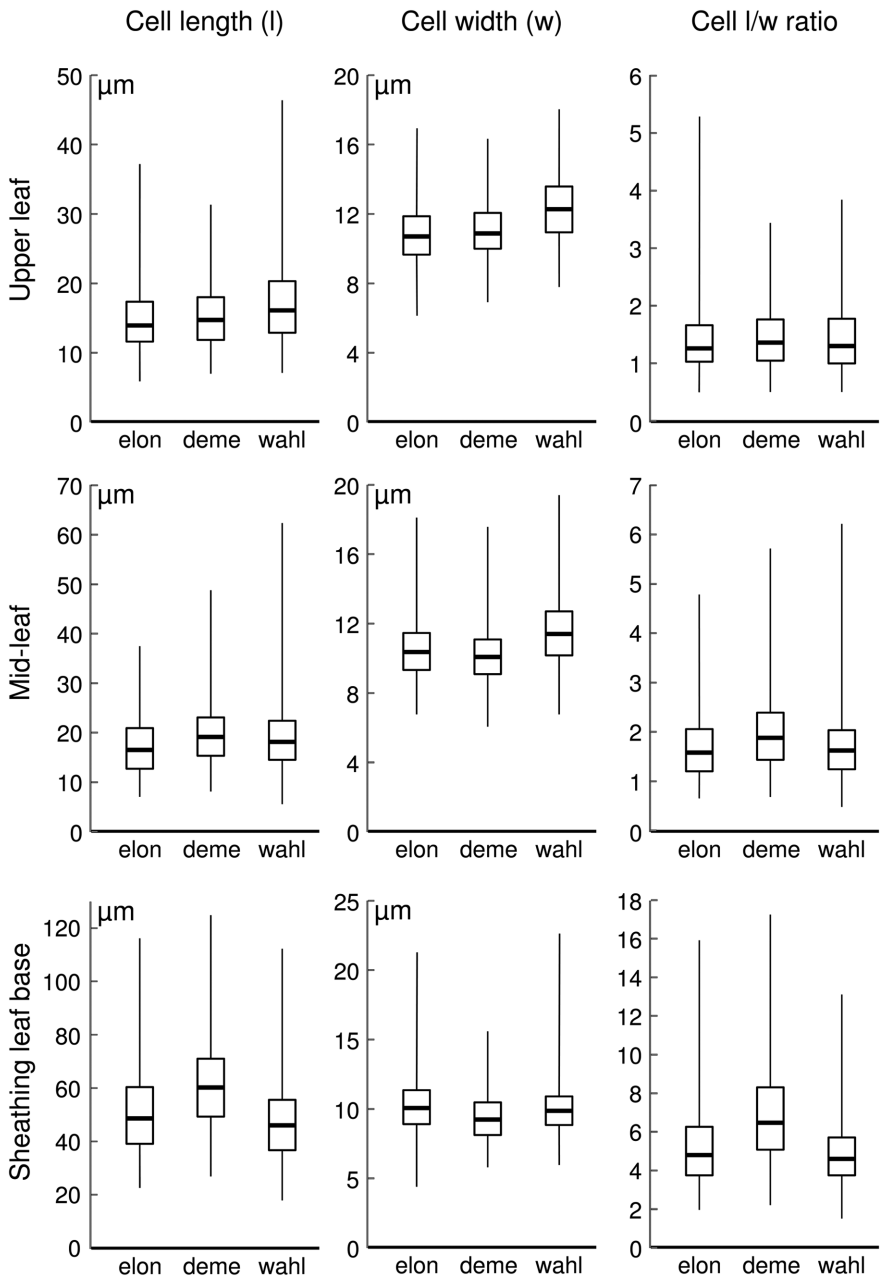


Figure 3. Boxplots with median values, quartiles, and whiskers from maximum to minimum values, for cell length, width, and length/width ratio in the upper, middle, and basal leaf portions for *Oncophorus elongatus* (elon; 18 specimens), *O. demetrii* (deme; 8) and *O. wahlenbergii* A plus C (wahl; 14) (cf. Fig. 1). From each molecularly identified specimen, three leaves were selected as described in the text, and 20 cells were measured at each position in the leaf. For each parameter, the number of measurements was 1080 in *O. elongatus*, 480 in *O. demetrii*, and 840 in *O. wahlenbergii* A plus C.

