



Research article

Scandinavian *Oncophorus* (Bryopsida, Oncophoraceae): species, cryptic species, and intraspecific variation

Lars HEDENÄS

Swedish Museum of Natural History, Department of Botany,
Box 50007, SE-104 05 Stockholm, Sweden.

E-mail: lars.hedenas@nrm.se

Abstract. Scandinavian members of the acrocarpous moss genus *Oncophorus* were revised after field observations had suggested unrecognized diversity. Based on molecular (nuclear: internal transcribed spacers 1 and 2, ITS; plastid: *trnG*_{UCC} G2 intron, *trnG*, *rps4* gene + *trnS-rps4* spacer, *rps4*) and morphological evidence, four morphologically distinguishable species are recognized, *Oncophorus elongatus* (I.Hagen) Hedenäs, *O. integerrimus* Hedenäs sp. nov. (syn. *O. virens* var. *elongatus* Limpr.), *O. virens* (Hedw.) Brid., and *O. wahlenbergii* Brid. (*O. sardous* Herzog, syn. nov.). *Oncophorus elongatus* was earlier recognized, but much of its variation was hidden within *O. wahlenbergii*. Its circumscription is here expanded to include plants with long leaves having mostly denticulate or sharply denticulate upper margins and with long and narrow marginal cells in the basal portion of the sheathing leaf lamina. The new species *O. integerrimus* sp. nov. differs from *O. virens* in having more loosely incurved leaves and entire or almost entire upper leaf margins. Besides these characters, the species in the respective pairs differ in quantitative features of the leaf lamina cells. Several cryptic entities were found, in several cases as molecularly distinct as some of the morphologically recognizable species, and phylogeographic structure is present within *O. elongatus* and *O. virens*.

Keywords. Geographic differentiation, habitat differences, morphology, *Oncophorus integerrimus* Hedenäs sp. nov., Principal Component Analysis.

Hedenäs L. 2017. Scandinavian *Oncophorus* (Bryopsida, Oncophoraceae): species, cryptic species, and intraspecific variation. *European Journal of Taxonomy* 315: 1–34. <https://doi.org/10.5852/ejt.2017.315>

Introduction

A significant proportion of species diversity is either not yet recognized, such as undescribed species, or hidden within morphologically closely similar or virtually identical species (Hawksworth 2001; Bickford *et al.* 2006; Crawford & Stuessy 2016). During the last years this has been shown repeatedly for different bryophyte genera (Heinrichs *et al.* 2010; Carter 2012a, 2012b; Buchbender *et al.* 2014; Hedenäs *et al.* 2014; Draper *et al.* 2015). *Oncophorus* Brid. (von Bridel 1826) is another example of a moss genus for which species' circumscriptions are still unclear, and where it has not yet been tested if the many existing names at levels below the species reflect high intraspecific variation (e.g., Limpricht 1886; Mönkemeyer 1927; Nyholm 1987). *Oncophorus* (Dicranales: Oncophoraceae; Goffinet *et al.* 2008; Stech & Frey 2008; Frey & Stech 2009) includes acrocarpous species with leaves having a sheathing basal portion and a mostly long, gradually tapering, and narrowly triangular to almost linear

upper portion. Species of *Oncophorus* are frequent in many wet or humid habitats in arctic to temperate regions of the Northern Hemisphere, and in addition some species occur in Sri Lanka or temperate areas of the Southern Hemisphere (Frahm *et al.* 1998; Frey & Stech 2009).

In a relatively recent global treatment of *Oncophorus*, Frahm *et al.* (1998) recognized six species, down from twelve before their revision. Since then additional species were distinguished or described (Hedenäs 2005; Hedderson & Blockeel 2006), and Frey & Stech (2009) recognized nine species in the genus. Two of the species that Frahm *et al.* (1998) recognized, *O. virens* (Hedw.) Brid. (von Bridel 1826) and *O. wahlenbergii* Brid. (von Bridel 1826) are widespread and frequent in many areas of northern and central Scandinavia, but are rare in the south of Scandinavia (e.g., Hallingbäck *et al.* 2006). Some of the Scandinavian material considered by Frahm *et al.* (1998) as belonging to *O. wahlenbergii* has later been recognized as a species of its own, *O. elongatus* (I.Hagen) Hedenäs, restricted mainly to the mountains and the far north (Hedenäs 2005). Hagen (1899) originally distinguished this taxon by its large, yellow-green, incoherent tufts, leaves 5.3 mm long and 1 mm wide, and a long-excurrent leaf costa.

Significant additional variation was observed during fieldwork in Norway and Sweden. Much of the variation could be interpreted as habitat-induced, but some was not possible to explain by this alone. For example, strikingly large plants forming lax tufts and with morphological affinities to *O. wahlenbergii* or *O. elongatus* occur along rocky shores of the Bothnian Sea and Bothnian Bay in Sweden, and *O. virens* s. lat. varies from tiny phenotypes in late snow-beds to large and lax phenotypes in fens. Finally, two specimens of *O. virens* s. lat. with very different appearances were found growing close to each other in the same habitat on Mt. Åreskutan in Jämtland (C. Sweden), suggesting that some of the morphological variation was likely to have a genetic basis.

Information from morphology alone is evidently insufficient to interpret the variation within Scandinavian *Oncophorus*, or the taxonomy would already be clear and agreed on. Here, an approach including a wide molecular sampling of the Scandinavian taxa is combined with detailed morphological studies to explore (1) the circumscriptions of the so-far accepted taxa, and (2) whether additional species occur in the area. Based on the gathered information the circumscriptions of *O. elongatus* and *O. wahlenbergii* are considerably emended and *O. virens* s. lat. is divided into two species. In addition, several cryptic entities were detected and are discussed.

Material and methods

Study species and material

For the molecular evaluation, 24 Scandinavian specimens of *O. elongatus*, 22 of *O. wahlenbergii*, and 48 of *O. virens* s. lat. were studied. The species were sampled to represent different areas and environments in Scandinavia, as well as to cover the known morphological variation. Two specimens of the recently described species *Oncophorus dendrophilus* Hedd. & Blockeel (Hedderson & Blockeel 2006), from Cyprus and Crete, and two specimens of each of two other members of the genus, *O. crispifolius* (Mitt.) Lindb. (Lindberg 1872) and *O. rauei* (Austin) Grout (Grout 1937), were included for an assessment of the positions of *O. virens* and *O. wahlenbergii* within the genus. Based on Stech *et al.* (2012) two specimens of each of the two species *Cynodontium strumiferum* (Hedw.) Lindb. (Lindberg 1864) and *Rhabdoweisia fugax* (Hedw.) Bruch & Schimp. (Bruch & Schimper 1846), which appear in the clade sister to *Oncophorus*, were used as outgroup. The molecularly studied specimens are listed in Table 1.

The morphological analysis was based on specimens of *O. elongatus*-*O. wahlenbergii* and *O. virens* s. lat. that were included in the molecular analysis, whereas the geographical distribution of the species that were recognized for Scandinavia was mapped based on all Scandinavian material present in the Swedish Museum of Natural History (S). All Scandinavian S specimens were checked for their identity

Table 1. (1/6) Specimen data and European Nucleotide Archive (EMBL-ENA) accession numbers for the sequences (sequence data available at: <http://www.ebi.ac.uk/ena/data/view/LT576466-LT576777>). Data format: species; sample no. (* = leaves and cells were measured in the detailed morphological study); country; locality; collection year; collector's name (LH = L. Hedenäs); collection no.; S herbarium registration no. (except sample no. P208, which is in Herb. T.L.Blockeel); EMBL-ENA accession numbers for ITS, *trnG*, *rps4*.

Species	Sample no.	Country	Locality	Year	Collector	Collection no.	S herbarium registration no.	ITS	<i>trnG</i>	<i>rps4</i>
<i>Oncophorus crispifolius</i> (Mitt.) Lindb.	P205	Japan	Honshu, Ibaraki Pref., Tsukuba	2000	M.Higuchi		B114640	LT576567	LT576574	LT576678
	P206	Japan	Honshu, Gifu-ken, Kanbora	1991	M.Mizutami		B205745	LT576470	LT576575	LT576679
	P207	Greece	Crete: Chania, White mountains	2004	T.L.Blockeel	33/203	B208472	LT576471	LT576576	LT576680
<i>Oncophorus dendrophilus</i> Hedd. & Blockeel (paratypes)	P208	Cyprus	W. Trodos, Stavros Forestry Station	2003	T.L.Blockeel	32/173	Herb. Blockeel	LT576472	LT576577	LT576681
	*P211	Norway	Finmark, Hammerfest, Sørøya	2010	LH		B176674	LT576474	LT576580	LT576684
	P212	Norway	Finmark, Sörøysund, Seiland	2001	LH		B63111	LT576475	LT576581	LT576685
	*P213	Norway	Nordland, Hattfjelldal, Greipfjellet/Låtakrøysa	2012	LH et al.		B195359	LT576476	LT576582	LT576686
	P214	Norway	Nordland, Saltådal, Vikfjellet	2013	LH		B197545	LT576477	LT576583	LT576687
	*P215	Norway	Nordland, Sørfold, Djupvik	2013	LH		B197521	LT576478	LT576584	LT576688
	*P216	Norway	Nord-Trøndelag, Røyrvik, Guelehtsjahke	2014	LH		B205326	LT576479	LT576585	LT576689
	*P217	Norway	Nord-Trøndelag, Røyrvik, Guelehtsjahke	2014	LH		B205327	LT576480	LT576586	LT576690
	*P218	Norway	Troms, Lyngen, Bensnes, Kvitberget	2003	LH		B81878	LT576481	LT576587	LT576691
	P219	Norway	Troms, Lyngen, N of Arøybukta	2003	LH		B82802	LT576482	LT576588	LT576692
	*P220	Sweden	Jämtland, Frostviken, Brakfjället area	2009	LH		B164433	LT576483	LT576589	LT576693
	*P221	Sweden	Jämtland, Undersåker, Snasahögarna	2013	LH		B198950	LT576484	LT576590	LT576694
P222	Sweden	Jämtland, Åre, Storlien, Skurdalshöjden	2010	LH		B177191	LT576485	LT576591	LT576695	
*P229	Sweden	Dalarna, Norrbärke, Spanssjön	1986	LH		B205753	LT576492	LT576598	LT576702	

Table 1. (2/6) Specimen data and European Nucleotide Archive (EMBL-ENA) accession numbers for the sequences (sequence data available at: <http://www.ebi.ac.uk/ena/data/view/LT576466-LT576777>). Data format: species; sample no. (* = leaves and cells were measured in the detailed morphological study); country; locality; collection year; collector's name (LH = L. Hedenäs); collection no.; S herbarium registration no. (except sample no. P208, which is in Herb. T.L.Bloekel); EMBL-ENA accession numbers for ITS, *trnG*, *rps4*.

Species	Sample no.	Country	Locality	Year	Collector	Collection no.	S herbarium registration no.	ITS	<i>trnG</i>	<i>rps4</i>
<i>Oncophorus elongatus</i> (L.Hagen) Hedenäs	*P233	Sweden	Härjedalen, Sveg, N Tävremstjärnen	1989	LH	HD89-4	B205362	LT576496	LT576602	LT576706
	*P236	Sweden	Jämtland, Frostviken, Brakfjället	2009	LH		B164571	LT576499	LT576605	LT576709
	*P248	Sweden	Torne Lappmark, Karesuando, Pulsujärvi	1990	LH & M.Aronsson	NT90-489	B33249	LT576510	LT576616	LT576720
	*P249	Sweden	Uppland, Riala, Starmora gård	1995	K.Hyllander	1120	B205357	LT576511	LT576617	LT576721
	*P250	Sweden	Uppland, Singö, Råstensudd	2003	LH		B81589	LT576512	LT576618	LT576722
	P251	Sweden	Ångermanland, Grundsunda, Skagsudden	2013	LH et al.		B199906	LT576513	LT576619	LT576723
	*P252	Sweden	Ångermanland, Grundsunda, Skagsudden	2013	LH et al.		B199951	LT576514	LT576620	LT576724
	P253	Sweden	Ångermanland, Grundsunda, Skagsudden	2013	LH et al.		B199955	LT576515	LT576621	LT576725
	*P254	Sweden	Ångermanland, Grundsunda, Skagsudden	2013	LH et al.		B199962	LT576516	LT576622	LT576726
	*P255	Sweden	Ångermanland, Grundsunda, Allön	2013	LH et al.		B200902	LT576517	LT576623	LT576727
<i>Oncophorus integerrimus</i> Hedenäs sp. nov.	*P256	Sweden	Ångermanland, Hemsö, Nordånö	2013	LH et al.		B199831	LT576518	LT576624	LT576728
	*P258	Norway	Finnmark, Hammerfest, Sorøya	2010	LH		B176577	LT576520	LT576626	LT576730
	*P266	Norway	Troms, Lyngen, Rotenvikvatnet	2003	LH		B82805	LT576528	LT576634	LT576738
	*P267	Sweden	Härjedalen, Hede, Östra Fröstsjöåsen	2007	LH et al.		B121290	LT576529	LT576635	LT576739
	P268	Sweden	Härjedalen, Hede, Västra Fröstsjöåsen	2007	LH et al.		B121296	LT576530	LT576636	LT576740
	P269	Sweden	Härjedalen, Linsell, Glöte	2007	LH et al.		B121448	LT576531	LT576637	LT576741
	*P270	Sweden	Härjedalen, Linsell, Glöte	2007	LH et al.		B122479	LT576532	LT576638	LT576742

Table 1. (3/6) Specimen data and European Nucleotide Archive (EMBL-ENA) accession numbers for the sequences (sequence data available at: <http://www.ebi.ac.uk/ena/data/view/LT576466-LT576777>). Data format: species; sample no. (* = leaves and cells were measured in the detailed morphological study); country; locality; collection year; collector's name (LH = L. Hedenäs); collection no.; S herbarium registration no. (except sample no. P208, which is in Herb. T.L.Bloekel); EMBL-ENA accession numbers for ITS, *trnG*, *rps4*.

Species	Sample no.	Country	Locality	Year	Collector	Collection no.	S herbarium registration no.	ITS	<i>trnG</i>	<i>rps4</i>
<i>Oncophorus integerrimus</i> Hedenäs sp. nov.	P271	Sweden	Härjedalen, Storsjö, Svaalefjähkh	2014	LH		B207580	LT576533	LT576639	LT576743
	P272	Sweden	Härjedalen, Storsjö, Svaalefjähkh/Veakefjähke	2014	LH		B207582	LT576534	LT576640	LT576744
	P273	Sweden	Härjedalen, Storsjö, Svaalefjähkh/Veakefjähke	2014	LH		B207584	LT576535	LT576641	LT576745
	P274	Sweden	Härjedalen, Storsjö, Svaalefjähkh	2014	LH		B207580	LT576536	LT576642	LT576746
	P275	Sweden	Härjedalen, Tämnäs, Hem-Kröket	2005	LH		B104165	LT576569	LT576643	LT576747
	P276	Sweden	Härjedalen, Tämnäs, Kliehpje	2014	LH		B207475	LT576537	LT576644	LT576748
	*P277	Sweden	Härjedalen, Tämnäs, Joltere	2014	LH		B207536	LT576538	LT576645	LT576749
	*P283	Sweden	Jämtland, Frostviken, Brakfjället	2009	LH		B163762	LT576544	LT576651	LT576755
	P287	Sweden	Jämtland, Åre, Fröätjärnen	2001	LH		B62703	LT576548	LT576655	LT576759
	*P288	Sweden	Jämtland, Åre, Åreskutan	2013	LH		B198956	LT576549	LT576656	LT576760
	P290	Sweden	Lule Lappmark, Padjelanta, Kierkevare	1998	T.-B.Engelmark		B63865	LT576551	LT576658	LT576762
	P291	Sweden	Lule Lappmark, Haraudden	1996	S.Westerberg		B126995	LT576552	LT576659	LT576763
	P292	Sweden	Lule Lappmark, Padjelanta, Kierkevare	2002	T.Hallingbäck	3838/	B182838	LT576553	LT576660	LT576764
	P293	Sweden	Lycksele Lappmark, Täma, Atofjället	2012	LH et al.		B195260	LT576554	LT576661	LT576765
	*P296	Sweden	Norrbotten, Pajala, Isonkivenmaa	1990	LH & M.Aronsson	NT90-78	B33257	LT576557	LT576664	LT576768
	P297	Sweden	Pite Lappmark, Arjeplog, Vuoggafälmejávrr	2006	LH et al.		B113630	LT576558	LT576665	LT576769
	*P298	Sweden	Pite Lappmark, Arjeplog, Jäkkvik	2006	LH et al.		B113741	LT576559	LT576666	LT576770
	P302	Sweden	Åsele Lappmark, Dorotea, Harrsjö	2004	LH		B93214	LT576563	LT576670	LT576774

Table 1. (4/6) Specimen data and European Nucleotide Archive (EMBL-ENA) accession numbers for the sequences (sequence data available at: <http://www.ebi.ac.uk/ena/data/view/LT576466-LT576777>). Data format: species; sample no. (* = leaves and cells were measured in the detailed morphological study); country; locality; collection year; collector's name (LH = L. Hedenäs); collection no.; S herbarium registration no. (except sample no. P208, which is in Herb. T.L. Blockeel); EMBL-ENA accession numbers for ITS, *trnG*, *rps4*.

Species	Sample no.	Country	Locality	Year	Collector	Collection no.	S herbarium registration no.	ITS	<i>trnG</i>	<i>rps4</i>
<i>Oncophorus integerrimus</i> Hedenäs sp. nov.	P303	Sweden	Åsele Lappmark, Dorotea, Kalvberget	2004	LH		B95248	LT576564	LT576671	LT576775
	*P304	Sweden	Åsele Lappmark, Vilhelmina, Klimpfjäll	2004	LH		B100018	LT576565	LT576672	LT576776
<i>Oncophorus rauei</i> (Austin) Grout	P209	United States	North Carolina, Graham County	1988	L.E.Anderson		B205741	LT576473	LT576578	LT576682
	P210	United States	North Carolina, Jackson County	1992	L.E.Anderson		B205742	LT576568	LT576579	LT576683
	*P259	Norway	Nordland, Fauske, Stranda	2014	LH & I.Bisang		B207020	LT576521	LT576627	LT576731
	*P260	Norway	Nordland, Fauske, Øyneshøgda	2014	LH & I.Bisang		B207038	LT576522	LT576628	LT576732
	*P261	Norway	Nord-Trøndelag, Røyrvik, Vester-Vallervatnet	2014	LH		B205261	LT576523	LT576629	LT576733
	P262	Norway	Nord-Trøndelag, Røyrvik, Hutnegejaevrie	2014	LH		B205296	LT576524	LT576630	LT576734
	P263	Norway	Oppland, Dovre, Öyadalen	2012	LH		B193269	LT576525	LT576631	LT576735
	P264	Norway	Oppland, Sel, Otta, Tolykkja	2012	LH		B193256	LT576526	LT576632	LT576736
	P265	Norway	Troms, Bardu, Salangsdalen	2008	LH		B138721	LT576527	LT576633	LT576737
	*P278	Sweden	Härjedalen, Tämnäs, Ösjövälen	2014	LH		B207606	LT576539	LT576646	LT576750
	P279	Sweden	Jämtland, Frostviken, Brakkfjället	2003	LH		B84935	LT576540	LT576647	LT576751
P280	Sweden	Jämtland, Frostviken, Sipmekjeppa	2003	LH		B84937	LT576541	LT576648	LT576752	
P281	Sweden	Jämtland, Frostviken, Lake Sannaren	2004	LH		B100565	LT576542	LT576649	LT576753	
P282	Sweden	Jämtland, Frostviken, Brakkfjället	2009	LH		B163254	LT576543	LT576650	LT576754	
*P284	Sweden	Jämtland, Frostviken, Brakkfjället	2009	LH		B164637	LT576545	LT576652	LT576756	
P285	Sweden	Jämtland, Kall, ESE of Stavattsberget	2005	LH		B107608	LT576546	LT576653	LT576757	

Table 1. (S/6) Specimen data and European Nucleotide Archive (EMBL-ENA) accession numbers for the sequences (sequence data available at: <http://www.ebi.ac.uk/ena/data/view/LT576466-LT576777>). Data format: species; sample no. (* = leaves and cells were measured in the detailed morphological study); country; locality; collection year; collector's name (LH = L. Hedenäs); collection no.; S herbarium registration no. (except sample no. P208, which is in Herb. T.L.Bloekel); EMBL-ENA accession numbers for ITS, *trnG*, *rps4*.

Species	Sample no.	Country	Locality	Year	Collector	Collection no.	S herbarium registration no.	ITS	<i>trnG</i>	<i>rps4</i>
<i>Oncophorus virens</i> (Hedw.) Brid.	*P286	Sweden	Jämtland, Undersåker, Ristafallet	2013	LH		B198964	LT576547	LT576654	LT576758
	*P289	Sweden	Jämtland, Åre, Åreskutan	2013	LH		B198957	LT576550	LT576657	LT576761
	P294	Sweden	Medelpad, Borgsjö, Rankleven	1987	LH		B1117389	LT576555	LT576662	LT576766
	*P295	Sweden	Medelpad, Torp, River Granån	2006	LH		B1116722	LT576556	LT576663	LT576767
	*P299	Sweden	Pite Lappmark, Arjeplog, Skåräm	2006	LH et al.		B1113753	LT576560	LT576667	LT576771
	P300	Sweden	Pite Lappmark, Arjeplog, Skåräm	2006	LH et al.		B1113754	LT576561	LT576668	LT576772
	P301	Sweden	Torne Lappmark, Jukkasjärvi, Al. Oumisjärvi	1990	LH & M. Aronsson	NT90-605	B33258	LT576562	LT576669	LT576773
	*P305	Sweden	Östergötland, Lemunda	1980	T.Hallingbäck	1905	B182840	LT576566	LT576673	LT576777
	*P223	Norway	Finnmark, Söröysund, Seiland	2001	LH		B63113	LT576486	LT576592	LT576696
	*P224	Norway	Nordland, Fauske, Øyneshøgda	2014	LH & I.Bisang		B207035	LT576487	LT576593	LT576697
<i>Oncophorus wahlenbergii</i> Brid.	*P225	Norway	Nord-Trøndelag, Røyrvik Raajnese	2014	LH		B205323	LT576488	LT576594	LT576698
	*P226	Norway	Nord-Trøndelag, Røyrvik, Guelehtstjahke	2014	LH		B205328	LT576489	LT576595	LT576699
	*P227	Norway	Troms, Lyngen, Bensnes, Vassbotn	2014	LH		B81875	LT576490	LT576596	LT576700
	*P228	Norway	Troms, Storfjord, Didnujokka	1992	LH		B48750	LT576491	LT576597	LT576701
	P230	Sweden	Hälsingland, Los, Lakes Takmyrtjärnarna	2008	LH et al.		B138525	LT576493	LT576599	LT576703
	*P231	Sweden	Hälsingland, Kårböle, River Ljusnan	1999	LH		B13846	LT576494	LT576600	LT576704
	*P232	Sweden	Härjedalen, Storsjö, Svaalestjahkh	2014	LH		B207491	LT576495	LT576601	LT576705

Table 1. (6/6) Specimen data and European Nucleotide Archive (EMBL-ENA) accession numbers for the sequences (sequence data available at: <http://www.ebi.ac.uk/ena/data/view/LT576466-LT576777>). Data format: species; sample no. (* = leaves and cells were measured in the detailed morphological study); country; locality; collection year; collector's name (LH = L. Hedenäs); collection no.; S herbarium registration no. (except sample no. P208, which is in Herb. T.L. Blockeel); EMBL-ENA accession numbers for ITS, *trnG*, *rps4*.

Species	Sample no.	Country	Locality	Year	Collector	Collection no.	S herbarium registration no.	ITS	<i>trnG</i>	<i>rps4</i>
<i>Oncophorus wahlenbergii</i> Brid.	*P234	Sweden	Härjedalen, Tämnäs, Kliefpic/Ioltere	2014	LH		B207527	LT576497	LT576603	LT576707
	*P235	Sweden	Jämtland, Frostviken, Brakkfjället	2009	LH		B163267	LT576498	LT576604	LT576708
	P237	Sweden	Jämtland, Undersåker, Väster-Dalsvallen	2002	LH		B74681	LT576500	LT576606	LT576710
	*P238	Sweden	Jämtland, Åre, Snasahögarna	2010	LH		B177400	LT576501	LT576607	LT576711
	*P239	Sweden	Lule Lappmark, Padjelanta, Unna Titir	1998	T.-B. Engelmark		B63945	LT576502	LT576608	LT576712
	P240	Sweden	Lule Lappmark, Messaureape	1997	O. Johansson		B127254	LT576503	LT576609	LT576713
	P241	Sweden	Lycксеle Lappmark, Täma, Hemavan	2012	LH et al.		B195174	LT576504	LT576610	LT576714
	*P242	Sweden	Lycксеle Lappmark, Täma, Atofjället	2012	LH et al.		B195230	LT576505	LT576611	LT576715
	P243	Sweden	Lycксеle Lappmark, Stensele, Slussfors	2012	LH et al.		B195990	LT576506	LT576612	LT576716
	*P244	Sweden	Norrbottnen, Rosmyran, 10 km NNV Vidsele	1997	S. Westerberg		B126184	LT576507	LT576613	LT576717
*P245	Sweden	Pite Lappmark, Arjeplog, Jäkkvik	2006	LH et al.		B114015	LT576508	LT576614	LT576718	
*P247	Sweden	Torne Lappmark, Jukkasjärvi, Stuor Sitsavaara	2002	LH		B74370	LT576509	LT576615	LT576719	
*P257	Sweden	Åsele Lappmark, Vilhelmina, Klimpfjäll area	2004	LH		B95629	LT576519	LT576625	LT576729	
OUTGROUP										
<i>Cynodontium strumiferum</i> (Hedw.) Lindb.	P201	Sweden	Hälsingland, Los, Takmyrtjärnarna	2008	LH et al.		B138612	LT576466	LT576570	LT576674
	P202	Sweden	Dalarna, Garpenberg, Vaktarbo	2011	LH et al.		B186665	LT576467	LT576571	LT576675
<i>Rhabdovestia fugax</i> (Hedw.) Bruch & Schimp.	P203	Sweden	Värmland, Boråshöjden	2003	T. Hallingbäck	39879	B183877	LT576468	LT576572	LT576676
	P204	Sweden	Södermanland, Ösmo, Vidby	2013	LH		B200941	LT576469	LT576573	LT576677

based on the results of the present study. Detailed information on these specimens is available at: <http://herbarium.nrm.se/>

Molecular methods

Total DNA was extracted using the DNeasy® Plant Mini Kit for DNA isolation from plant tissue (QIAGEN) or the KingFisher Duo magnetic particle processor and the KingFisher Pure DNA Plant Kit (Thermo Fisher Scientific). Double stranded DNA templates were prepared by polymerase chain reaction (PCR). PCR was performed using Illustra™ Hot Start Mix RTG (GE Healthcare) in a 25 µl reaction volume according to the manufacturer's instructions.