towards insertion) with gradually narrowed, usually long and narrow upper portion, apex acuminate or mostly narrowly acuminate; leaf margin plane throughout, below entire, above often with one or a few indistinct, mostly obtuse teeth, especially close to leaf apex, cell walls projecting along upper 5–25% of margin, margin unistratose or partly bistratose; costa 39–88 µm wide near base, excurrent, with dorsal and ventral epidermis cells slightly widened but incrassate, one layer of large guide cells, 1–2 layers of ventral stereids and 1–2 layers of dorsal stereids, upper back and often sides of excurrent costa rough from projecting cell walls or cell portions, at least close to apex; lamina cells in acumen incrassate, 10–20 × 9–12 µm, 0.9–2.0 times as long as wide, in mid-leaf incrassate, 15–27 × 9–13 µm, 1.6–2.8 times as long as wide, and in sheathing lamina strongly incrassate and porose or indistinctly so, rarely eporose, 44–84 × 7–12 µm, 4.8–10.2 times as long as wide, transition between mid-leaf and basal cells gradual, due to relatively long lower mid-leaf cells, lamina of basal, sheathing portion of leaf with quadrate or rectangular cells extending down along margin from spreading lamina; alar cells undifferentiated or a few cells wider than other basal cells, unistratose, not or shortly and narrowly decurrent. *Perigonia* lateral on stem, not or shortly stalked, antheridia protected by oblong-triangular perigonial

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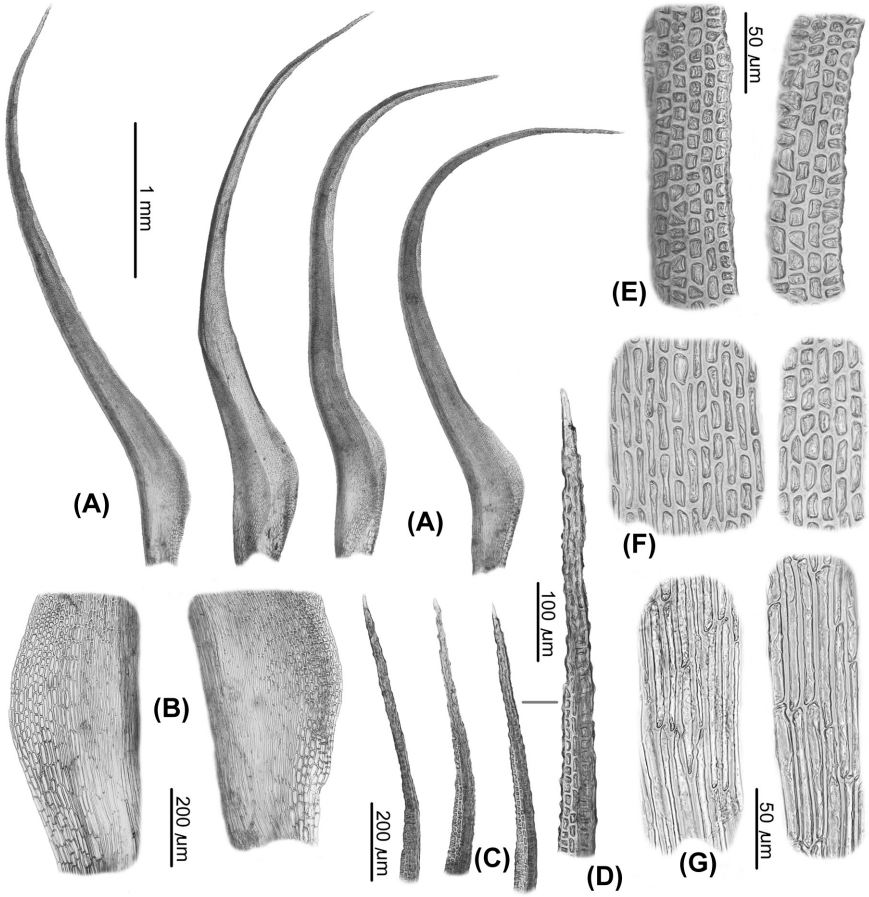


Figure 4. Isotype of *Dicranum demetrii* Renauld & Cardot (S, reg. no. B249252). (A) Stem leaves. (B) Sheathing leaf base. (C, D) Apical leaf portions. (E) Upper leaf lamina cells with leaf margin to the right. (F) Median leaf lamina cells. (G) Lamina cells of sheathing leaf base.