Initially, variation in the nuclear internal transcribed spacers 1 and 2 (ITS) and a portion of glyceraldehyde 3-phosphate dehydrogenase (*gpd*), and the plastid *atpB-rbcL* spacer (*atbB-rbcL*), *rpl16* G2 intron (*rpl16*), the *rps4* gene + *trnS-rps4* spacer (*rps4*), *trnG_{UCC}* G2 intron (*trnG*), and *trnL_{UAA}* intron plus *trnL_{UAA}-trnF_{GAA}* spacer (*trnL-trnF*) were explored for 4–5 specimens each of *O. elongatus*, *O. virens* s. lat., and *O. wahlenbergii*. The three most variable ones, ITS, *trnG*, and *rps4* were selected for the investigation. ITS was amplified with the primers '18SF' and '26SR' (Rydin *et al.* 2004), in a few cases with the internal primers '5.8F-Chrys' (Howis *et al.* 2009) and '5.8SRPEny' (Nylinder *et al.* 2013), *trnG* with the primers 'trnGf' and 'trnGr' (Pacak & Szweykowska-Kulińska 2000), and *rps4* with 'rps5F' (Nadot *et al.* 1994) and 'trnS' (Souza-Chies *et al.* 1997). For all three markers the following PCR program was used: 5 min at 95°C followed by 4 cycles of 30 sec at 95°C, 30 sec at 57°C, 1 min at 72°C, 4 cycles of 30 sec at 95°C, 30 sec at 55°C, 1 min at 72°C and 34 cycles of 30 sec at 95°C, 30 sec at 57°C, 1 min at 72°C and a final elongation step of 8 min at 72°C.

Twenty µl of each amplified fragment were cleaned using a mixture of 20 units of Exonuclease I from *E. coli* and 4 units of FastAP™ Thermosensitive Alkaline Phosphatase (Fermentas LIFE SCIENCE), mixed and incubated at 37°C for 30 min and inactivated at 80°C for 15 min. Cycle sequencing was performed using the ABI BigDye Terminator Kit (Applied Biosystems) according to the instructions on the kit (BDT ver. 3.1), and the sequencing products were cleaned using the DyeEx® 96 Kit (QIAGEN). The same primers as for the initial PCR were used. Sequencing products were resolved on an ABI3130xl automated sequencer. Double stranded sequencing was performed.

Sequence editing and analysis of molecular data

Nucleotide sequence fragments were edited and assembled for each DNA region using PhyDE® 0.9971 (<http://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 & Ochoterena 2000), using SeqState (Müller 2005). The sequence alignments used in the analyses are available on request. European Nucleotide Archive (EMBL-ENA) accession numbers are listed in Table 1.

Paralogous ITS haplotypes are rarely 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 & Rosselló 2007). The revealed ITS variation is thus interpreted as being among homologous haplotypes.

The program TCS (Clement *et al.* 2000) with a cut-off level of 0.95 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 4.12.6 (Huson & Bryant 2006) to visualize similarities or relationships among samples. A Jackknife 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 both visual inspection of the split networks, Jackknife trees, and the ILD test (Farris *et al.* 1995; 200 replicates, $p = 0.005$) indicated that the two are incongruent.

Morphological study and analysis of measurements

After the molecular relationships among the studied *O. elongatus*, *O. wahlenbergii*, and *O. virens* s. lat. specimens had been clarified, the morphology of selected specimens belonging to the distinguished molecular entities was studied. Earlier studies (e.g., Frahm *et al.* 1998) based only on morphology had clearly separated *O. elongatus*-*O. wahlenbergii* from *O. virens* s. lat., but had failed to correctly identify the further morphological entities distinguished by the molecular study. Therefore, an approach including both standard comparisons of qualitative and quantitative characters and the quantification of vegetative leaf size and especially leaf cell size and shape was used. Since vegetative leaves are invariably present in a plant it was expected that the latter approach, which had not been explored previously within *Oncophorus*, would reveal quantitative differences supporting the molecularly recognized entities.

Among molecularly identified *O. virens* s. lat., the two main entities *O. virens* s. str. and *O. integerrimus* Hedenäs (sp. nov.; see below) were sampled with 10 specimens each. The seemingly more heterogeneous *O. elongatus* was sampled with 18 specimens and *O. wahlenbergii* with 17 specimens. These 17 specimens included those belonging to the two small, molecularly well-supported *O. wahlenbergii* clades B and C in Fig. 1. The morphologically sampled specimens are indicated with an asterisk (*) in Table 1. For each of these specimens, three vegetative leaves were sampled from two shoots (2 leaves from one stem and 1 from the other, to avoid sampling all leaves from an untypical shoot for the specimen). For each leaf, length and maximal width was 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 1.13 software (Olympus Corporation) for automatic and continuous image stacking. Measurements were then made from these leaf and cell images, using the Olympus cellSens Standard 1.13 software.

Comparisons among the four entities within *O. elongatus*-*O. wahlenbergii* and between the two within *O. virens* s. lat., respectively, are based on two approaches. First, the cell measurements were compared between the entities within each of the two groups. 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 (normality) showed that the data do not meet the criteria of normality and homogeneity of variance. Thus, for *O. elongatus*-*O. wahlenbergii* the nonparametric Kruskal-Wallis test for multiple comparisons and for *O. virens* s. lat. the nonparametric Mann Whitney-U-test for comparing two groups were used to compare the cell measurements among or between the entities, respectively. 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 the molecularly identified entities. All statistical calculations were made in STATISTICA 12 (StatSoft 2013).

Herbarium data

Herbarium acronyms follow *Index Herbariorum* (Thiers continuously updated). For specimens citations, double quotes “...” indicates that citation is exactly as on label; square brackets [...] indicates that information is interpreted from label data.

Results

Molecular relationships

The total number of aligned ITS sites in the 100 studied *Oncophorus* specimens, and outgroup of two *Cynodontium strumiferum* and two *Rhabdoweisia fugax* specimens, after deletion of regions at the beginnings and ends that were incomplete for some specimens, was 1022. Of these, 212 sites were variable (122 in the species complexes around *Oncophorus virens* and *O. wahlenbergii*), with 95.8% (95.1%) of the variable ones parsimony-informative; 181 (85) indels were present, with 93.9% (96.5%) informative. For *trnG* the length was 618, 91 (63) were variable, and 96.7% (95.2%) of these were parsimony-informative; 25 (10) indels with 92% (90%) informative. For *rps4* the length was 628, 73 (35) were variable, and 98.6% (97.1%) of these were parsimony-informative; 4 (3) indels with 100% (100%) informative. The sequence lengths for the species were: *Oncophorus crispifolius* (n = 2): 827 (ITS), 574 (*trnG*), 621 (*rps4*); *O. dendrophilus* (2): 818, 581, 628; *O. elongatus* (24): 812–823, 588, 621; *O. rauei* (2): 819–823, 579, 610; *O. virens* (22): 835–838, 578–596, 620; *O. wahlenbergii* (22): 803–826, 581–582, 612; *O. integerrimus* sp. nov. (26): 837–840, 579, 627; *Cynodontium strumiferum* (2): 773, 576, 621; *Rhabdoweisia fugax* (2): 782–784, 571, 621.

The NN split networks and the corresponding haplotype networks identified by TCS are shown with indications of branches having Jackknife support of at least 75 in Fig. 1. Both the nuclear and plastid data provide support for the three *O. elongatus* entities A–C, except that P218 belongs to B according to the ITS data and A in the plastid data. Support is provided for the three *O. wahlenbergii* entities A–C. Both data sets also support the two main entities *O. virens* and *O. integerrimus* (sp. nov.; see below) in *O. virens* s. lat., with additional differentiation within *O. virens* s. str., although the latter is incongruent between the two data sets except for *O. virens* B, that differs from *O. virens* A in 2 (ITS) or 3 mutations (Fig. 1).

Morphological evaluation

No differences could be found between *O. wahlenbergii* A and C (not shown), and these are therefore merged in the following (*O. wahlenbergii* AC). The PCA based on leaf and leaf cell measurements revealed that *O. elongatus* differs from *O. wahlenbergii* AC, with some overlap between the two (Fig. 2A). The differentiation is along PCA axis 2, showing that leaf length and width, as well as the width of cells in the apical and middle portions of the leaves, are most important in explaining this separation (Fig. 2A:1). *Oncophorus elongatus* and *O. wahlenbergii* AC differ from each other in five out of nine individual leaf lamina cell sizes or length-to-width ratios, whereas *O. wahlenbergii* B is sometimes most similar to either *O. elongatus* or *O. wahlenbergii* AC, sometimes intermediate between these, or its mean values are larger or smaller than those of both the other two (Table 2; cf., Fig. 2A). Also *O. virens* and *O. integerrimus* sp. nov. differ from each other in the PCA based on these parameters, again with a small overlap (Fig. 2B). The main differentiation is along PCA axis 1, and leaf length, length of the apical leaf lamina cells and width of the middle ones, as well as the length-to-width ratio of the apical and middle lamina cells contribute most to this pattern (Fig. 2B:1). These two species differ in all cell measurements (Table 3). Finally, despite the found statistical differences, which are based on large numbers of measurements from molecularly identified groups, the overlap among *O. elongatus*-*O. wahlenbergii* entities and between *O. virens*-*O. integerrimus* sp. nov. in individual characters is large (Supplementary file: Figs S1, S2).

Geographical distribution and habitat

The distribution of the four Scandinavian *Oncophorus* species is mapped in Fig. 3, based on the material in S. All species can grow in several habitat types, but each species is most commonly found in one or two of these (Fig. 4). Three members of the genus (*O. elongatus*, *O. wahlenbergii*, *O. integerrimus* sp. nov.)

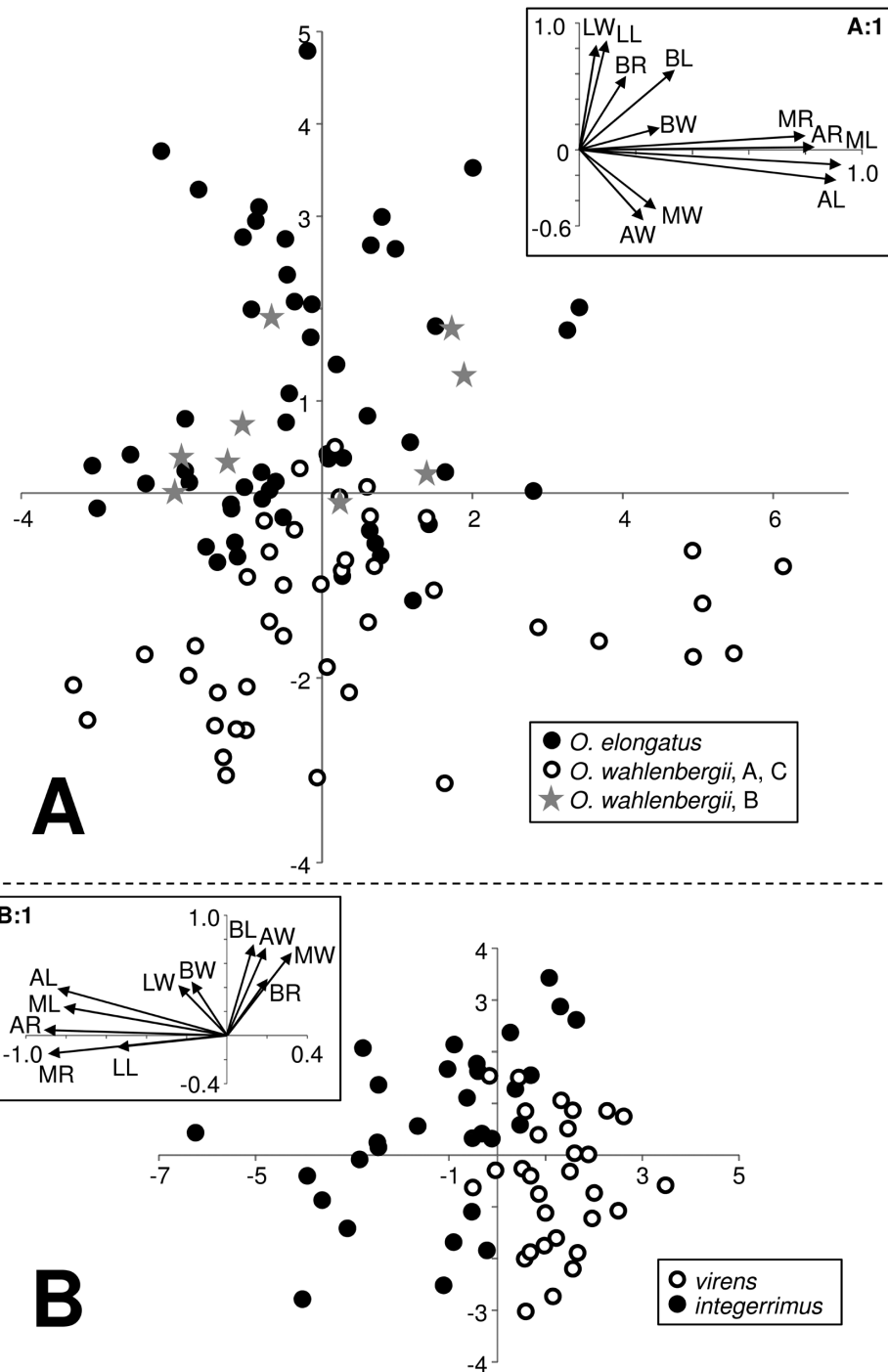


Fig. 2. The positions of three leaves from each of 18 molecularly identified specimens of *O. elongatus*, 14 of *O. wahlenbergii* A and C, and 3 of *O. wahlenbergii* B (cf. Fig. 1) (A), and of 10 specimens of *O. virens* and 10 of *O. integerrimus* Hedenäs sp. nov. (B), along the first two axes in a 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 (x) and 2 (y) explain 30.69% and 25.24% of the variation in A, and 32.56% and 22.01% of the variation in B. Insert diagrams **A:1** and **B:1** depict explanatory factors in the plane of these two axes.

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*, three specimens of *O. wahlenbergii* B, and 14 specimens of *O. wahlenbergii* A and C (AC). The number of measured cells at each position, n, is indicated after the species. Significant pair-wise differences between species revealed by the Kruskal-Wallis test are indicated by different letters appended after the values in the respective columns, for the Bonferroni corrected p values corresponding with $p < 0.05$.

Position; measurement	<i>elongatus</i> (1080)	<i>wahl. B</i> (180)	<i>wahl. AC</i> (840)
Acumen; length (AL)	14.6 (0.1) a	14.8 (0.4) a	17.3 (0.2) b
Acumen; width (AW)	10.8 (0.1) a	11.4 (0.1) b	12.3 (0.1) c
Acumen; AL/AW ratio (AR)	1.40 (0.02) -	1.31 (0.03) -	1.45 (0.02) -
Mid-leaf; length (ML)	17.4 (0.2) a	17.9 (0.4) ab	19.4 (0.2) b
Mid-leaf; width (MW)	10.4 (0.0) a	10.1 (0.1) a	11.5 (0.1) b
Mid-leaf; ML/MW ratio (MR)	1.72 (0.02) -	1.84 (0.05) -	1.74 (0.02) -
Base; length (BL)	51.1 (0.5) a	55.3 (1.1) b	47.5 (0.5) c
Base; width (BW)	10.2 (0.1) a	9.5 (0.1) b	10.0 (0.1) ab
Base; BL/BW ratio (BR)	5.20 (0.06) a	6.07 (0.16) b	4.87 (0.06) a

Table 3. 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 ten specimens of *Oncophorus virens* and *O. integerrimus* Hedenäs sp. nov. The number of measured cells at each position, n, is indicated after the species. Significant differences between species revealed by the Mann-Whitney U-test are indicated by different letters appended after the values in the respective columns, for the Bonferroni corrected p values corresponding with $p < 0.05$.

Position; measurement	<i>virens</i> (600)	<i>integerrimus</i> (600)
Acumen; length (AL)	13.7 (0.2) a	16.3 (0.2) b
Acumen; width (AW)	10.6 (0.1) a	9.6 (0.1) b
Acumen; AL/AW ratio (AR)	1.34 (0.02) a	1.76 (0.03) b
Mid-leaf; length (ML)	14.2 (0.2) a	16.1 (0.2) b
Mid-leaf; width (MW)	9.9 (0.1) a	8.5 (0.1) b
Mid-leaf; ML/MW ratio (MR)	1.48 (0.02) a	1.97 (0.03) b
Base; length (BL)	48.0 (0.6) a	41.0 (0.5) b
Base; width (BW)	9.6 (0.1) a	9.2 (0.1) b
Base; BL/BW ratio (BR)	5.27 (0.08) a	4.67 (0.07) b

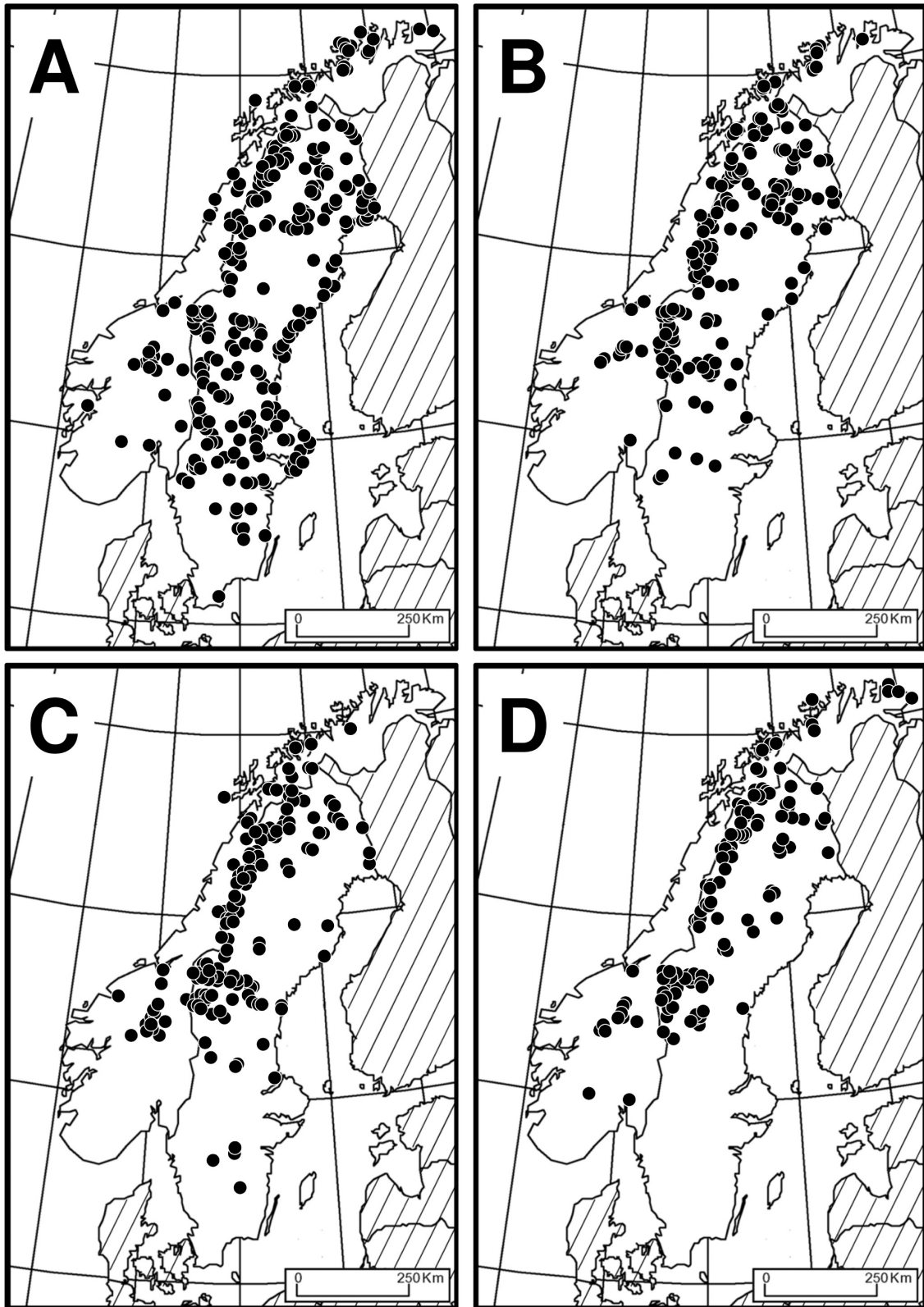


Fig. 3. Geographical distributions in Scandinavia. **A.** *Oncophorus elongatus* (n = 459). **B.** *O. wahlenbergii* (n = 333). **C.** *O. virens* (n = 361). **D.** *O. integerrimus* Hedenäs sp. nov. (n = 247). The distribution maps are based on the S material for which geographical origin could be determined.

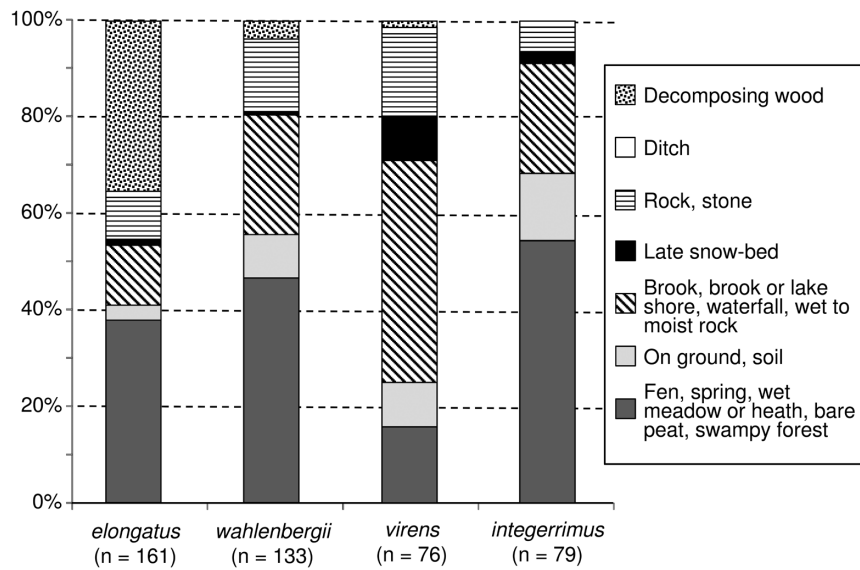


Fig. 4. Habitat preferences of *Oncophorus elongatus*, *O. wahlenbergii*, *O. virens*, and *O. integerrimus* Hedenäs sp. nov. in Scandinavia, based on label information from studied material in S.

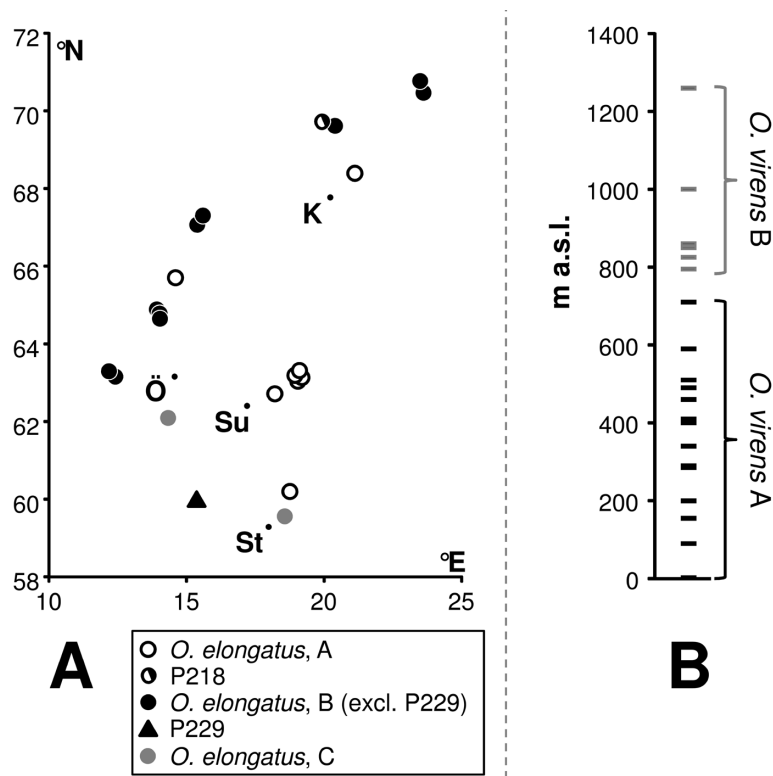


Fig. 5. A. Latitudinal and longitudinal distribution of *Oncophorus elongatus* samples belonging to different haplotypes or groups of haplotypes (cf., Fig. 1) based on ITS and plastid (*trnG*, *rps4*) data. Sample P218 is related to *O. elongatus* B according to ITS data and *O. elongatus* A according to plastid data (Fig. 1). The positions of the Swedish towns Kiruna (K), Stockholm (St), Sundsvall (Su), and Östersund (Ö) are indicated as references. **B.** Elevational distribution of the molecularly sampled *Oncophorus virens* A and B (P278-P280, P282, P289, P299, P300) in Scandinavia.

have between 40 and 55% of their recorded occurrences in fens, springs, wet meadows and similar habitats. In addition, 35% of the finds of *O. elongatus* are from decomposing wood, an unimportant habitat for the other species, and for *O. wahlenbergii* and *O. integerrimus* sp. nov. 20–25% of the records are from shores of brooks and lakes, wet rocks, and similar habitats. Shores and wet rocks are the most important habitats for *O. virens*, which has more than 45% of its records there. This species is the only one with a significant number of occurrences in late snow-beds.