leaves, sometimes with broad acumen to as long as basal leaf, apex obtuse or acute. *Inner perichaetial leaves* 3.57–4.68 mm long, lower (25)30–50% oblong and broadly sheathing, above suddenly narrowed to long, narrow acumen. *Calyptra* cucullate, smooth, naked. *Seta* tall, 8–22 mm, yellowish when young, orange-red when mature; capsule obloid or cylindrical, curved or slightly curved, rarely almost straight, with distinct struma, when dry 1.0–1.4 × 0.3–0.5 mm, 2.0–3.3 times as long as broad, more or less orthogonal or occasionally homotropous, when empty and dry furrowed or strongly so; exothecial cells incrassate, sometimes more strongly so in longitudinal walls, not or weakly collenchymatous, sometimes alternating with zones having thin-walled or slightly incrassate cells; stomata few, ovate-pored or lacking pore, surrounded by radially arranged cells, near base of capsule; annulus not separating; operculum conical-rostrate; peristome red, teeth cleft or perforated to one fourth or further down, with longitudinal rows of pits on outside; spores 21–27 µm, finely papillose.

Oncophorus demetrii is on the average intermediate in size between *O. wahlenbergii* (A plus C) and *O. elongatus*. Contrary to *O. elongatus*, but similar to *O. wahlenbergii*, *O. demetrii* has quadrate or rectangular marginal cells in the middle and basal portions of the basal, sheathing lamina. Its vegetative leaves are shorter than in *O. elongatus* (see the key to the species), and in their upper (10)25–35(50)% the margins and back of costa are never distinctly or sharply denticulate or dentate (Hedenäs 2017). *Oncophorus demetrii* has acuminate or mostly narrowly acuminate leaves, whereas in *O. wahlenbergii* the leaves frequently end in a clearly obtuse point. In *O. wahlenbergii* specimens with narrowly acuminate leaves, the leaves can have very obtusely denticulate uppermost margins (high magnification), where the denticles are formed by projecting cell walls. In *O. demetrii*, on the other hand, many leaves have the leaf margins uneven due to projecting cell walls in their upper 5–25%, which was nicely illustrated in Plate 3A by Renauld and Cardot (1896) in their description of the species, and the excurrent costa is at least partly rough from projecting cells or cell walls.

Nomenclatural notes

The leaves in the isotype of *Dicranum demetrii* Renauld & Cardot (Fig. 4) are slightly worn, but the features of the type material agree well with those of the Scandinavian material (Fig. 5) that was called *O. wahlenbergii* B by Hedenäs (2017).

The names cited as synonyms under *O. wahlenbergii* Brid. by Hedenäs (2017) all belong to *O. wahlenbergii* (A plus C) rather than to *O. demetrii*. *Oncophorus compactus* (Bruch & Schimp.) Kindb. (*Dicranum virens* var. *compactum* Bruch & Schimp.) was not treated by Hedenäs (2017). Bruch et al. (1836–1851) cite *Dicranum homannii* Boeck as a synonym of their *D. virens* var. *compactum*. Since the S isotype (S-B231701!) of *D. homannii* belongs to *O. wahlenbergii*