Within *O. elongatus*, the molecular differentiation corresponds with a geographic pattern. Samples from the lowlands and along the Bothnian coast mostly belong to *O. elongatus* A, whereas samples from the mountain range and the Norwegian coast are predominantly *O. elongatus* B (Fig. 5A). No such geographic pattern was found within the other species. Within *O. virens*, on the other hand, we find a very clear differentiation between low (*O. virens* A) and high (B) elevation haplotypes (Fig. 5B).

Key to Scandinavian *Oncophorus* species

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 differentiated3

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 mm1. ***O. elongatus*** (I.Hagen) Hedenäs
 - 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, with an occasional and mostly obtuse and irregular denticle (mostly close to leaf apex), or sometimes with projecting cell walls. Vegetative leaves 1.4–4.4 × 0.3–0.8 mm2. ***O. wahlenbergii*** Brid.

3. 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 twisted3. ***O. virens*** (Hedw.) Brid.
 - 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 twisted4. ***O. integerrimus*** Hedenäs sp. nov.

Taxonomy

For all species, the total number of studied specimens is indicated in Fig. 3, and a selection of studied specimens is found in Table 1.

Class Bryopsida Pax (Pax 1900)
 Subclass Dicranidae Doweld (Doweld 2001)
 Order Dicranales M.Fleisch. (Fleischer 1920)
 Family Oncophoraceae M.Stech (Stech & Frey 2008)

Genus *Oncophorus* Brid. (von Bridel 1826)

Bryologia Universa 1: 389 (von Bridel 1826). – Type: *Oncophorus virens* (Hedw.) Brid.

1. *Oncophorus elongatus* (I.Hagen) Hedenäs

Fig. 6

Lindbergia 30: 36 (Hedenäs 2005). – *Oncophorus wahlenbergii* var. *elongatus* I.Hagen, *Tromsø Museums Aarshefter* 21–22: 13 (Hagen 1899). – *Cynodontium wahlenbergii* var. *elongatum* (I.Hagen) Mönk., *Die Laubmoose Europas*: 195 (Mönkemeyer 1927). – Type: “Norway. Nordland, Saltdalen, Rognanfjeld, 67° 6' N, 600 m asl, 21 July 1889, R. E. Fridtz” (lecto-: O!, designated by Hedenäs 2005).

Description

Plants up to ten cm high, mostly in loose tufts, green or yellow-green. Stem with large central strand, a cortex plus epidermis of 1–2 layers of incrassate cells, epidermis not differentiated as a hyalodermis; axillary hairs with 2–8-celled, hyaline upper portion, 8–10 µm wide, basal 1–2 cells rectangular, brown; rhizoids strongly branched, red-brown, smooth, in leaf axils or shortly above. Leaves 2.5–6.4 × 0.4–1.2 mm, when moist from strongly sheathing base erect, or erect-patent to spreading and straight or slightly curved, when dry with middle leaf spreading and gradually curved upwards or upwards-inwards and curled or slightly curled, from oblong-obovate or ovate sheathing portion (narrowed or strongly narrowed towards insertion) with long and almost linear, gradually narrowing upper portion, apex long- or very long-acuminate; leaf margin plane throughout, below entire, in upper 20–25(–35)% partly irregularly dentate or denticulate with sharp forwards-directed teeth, or sometimes relatively weakly denticulate, or some leaves almost entire and other leaves with scattered teeth along upper margin, teeth single or occasionally double, sometimes with cell walls projecting along upper margin, margin varying from unistratose to bistratose; costa 53–125 µm wide near base, with dorsal and ventral epidermis cells slightly widened but incrassate, one layer of large guide cells, 1–3 layers of ventral stereids and 2–3(–4) layers of dorsal stereids, sometimes with mammillae, or erect to forwards-directed teeth on upper back; lamina cells in acumen incrassate or strongly so, 10–21 × 9–14 µm, 0.9–2.0 times as long as wide, in mid-leaf incrassate or strongly so, 11–29 × 8–13 µm, 1–3 times as long as wide, and in sheathing lamina strongly incrassate and eporose or indistinctly porose, 36–88 × 8–14 µm, 3.5–9.1 times as long as wide, transition between mid-leaf and basal cells gradual, due to relatively long mid-leaf cells and relatively short basal cells, lamina of basal, sheathing portion of leaf in middle and below with long and narrow cells also along margin; alar cells undifferentiated or a few cells slightly wider than other basal cells and sometimes brownish, unistratose, not or shortly and narrowly decurrent. Perigonia lateral on stem, not or shortly stalked, antheridia protected by oblong-triangular perigonial leaves having obtuse to narrowly acuminate acumen. Inner perichaetial leaves 5.36–7.14 mm long, lower 26–42% oblong and broadly sheathing, above suddenly narrowed to long, narrow acumen. Seta tall, (6–)12–25 mm; capsule obloid, slightly curved, with distinct struma, 0.9–1.4 × 0.5–1.0 mm, 1.3–2.1 times as long as broad, more or less orthogonal; exothecial cells slightly incrassate, mostly slightly collenchymatous; stomata ovate-pored, surrounded by indistinctly radially arranged cells, near base of capsule; peristome orange-red, teeth cleft or perforated to one- or two-thirds down, with longitudinal rows of pits on outside; spores 23–30 µm, very finely rough.

Remarks

Well-developed *O. elongatus* has very long leaves, which are narrow above their sheathing base. In oceanic portions of the Scandinavian mountain range and along the Norwegian coast the species often grows in open fens or wet heaths or meadows and then the leaves are mostly spreading and give the plants a very characteristic appearance. This is the kind of plants that made Hagen (1899) distinguish *O. wahlenbergii* var. *elongatus* and Hedenäs (2005) raise it to the species level. However, molecular data show that this species is variable both molecularly and morphologically and with the present circumscription, the species includes also plants with different leaf orientations and from different habitats than the plants originally referred to it. Morphologically, this species differs from *O. wahlenbergii* in that the middle and basal portions of the basal, sheathing lamina have long and narrow cells also along its margin. In

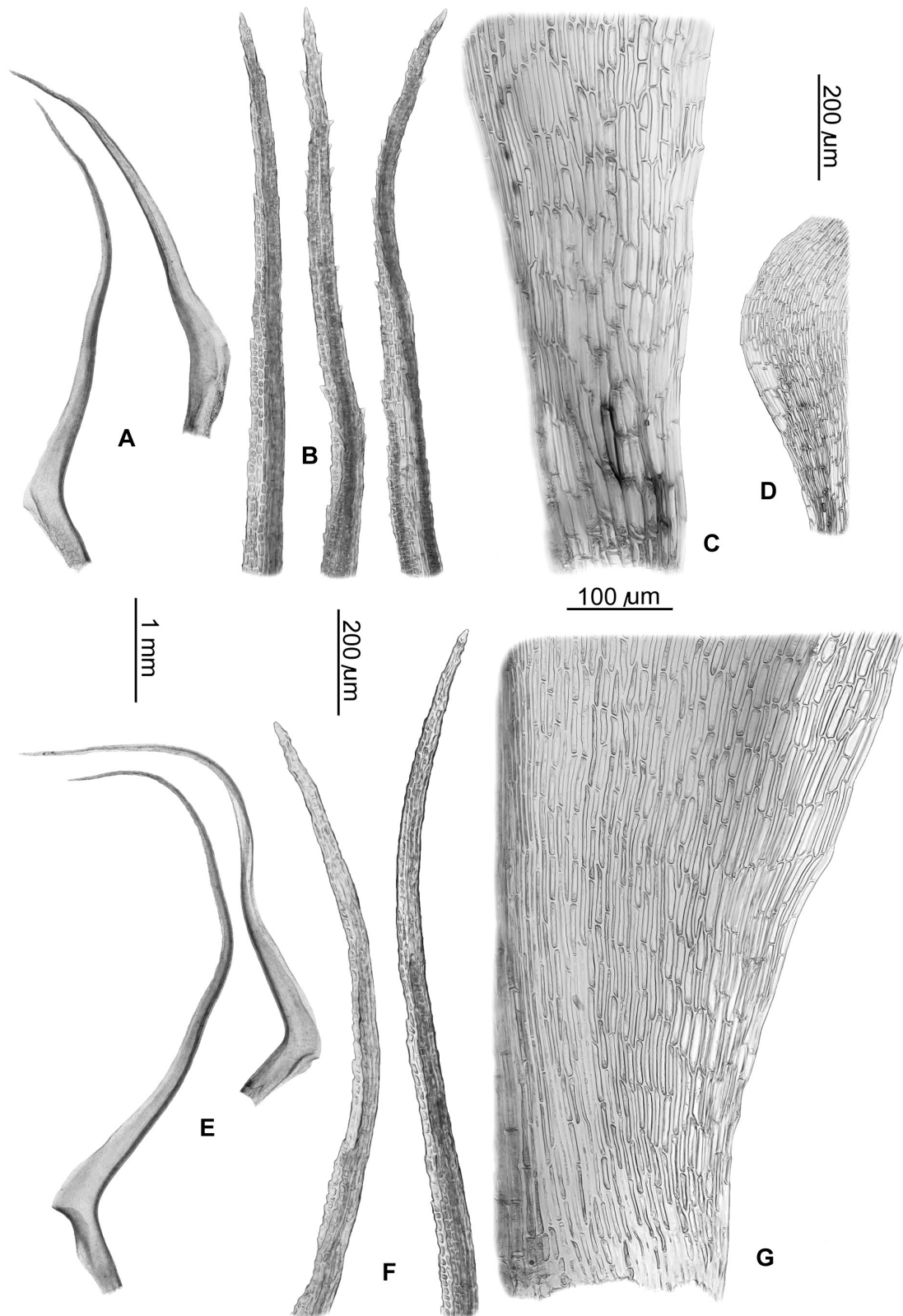


Fig. 6. A–D. *Oncophorus elongatus* A (specimen P251; cf., Table 1). E–G. *O. elongatus* B (specimen P221, cf. Table 1). A, E. Stem leaves. B, F. Upper leaf acumen. C, G. Marginal and alar portions of sheathing leaf base (margin to the right). D. Portion of leaf at widest point, showing the flat margin.

addition, *O. elongatus* has longer vegetative leaves than *O. wahlenbergii*, and some or many leaves have almost always got denticulate or sharply denticulate upper margins, often with denticles on the back of the costa also. Rarely some plants have only a few leaves with denticles along the margin, and their denticles are in addition scattered and obtuse. In such cases the cell pattern of the sheathing lamina can be used to distinguish the two species. As noted by Hedenäs (2005) the spore capsules of *O. elongatus* mature somewhat before those of *O. wahlenbergii*.

Habitat and distribution in Scandinavia

This species is most frequent in open wetlands and humid forests, where it is found on humus-rich substrates and decomposing wood (Fig. 4). It occurs also on rocks, wet rocks, and on shores. *Oncophorus elongatus* is the most frequent and widespread member of the genus in Scandinavia (Fig. 3A), and is the only member of the genus that is relatively frequent also in large portions of the southern third of Sweden.

2. *Oncophorus wahlenbergii* Brid.

Figs 7, 8

Bryologia Universa 1: 400 (von Bridel 1826). – *Dicranum wahlenbergii* (Brid.) Schultz, *Sylloge Plantarum Novarum* 2: 149 (Schultz 1828). – *Dicranum virens* var. *wahlenbergii* (Brid.) Huebener, *Muscologia Germanica*: 231 (Hübener 1833). – *Aongstroemia wahlenbergii* (Brid.) Müll.Hal., *Synopsis muscorum frondosorum omnium hucusque cognitorum* 2: 610 (Müller 1851). – *Cynodontium wahlenbergii* (Brid.) Hartm., *Handbok i Skandnaviens Flora*, Ed. 10, 2: 113 (Hartman 1871). – Type: no potential type material is extant in B (cf., Frahm *et al.* 1998; Hedenäs 2005), and the typification will be dealt with separately (Hedenäs & Ochyra, in prep.).

Dicranum homannii Boeck in Hartman, *Handbok i Skandnaviens Flora*, Ed. 2: 314. (Hartman 1832). – Type: [Norway] “Dicr. Homanni, Sp. nov. e Gudbrandsdal, dedit Boeck, lectum 1830 Jun. 1. Jul., Ahnfeldt” in Herbarium Claës Gustaf Myrin, in Herb. Hj. Möller (iso-: S-B231701!).

Oncophorus virens var. *gracilis* Broth., *Acta Societatis pro Fauna et Flora Fennica* 6 (4): 75 (Brotherus & Saelan 1890). – *Oncophorus wahlenbergii* var. *gracilis* (Broth.) Arnell & C.E.O.Jensen, *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar* 21 Afd. 3 (10): 52 (Arnell & Jensen 1896). – *Cynodontium virens* var. *gracile* (Broth.) Paris, *Index Bryologicus Supplementum Primum* 111 (Paris 1900). – *Cynodontium wahlenbergii* var. *gracile* (Broth.) Mönk., *Die Laubmoose Europas*: 195 (Mönkemeyer 1927). – Type: [Russia] “V. F. Brotherus M. F. E. 434. *Oncophorus virens* (Sw.) Brid. var. *gracilis* Broth., Lapponia murmanica, in ripa arenosa fluvii Varsina, Aug. 11, 1887, leg. V. F. B.” (iso-: S-B234603!).

Oncophorus sardous Herzog (syn. nov.), *Allgemeine Botanische Zeitschrift für Systematik, Floristik, Pflanzengeographie* 16: 84 (Herzog 1910). – Type: [Italy] “Fl. v. Sardinien, Auf Baumstumpf im Steineichenwald under d. Tonneri, 1100 m., leg. Th. Herzog, 4.1904, Typus!”, S; reg. no. B107132 (holo-: JE, n.v.; iso-: S-B107132!, H, n.v.).

Oncophorus gracillimus Dixon, *Records of the Botanical Survey of India* 9 (5): 304. pl. 1: f. 1 (Dixon 1926). – Type: [India] “On wood, Kamri Pass & Kishenganga Valley, India, 8,000–14,000 ft. alt., J. Garrett & W. Lillie, Aug. 1924, Comm. D. Lillie (Herb. H. N. Dixon Ref. No. 1138)” (holo-: BM, n.v. – synonymized by Frahm *et al.* 1998).

Description

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 1–2 layers of incrassate cells, epidermis not differentiated as a hyalodermis; axillary hairs with (1–)2–4-celled, hyaline upper portion, 7–12 µm wide, basal 1–2 cells rectangular, hyaline or pale brown; rhizoids strongly branched, red-brown,

smooth, in leaf axils or shortly above. Leaves $1.4\text{--}4.4 \times 0.3\text{--}0.8$ mm, when moist from sheathing base erect to spreading and straight or slightly curved, when dry with middle leaf spreading and gradually curved upwards-inwards and slightly curled or weakly curled, from oblong or slightly oblong-obovate sheathing portion (narrowed towards insertion) with narrowly triangular to almost linear upper portion, gradually narrowing upper portion, apex obtuse, acute, acuminate or narrowly acuminate; leaf margin plane throughout, below entire, above entire or with one or few occasional and indistinct, mostly obtuse teeth, especially close to leaf apex, sometimes with cell walls distinctly projecting along upper margin, margin varying from unistratose to bistratose; costa $31\text{--}88$ μm wide near base, with dorsal and ventral epidermis cells slightly widened but incrassate, one layer of large guide cells, 1–2 layers of ventral stereids and 1–3 layers of dorsal stereids, sometimes with projecting cell walls or cell portions in upper costa; lamina cells in acumen incrassate, $10\text{--}33 \times 10\text{--}15$ μm , 0.9–2.4 times as long as wide, in mid-leaf

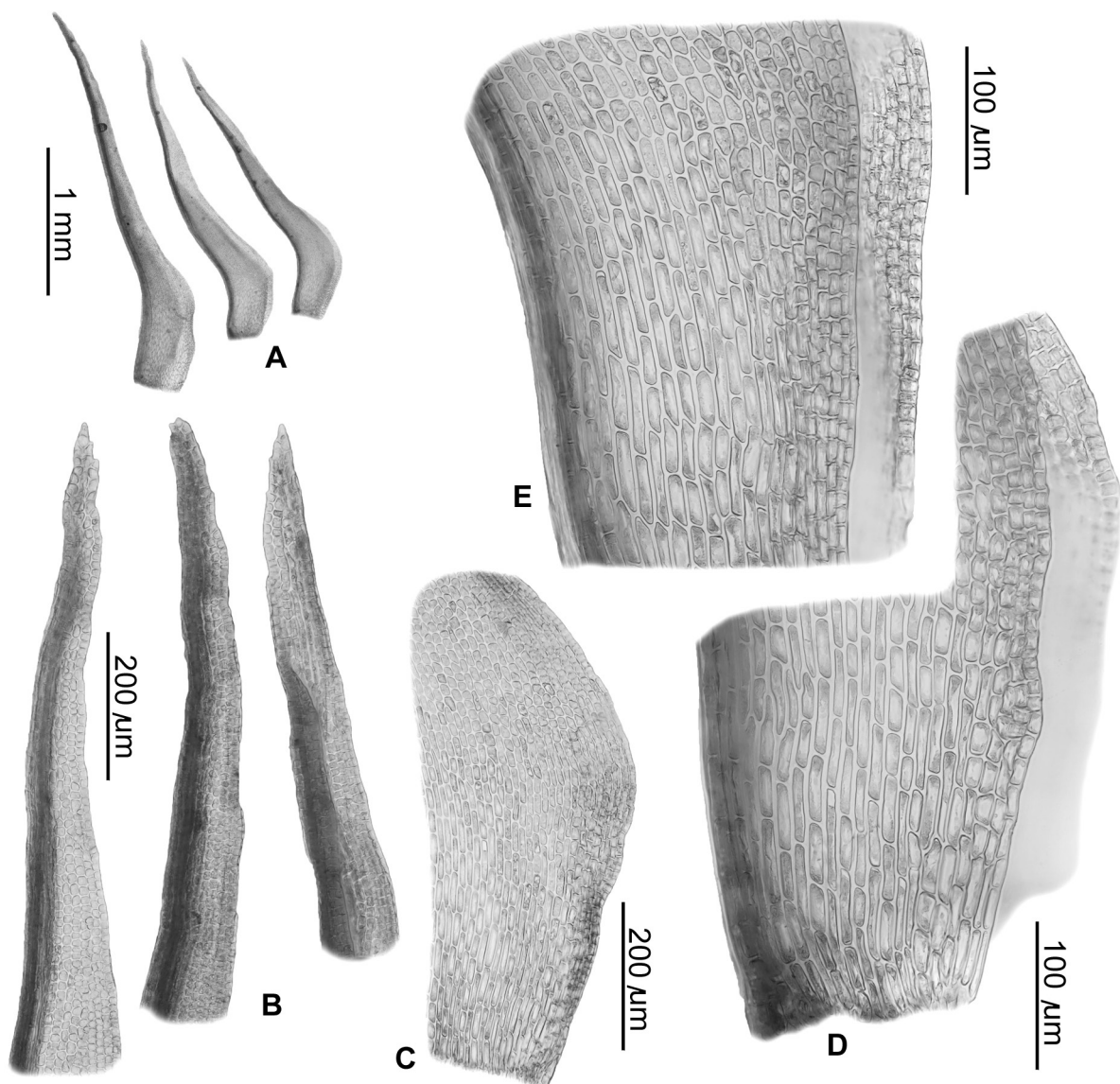


Fig. 7. *Oncophorus wahlenbergii* A (specimen P225; cf., Table 1). **A.** Stem leaves. **B.** Upper leaf acumen. **C.** Portion of leaf at widest point, showing the flat margin. **D, E.** Sheathing leaf portions, showing short marginal leaf cells (margin to the right) and, in D, alar region.

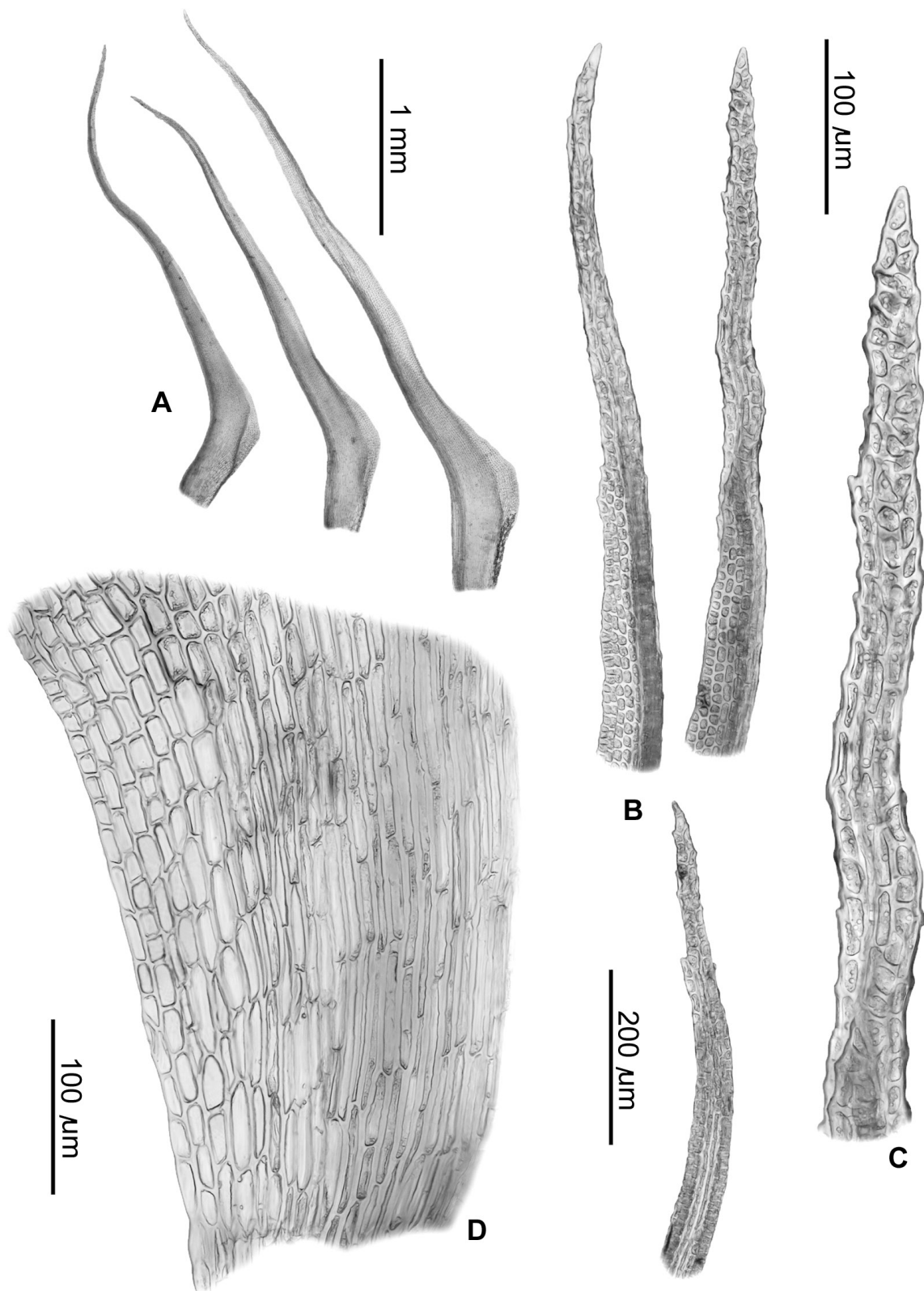


Fig. 8. *Oncophorus wahlenbergii* B (specimen P234; cf., Table 1). **A.** Stem leaves. **B.** Upper leaf acumen. **C.** Uppermost leaf acumen at higher magnification. **D.** Sheathing leaf portion, showing short marginal leaf cells and alar region (margin to the left).

incrassate, $10\text{--}33 \times 8\text{--}17 \mu\text{m}$, 0.9–3.0 times as long as wide, and in sheathing lamina strongly incrassate and eporose or indistinctly porose, $30\text{--}72 \times 7\text{--}15 \mu\text{m}$, 3.4–8.3 times as long as wide, transition between mid-leaf and basal cells gradual, due to relatively long mid-leaf cells and relatively short basal 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 leaves with obtuse or acute apex. Inner perichaetial leaves 2.73–4.24 mm long, lower 34–67% oblong and broadly sheathing, above suddenly narrowed to long, narrow acumen. Seta tall, 9–22 mm; capsule obloid, curved or slightly curved, with distinct struma, $0.5\text{--}1.3 \times 0.3\text{--}0.7 \text{ mm}$, 1.2–2.5 times as long as broad, more or less orthogonal; exothecial cells incrassate, sometimes more strongly so in longitudinal walls, not or weakly collenchymatous; stomata sparse, ovate-pored or lacking pore, surrounded by radially arranged cells, near base of capsule; peristome red, teeth cleft or perforated to one-fourth or further down, with longitudinal rows of pits on outside; spores 21–29(–32) μm , finely rough.

Remarks

Oncophorus wahlenbergii is the smallest Scandinavian species. Contrary to *O. elongatus* it has quadrate or rectangular marginal cells in the middle and basal portions of the basal, sheathing lamina. In addition, its vegetative leaves are shorter than in *O. elongatus*, and in their upper portions the margins are entire or have occasionally one or a few indistinct teeth, especially close to the leaf apex. In some plants the cell walls project distinctly along the upper margin, and sometimes on the uppermost back of the costa.

Habitat and distribution in Scandinavia

Oncophorus wahlenbergii is most often found in open wetlands, but occurs also on soil, rocks, wet rocks, and on shores (Fig. 4). The species is widespread, but compared with *O. elongatus* it is much less common outside the mountain range and the far north (Fig. 3B), and has only been collected a few times in the southern third of Sweden.