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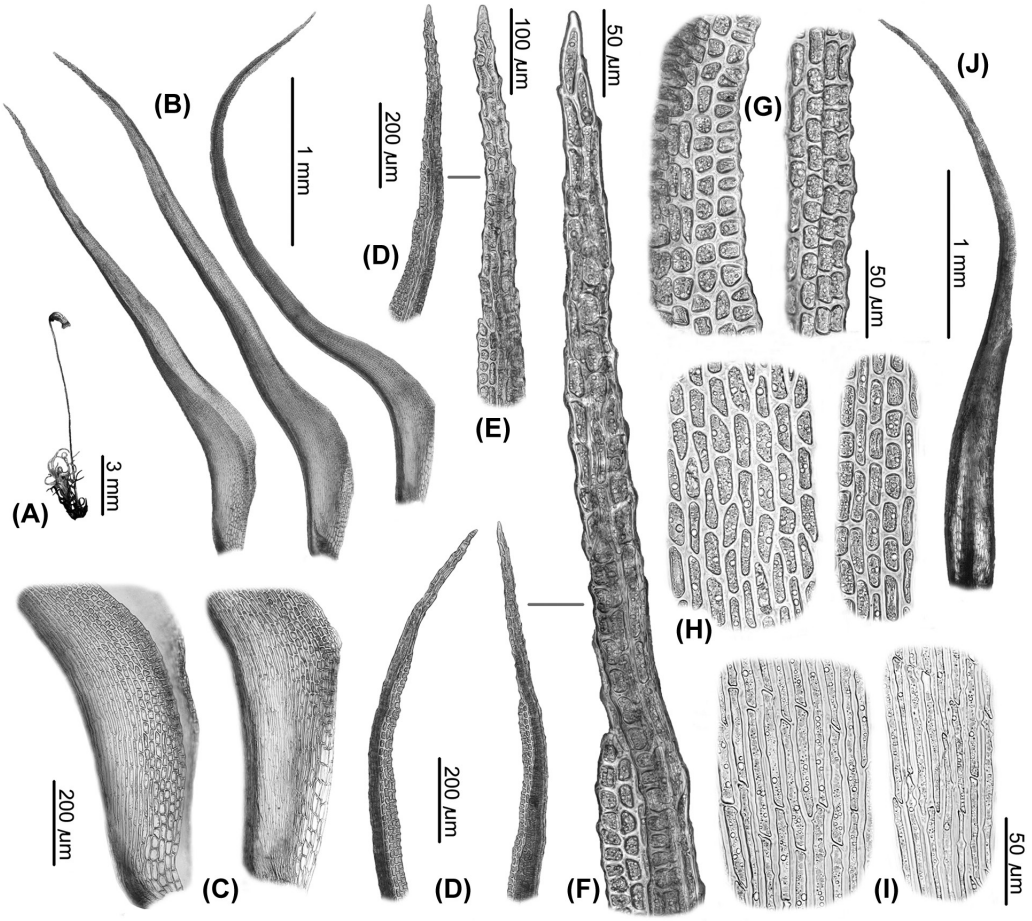


Figure 5. *Oncophorus demetrii* (Renauld & Cardot) Hedenäs (Sweden. Jämtland, Frostviken, 2 August 2009, L. Hedenäs; S, reg. no. B163267). (A) Habit, dry. (B) Stem leaves. (C) Sheathing leaf base. (D–F) Apical leaf portions. (G) Upper leaf lamina cells with leaf margin to the right. (H) Median leaf lamina cells. (I) Lamina cells of sheathing leaf base. (J) Inner perichaetial leaf.

(A plus C) (Hedenäs 2017), *O. compactus* is also a synonym of *O. wahlenbergii* Brid.

Habitat and distribution in Scandinavia

Oncophorus demetrii occurs in the Scandinavian mountain range from the sea level at the northern Norwegian coast to 1300 m a.s.l. (Fig. 6). In the lowlands to the east of the mountains, there is one find from the shore of the Swedish river Indalsälven, which sources are in the mountain range. It is the Scandinavian *Oncophorus* species with the most restricted geographical distribution; maybe this is why it has remained undetected until now. Outside Scandinavia, the species is known from Labrador in Canada (type locality for *Dicranum demetrii*), which suggests that it occurs also in other northern areas.

According to label information and field observations in the rich north-facing slopes between Björkliden and Vassijaure, west of Lake Torneträsk (northern Swedish Lappland) in 2017, the species often grows in base-rich or calcareous habitats. This includes meadows and wet meadows, heaths and wet mountain heaths, including *Dryas-Cassiope* heaths, rich fens, wet or periodically wet rocks and rock crevices, and brook and river shores, where it can occasionally grow on rotten wood. In its habitat, *O. demetrii* therefore deviates from *O. wahlenbergii* (A plus C) and *O. elongatus*, which occur predominantly in base-poor habitats.

Discussion

In the previous study of Scandinavian *Oncophorus* (Hedenäs 2017), three *O. wahlenbergii* lineages were identified by molecular data. Two lineages included only three or four specimens, respectively, and these were included per chance thanks to a sufficiently large sample size. To reveal such unexpected species-level diversity, it is necessary to study a relatively large number of representative specimens from different geographical regions. The three specimens of the poorly represented lineage that corresponds with *O. demetrii* differ from those of the other two lineages in a few morphological traits. A molecular examination of additional specimens with *O. demetrii* morphology shows that this species is distinguishable also by morphology. Within the genus *Oncophorus* in Scandinavia, we have thus five morphologically distinguishable species, and an additional cryptic one which morphology is similar to that of *O. wahlenbergii*.