Nomenclatural notes

The isotype of *Oncophorus sardous* Herzog (Herzog 1910) in S has plane leaf margins and no or few marginal teeth near the leaf apex, and several rows of short cells along the leaf margin in the sheathing lamina. Despite an earlier synonymisation with *O. virens* Hedw. (Frahm *et al.* 1998), the material unambiguously belongs to *O. wahlenbergii* Brid. The partly mammillose apical costa back and few marginal teeth or projecting cell walls remind about the molecularly identified *O. wahlenbergii* B (Fig. 1). However, since the geographical origin of the *O. sardous* type is distant from Scandinavia, further information is required to confidently judge its relationship with other *O. wahlenbergii* specimens.

The protologue of *Oncophorus gracillimus* Dixon (Dixon 1926) mentions entire or almost entire leaf margins, which indicates that the synonymy with *O. wahlenbergii* suggested by Frahm *et al.* (1998) is correct.

3. *Oncophorus virens* (Hedw.) Brid.

Fig. 9

Bryologia Universa 1: 399 (von Bridel 1826). – *Dicranum virens* Hedw., *Species Muscorum Frondosorum*: 142 (Hedwig 1801). – *Aongstroemia virens* (Hedw.) Müll.Hal., *Synopsis Muscorum Frondosorum omnium hucusque Cognitorum* 2: 609 (Müller 1851). – *Cynodontium virens* (Hedw.) Schimp., *Corollarium Bryologiae Europaeae*: 12 (Schimper 1856). – Type: no potential type material

is extant in G (cf., Frahm *et al.* 1998; <http://www.ville-ge.ch/musinfo/bd/cjb/hedwig/>; accessed 4 Feb. 2016), and the typification will be dealt with separately (Hedenäs & Ochyra in prep.).

Dicranum virens var. *serratum* Bruch & Schimp., *Bryologia Europaea* 1: 119. 49g (fasc. 37–40. Mon. 13. 3g) (Bruch & Schimper 1847). – *Cynodontium virens* var. *serratum* (Bruch & Schimp.) Schimp., *Corollarium Bryologiae Europaeae*: 12 (Schimper 1856). – *Oncophorus virens* var. *serratus* (Bruch & Schimp.) Braithw., *The British Moss-Flora* 1: 116 (Braithwaite 1883). – Type: “secus rivulos” (BM, n.v.; cf., below).

Aongstroemia curvicaulis Müll.Hal., *Nuovo Giornale Botanico Italiano*, n.s. 5 (2): 169 (Müller 1898). – *Cynodontium curvicaule* (Müll.Hal.) Paris, *Index Bryologicus Supplementum Primum* 111 (Paris 1900). – *Oncophorus curvicaulis* (Müll.Hal.) Broth., *Die Natürlichen Pflanzenfamilien* 1 (3): 319 (Brotherus 1901). – Type: “Bryotheca E. Levier. *Oncophorus curvicaulis* C. Müll., c.fr., *Nuovo Giornale italiano* 1898, p. 169 (sub. *Angstroemia*), China interior, provincia Schen-si sept., in monte Thae-peisan, Aug. 1896, legit Rev. Jos. Giraldi, determ. Prof. C. Müller sub. No. 1969” (lecto-: BM-000517729!, designated here).

Cynodontium bicolor Paris, *Index Bryologicus Supplementum Primum*: 111 (Paris 1900) (*Aongstroemia bicolor* Müll.Hal., *Nuovo Giornale Botanico Italiano*, n.s. 5: 170 (Müller 1898), nom. illeg.; later homonym). – *Oncophorus bicolor* (Paris) Broth., *Die Natürlichen Pflanzenfamilien* 1 (3): 319 (Brotherus 1901). – Type: “Bryotheca E. Levier. *Oncophorus bicolor* (C. Müll. sub *Angstroemia*, in N. Giorn. bot. ital. 1898, p. 170) Broth., China interior, provinc. SchenSi sept., in monte Tui-kio-san, 21 Sept. 1896, legit. Rev. Jos. Giraldi, determ. Dr. C. Müller n. 1970” (lecto-: BM-000517728!, designated here).

Description

Plants up to 8 cm high, usually in loose tufts, green or yellow-green. Stem with large central strand, a cortex plus epidermis of 1–2 layers of incrassate cells, epidermis not differentiated as a hyalodermis; axillary hairs with 2–4-celled, hyaline upper portion, 10–11 µm wide, basal 1–2 cells rectangular, hyaline; rhizoids strongly branched, red-brown, smooth, in leaf axils. Leaves 2.1–4.2 × 0.6–1.0 mm, when moist from sheathing base patent to spreading, straight or screwed, when dry above sheathing base erect and tightly incurved to spreading, above strongly twisted, from ovate or rounded oblong base with narrowly triangular acumen, apex acuminate to longly acuminate; leaf margin at least partly distinctly recurved in lower leaf, below entire, upper margin in all or many leaves regularly to irregularly dentate or coarsely and somewhat irregularly denticulate, sometimes only close to leaf apex but mostly in at least some leaves down to mid-leaf or almost so, teeth single or double, mostly sharp and when strong often directed forwards, margin varying from unistratose to bistratose; costa 83–120 µm wide near base, with dorsal and ventral epidermis, one layer of large guide cells, 1(–2) layers of ventral stereids and 2–3 layers of dorsal stereids; lamina cells in acumen incrassate, 6–30 × 6–18 µm, 0.5–3.3 times as long as wide, in mid-leaf incrassate, 6–33 × 6–15 µm, 0.6–3.8(–4.2) times as long as wide, and in sheathing lamina incrassate and slightly porose, 20–109 × 5–19 µm, 1.6–15.8 times as long as wide, transition between mid-leaf and basal cells relatively sudden, due to relatively short upper lamina cells and relatively long basal cells; alar cells differentiated, rectangular, slightly to strongly inflated and forming a diffusely delimited group of 3–4 cells wide and 2–4(–5) cells long, partly bistratose, decurrent. Perigonia lateral on stem, not stalked, antheridia protected by oblong perigonial leaves with “cut-off” or acute apex. Inner perichaetial leaves 3.27–6.18 mm long, lower 29–50% oblong and broadly sheathing, above suddenly narrowed to long, narrow acumen. Seta tall, 12–29 mm; capsule cylindrical or shortly so, curved or slightly curved, with distinct struma, 0.9–1.5 × 0.5–0.6 mm, 1.6–2.9 times as long as broad, more or less orthogonal to homotropus; exothecial cells incrassate or longitudinally incrassate, slightly collenchymatous or not; stomata ovate-pored, surrounded by radially arranged cells, near base of capsule; peristome red, teeth cleft or perforated to one-third or further down, with longitudinal rows of pits on outside; spores 23–38 µm, very finely rough.

Remarks

This species is on the average weaker than *O. integerrimus* sp. nov. In addition, it differs by its usually strongly dentate leaf margins and in that dry leaves are more tightly incurved. Plants from high elevations, which can be molecularly differentiated from lowland ones, are often relatively small. However, neither this nor other morphological features consistently distinguish plants from different elevations.

Habitat and distribution in Scandinavia

Oncophorus virens occurs on rocks, especially wet rocks, and on brook and lake shores (Fig. 4). It is the only member of *Oncophorus* that is frequent in late snow-beds, and it grows also on soil and in open wetlands. This species is frequent mainly in the mountain range and the base- or calcium-rich lowland regions of northern Sweden (Fig. 3C). Like *O. wahlenbergii*, it has only been collected a few times in the southern third of Sweden.

Nomenclatural notes

Dicranum virens var. *serratum* Bruch & Schimp. (Bruch & Schimper 1847) should differ from *Oncophorus virens* (Hedw.) Brid. var. *virens* in having strongly serrate leaf margins (Bruch *et al.* 1836–1851). However, since *O. virens* has serrate to strongly serrate upper leaf margins, the var. *serratus* belongs within this variation (cf., Ignatov & Afonina 1992; Newmaster 2007). The types of *Aongstroemia curvicaulis* Müll.Hal. (Müller 1898) and *Cynodontium bicolor* Paris (Paris 1900) also have strongly serrate leaf margins and clearly belong to *O. virens* as this species is understood here. The types of latter two names were checked to exclude that they belong to the next species.

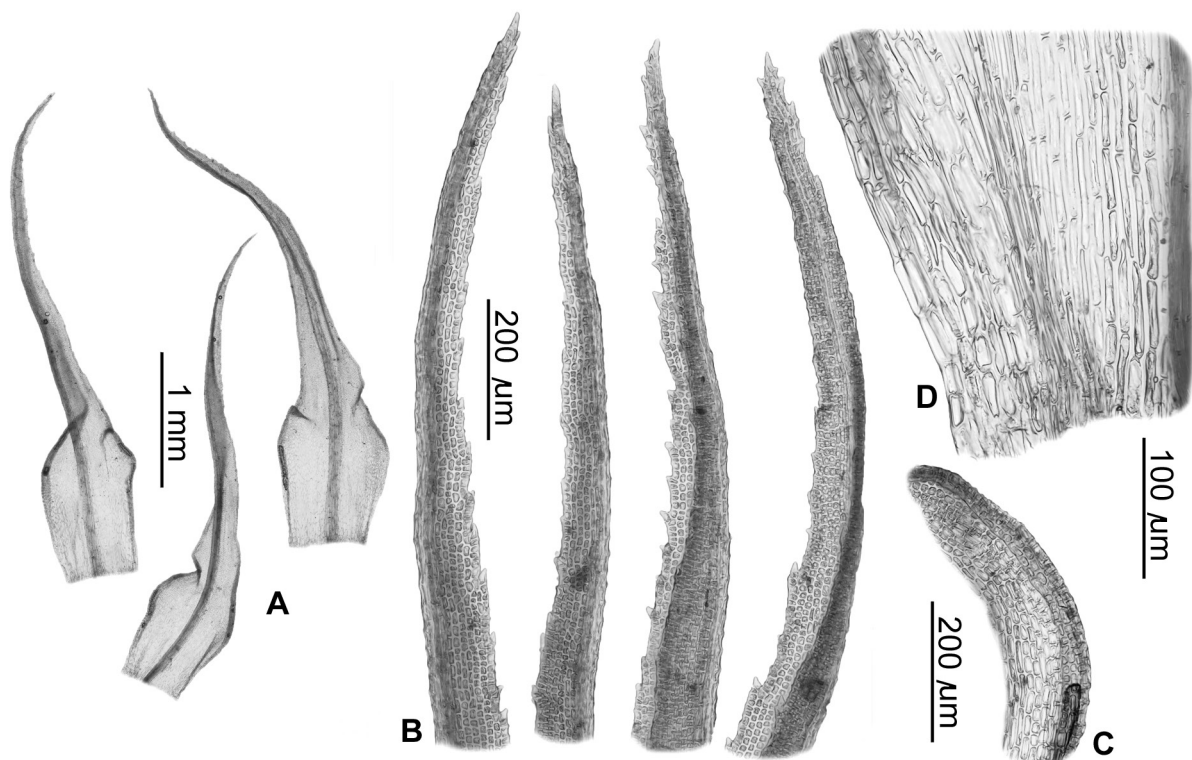


Fig. 9. *Oncophorus virens* (specimen P286; cf., Table 1). **A.** Stem leaves. **B.** Upper leaf acumen. **C.** Portion of leaf at widest point, showing the broadly recurved margin. **D.** Lower part of sheathing leaf portion, showing differentiated alar region (margin to the left).

4. *Oncophorus integerrimus* Hedenäs sp. nov.

Fig. 10

Oncophorus virens var. *elongatus* Limpr., *Die Laubmoose Deutschlands, Oesterreichs und der Schweiz* 1: 309 (Limpricht 1886). – *Cynodontium virens* var. *elongatum* (Limpr.) Mönk., *Die Laubmoose Europas*: 195 (Mönkemeyer 1927). – Type: “An Quellen bei Innervillgraten in Tirol (Gander) und im Valée d’Eyne in den Pyrenäen 200 m (Renauld)” (syn-: BP, n.v.).

Diagnosis

Oncophorus integerrimus sp. nov. differs from *O. virens* (Hedw.) Brid. by its more loosely incurved leaves when dry, and in having entire or almost entire upper leaf margins.

Etymology

The epithet ‘*integerrimus*’ refers to the mostly entire leaf margin.

Type material

SWEDEN: Härjedalen, Tännäs, SW slope of Mt. Joltere (Lill-Mittåkläppen), 960 m a.s.l., periodically wet depression at margin of fen, 2 Sep. 2014, *Lars Hedenäs s.n.* (holo-: S, B207536!; iso-: BM!, NY!).