Oncophorus occurs mainly in arctic to temperate regions of the Northern Hemisphere (Frahm et al. 1998), also in the high-arctic (Frisvoll and Elvebakk 1996), and diversification

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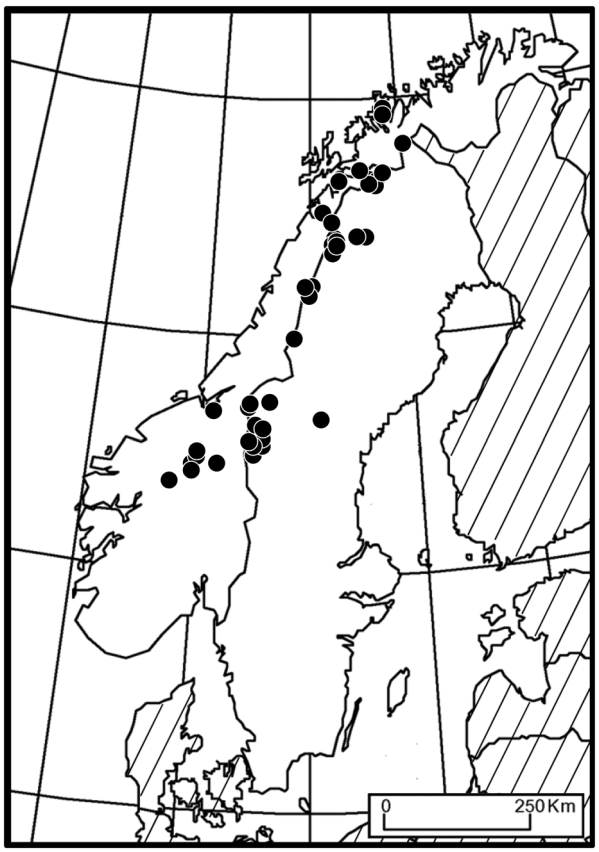


Figure 6. Distribution of *Oncophorus demetrii* in Scandinavia based on material present in S.

within the genus therefore likely occurred in environments and climates similar to what we find in these areas today. *Oncophorus* species are present in the fossil record from the late Pliocene and Quaternary periods (Janssens 1983, Hedenäs 1994a, Hedenäs and Bennike 2009), showing that its diversification has a history of at least 2.5 MY. For northern, cold-adapted taxa like *Oncophorus* an important driver for diversification could therefore have been the glacial fluctuations that repeatedly segregated independently evolving populations in isolated refugia, also small northern ones, during the glacial periods. However, to establish if this is likely as an explanation or partial explanation, the timing of the diversification events needs to be established, which requires a better fossil record for *Oncophorus* and related taxa than is available at present.

Compared with the two European species accepted by Frahm et al. (1998) the increase to six, including *O. dendrophilus* Hedd. & Blockeel (Hedderson and Blockeel 2006), or with the cryptic *O. wahlenbergii* one, even seven species, is highly significant. During the last decades, the number of accepted species has increased in several European moss groups. This was first a result of classical taxonomic studies (Frisvoll 1983, 1988, Hedenäs 1994b, Blom 1996), and this trend continues in the age of integrative taxonomy (Köckinger et al. 2010, Köckinger and Kučera 2011, 2016, Medina et al. 2013, Buchbender et al. 2014, Hedenäs et al. 2014, Caparrós et al. 2016, Ignatova et al. 2016, Köckinger and Hedenäs 2017). In addition, cryptic species diversity is revealed, as in *O. wahlenbergii* (Hedenäs 2017) and *Hamatocaulis vernicosus* (Mitt.) Hedenäs (Hedenäs and Eldenäs 2007). It now seems very likely that diversity losses at the intraspecific level have been significant (Hedenäs 2016), and based on the just cited information on species we may ask 1) how much of the European species level diversity that still hides among synonyms or undescribed species and 2) how much of this is threatened or has already been lost? Bryophyte taxonomy and systematics are declining disciplines in many European countries today, despite the obvious lack of knowledge regarding even which species actually exist on the continent.

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