Description

Plants up to ten cm high, usually in loose tufts, green or yellow-green. Stem with large central strand, a cortex of (0–)1–3 layers of strongly incrassate cells, and an epidermis of one layer of thin-walled or slightly incrassate cells, sometimes partly differentiated as a hyalodermis; axillary hairs with 2–8-celled, hyaline upper portion, 8–12 µm wide, basal 1–2 cells rectangular, hyaline; rhizoids strongly branched, red-brown, smooth, in leaf axils. Leaves 2.7–5.0 × 0.6–1.1 mm, when moist from sheathing base erect-patent to spreading, straight or screwed, when dry loosely incurved and curled or twisted, from ovate or rounded-oblong base with longly and narrowly triangular acumen, apex longly acuminate; leaf margin at least partly distinctly recurved in lower leaf, below entire, in upper leaf mostly entire or indistinctly and obtusely denticulate, occasionally distinctly denticulate close to leaf apex, denticles single, margin varying from unistratose to bistratose; costa 75–146 µm wide near base, with dorsal and ventral epidermis, one layer of large guide cells, 1–4 layers of ventral stereids and 2–4 layers of dorsal stereids; lamina cells in acumen incrassate, 6–38(–49) × 5–15 µm, 0.6–4.5(–5.8) times as long as wide, in mid-leaf incrassate, 6–42 × 4–12 µm, 0.6–6.1(–7.2) times as long as wide, and in sheathing lamina slightly incrassate or incrassate and slightly porose, 16–91 × 5–22 µm, 1.4–12.4 times as long as wide, transition between mid-leaf and basal cells gradual, due to relatively long mid-leaf cells and relatively short basal cells; alar cells differentiated, rectangular, slightly to strongly inflated and forming a diffusely delimited group of 3–5 cells wide and 3–5(–6) cells long, partly bistratose, decurrent. Perigonia lateral on stem, not stalked, antheridia protected by oblong perigonial leaves with “cut-off” or acute apex. Inner perichaetial leaves 4.29–6.02 mm long, lower 32–58% oblong and broadly sheathing, above suddenly narrowed to long, narrow acumen. Seta tall, 18–27 mm; capsule cylindric, curved, with distinct struma, 1.3–1.8 × 0.5–0.8 mm, 1.8–2.6 times as long as broad, more or less orthogonal to homotropus; exothecial cells slightly incrassate or longitudinally incrassate, collenchymatous or not; stomata ovate-pored, surrounded by radially arranged cells, near base of capsule; peristome red, teeth cleft or perforated to middle or further down, with longitudinal rows of pits on outside; spores 18–28 µm, very finely rough.

Remarks

When well developed this is a large species, with on the average more longly and narrowly acuminate leaves than in *O. virens*. When dry, the leaves are loosely incurved or curved upwards, and the upper acumen is loosely but relatively strongly twisted. The leaf margin in the acumen is mostly entire, but

sometimes slightly uneven or has a few and usually low and irregular obtuse teeth. Occasionally one or a few sharp teeth may occur, especially close to the leaf apex.

Habitat and distribution in Scandinavia

Oncophorus integerrimus sp. nov. is found most often in open wetlands, but occurs also on soil and wet rocks, often on shores (Fig. 4). The distribution of *O. integerrimus* sp. nov. is similar to that of *O. virens*, but geographically more restricted (Fig. 3D). Of the four Scandinavian *Oncophorus* species it is the only one that has not been found in southern Sweden, although there are few finds from southern Norway.

Nomenclatural note

The synonymy of *Oncophorus virens* var. *elongatus* Limpr. is based on protologue information (Limpricht 1886) and on material collected by Gander at the type locality two years after the description of the taxon (S-B232585). The name of the variety cannot be used at the species level, since it is blocked by *Oncophorus elongatus* (I.Hagen) Hedenäs.

Discussion

Although the monophyly of *Oncophorus* was not an issue in the present study, the positions of its species in relation to *Cynodontium strumiferum* and *Rhabdoweisia fugax* do not suggest otherwise. Neither in the ITS- nor chloroplast-based analyses, *O. crispifolius*, *O. dendrophilus*, and *O. rauei* were found in positions that suggested that they are especially closely related to any of the Scandinavian species. The molecular evidence presented here supports the recognition of the recently described *O. dendrophilus* (Hedderson & Blockeel 2006).

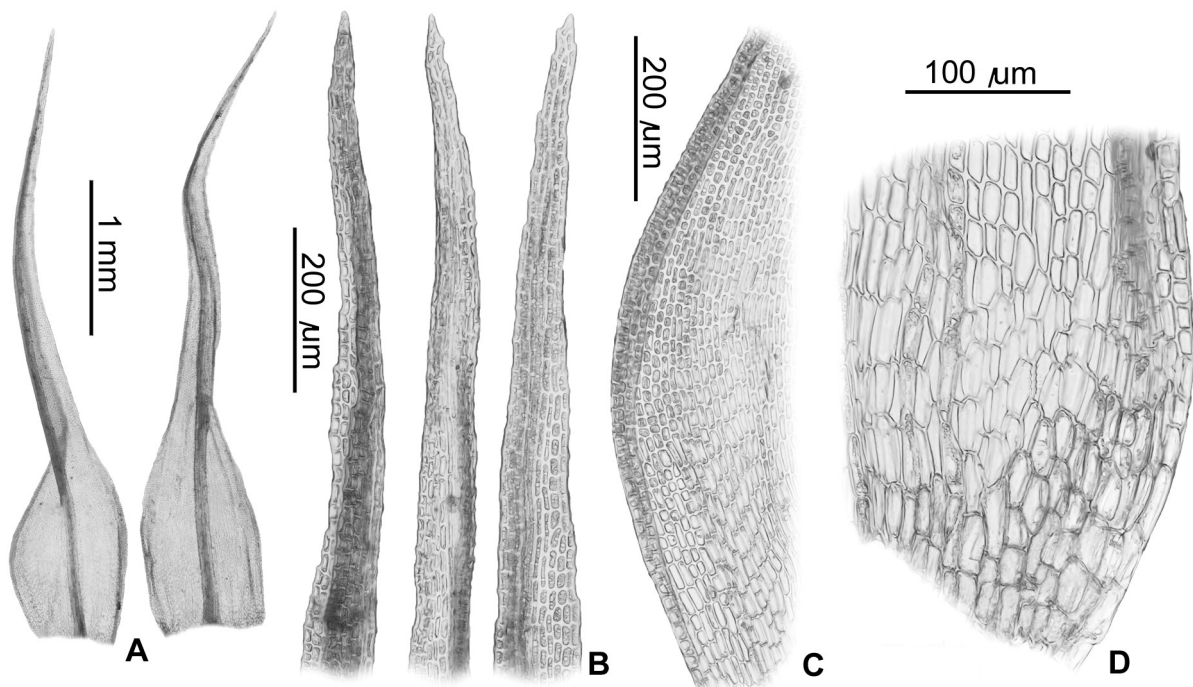


Fig. 10. *Oncophorus integerrimus* Hedenäs sp. nov. (holotype). **A.** Stem leaves. **B.** Upper leaf acumen. **C.** Portion of leaf at widest point, showing the broadly recurved margin. **D.** Lower part of sheathing leaf portion, showing differentiated alar region (margin to the right).

The molecular information available for Scandinavian *Oncophorus* suggests that species additional to the ones so-far accepted exist in the area. Four molecularly supported entities can also be distinguished based on their morphology, by a few qualitative characters, statistically significant differences in leaf cell measurements or on PCA scores based on these and leaf size. Four is therefore the minimum number of species to be recognized in the area. However, additional evolutionary lineages and in some cases most likely also biologically distinct cryptic species occur among the Scandinavian *Oncophorus*, considering the number of mutational differences between lineages as well as the lack of intermediates between these lineages. Cryptic species are here understood as lineages that are molecularly as distinct as those of the morphologically recognized species but which lack (known) morphological distinguishing features. For semi-cryptic species, weak quantitative morphological differentiation towards other molecularly identified entities is presently suggested by the data.

The two species *Oncophorus elongatus* and *O. wahlenbergii* are easily distinguished from *O. virens* and *O. integerrimus* sp. nov. by their plane rather than partially recurved leaf margins. *Oncophorus elongatus* differs from *O. wahlenbergii* in the shape of the marginal cells of the sheathing leaf portion, the denticulation or dentation of the upper leaf margins and costa, and overall leaf size, and except for *O. wahlenbergii* B in the quantitative leaf characters included in the PCA (Fig. 2A). Within *O. elongatus* one specimen shifted between *O. elongatus* A and B depending on whether ITS or chloroplast data were analysed. Such incongruence could be a result of several processes, such as incomplete lineage sorting or hybridization, but to determine the cause additional evidence is required (cf., Wendel & Doyle 1998; Harris 2008). On the other hand, there appears to be a phylogeographic signal distinguishing *O. elongatus* B as a western, oceanic or sub-oceanic entity that was mostly collected in fens and had usually got the long leaf portions above the sheathing base widely spreading, in contrast with the predominantly more eastern *O. elongatus* A that was mainly collected on dead wood or rocks and mostly presented less or not spreading leaves. Combined with the incomplete congruence between the two molecular data sets, this could be interpreted as two lineages that are still in the process of diverging. The distinct habit of *O. elongatus* B made Hedenäs (2005) believe that only this kind of plants belongs to *O. elongatus*, which is now shown to be incorrect. *Oncophorus elongatus* C is clearly distinct from *O. elongatus* A and B by 5–6 mutational changes according to both ITS and chloroplast data. Because only two of the sampled specimens belong to this lineage and no morphological feature was found that supports it, *O. elongatus* C is best treated as a potential cryptic species that requires further study.

Within *O. wahlenbergii* several well-supported molecular lineages that are differentiated by numerous mutations and have a high jackknife support exist. It seems likely that the three distinct lineages that are present in *O. wahlenbergii* represent cryptic species, or in the case of *O. wahlenbergii* B, which in some quantitative morphological traits overlaps more with *O. elongatus* than with *O. wahlenbergii* (Fig. 2A, Table 2), semi-cryptic species. The sampling of specimens from two of these three lineages occurred by pure chance, since neither *O. wahlenbergii* B nor C was clearly distinguishable by morphology alone. It is possible that a fuller sampling of *O. wahlenbergii* B, that allows comparing additional specimens with *O. wahlenbergii* A and C, would make it possible to refer at least a significant proportion of *O. wahlenbergii* B specimens to this lineage by morphology. According to ITS data, *O. wahlenbergii* C appears on another side of a major split than *O. wahlenbergii* A and B, *O. crispifolius*, *O. dendrophilus*, and *O. rauei*, which suggests that this lineage is more isolated than *O. wahlenbergii* B from *O. wahlenbergii* A, despite that *O. wahlenbergii* B is the one that may deviate morphologically from the latter.

Oncophorus integerrimus sp. nov. includes no jackknife-supported intraspecific variation. The leaf margins of *O. integerrimus* are entire, or occasionally denticulate near leaf apex, whereas *O. virens* has predominantly dentate or coarsely denticulate upper leaf margins; the species also differ in the quantitative leaf characters that were included in the PCA (Fig. 2B). *Oncophorus virens* displays intraspecific variation that is mainly incongruent between ITS and chloroplast data (cf., *O. elongatus*

above), except that *O. virens* B is distinct from *O. virens* A in both data sets. All seven specimens of *O. virens* B came from higher elevations than any of the 15 *O. virens* A specimens (Fig. 5B). This is highly unlikely as a chance result and therefore suggests that *O. virens* B is restricted to the cold climate of higher mountains. Since the temperature in the mountains is expected to increase with several degrees until the year 2100 (Berglöv *et al.* 2015a, 2015b; Nylén *et al.* 2015), it is urgent to examine the distribution of *O. virens* B and similarly distributed species and intraspecific entities in more detail. Organisms restricted to cold environments, such as *O. virens* B and the northern haplotypes of *Scorpidium cossonii* (Schimp.) Hedenäs (Hedenäs 1989) (Hedenäs 2009), will likely decline when the areas of suitably cold habitats shrink.

All four species that can be clearly distinguished by morphology have relatively northern distributions and are especially common in the mountain range and the lowlands of the far north (Fig. 3). The mapped distributions clearly underestimate the frequency of the species in Norway, since the mapped occurrences are based on S material only and the distribution of members of the genus *Oncophorus* is much wider according to ‘Artskart’ (<https://artskart.artsdatabanken.no/>; accessed 9 Feb. 2016).

All four species occur with different frequencies in several humid to wet habitats (Fig. 4). *Oncophorus elongatus* obviously prefers organic substrates, such as decomposing wood and peaty soil in mires, whereas *O. virens* is clearly a species of brook and lake shores, and wet rocks, and is the only species that is often found in late snow-beds. The two remaining species are most frequently found in mire habitats, but are relatively abundant also on brook and lake shores, and wet rocks. *Oncophorus elongatus* and *O. wahlenbergii* occur in relatively base-poor environments, whereas *O. virens* and *O. integerrimus* sp. nov. are mostly found in base-rich to calcareous habitats. Whether entities within species that display clear intraspecific molecular variation also differ from each other in habitat preferences should be explored when molecular information exists for additional specimens.

From a biodiversity and conservation point of view the cryptic diversity in *Oncophorus* deserves serious attention (Hedenäs 2016). A fuller sampling of *O. virens*, *O. elongatus*, and *O. wahlenbergii* is required to understand their cryptic and semi-cryptic diversities, as well as intrinsic geographic and habitat components. Additionally, this would possibly allow the discovery of morphologically stable characters to distinguish at least *O. wahlenbergii* B. However, at the present state of knowledge, and considering the wish by most biologists to be able to distinguish species by morphology, four ‘species’ of *Oncophorus* are here recognized for Scandinavia.

Acknowledgements

I thank Bodil Cronholm for her excellent laboratory work, L. Ellis at BM for a loan of type material, and T.L. Blockeel for a gift and a loan of *O. dendrophilus* material. Two reviewers provided comments that significantly improved the text. Financial support for the molecular work was received from the Swedish Taxonomy Initiative (dha 2014-79 4.3).

References

- Arnell H.W. & Jensen C. 1896. Ein bryologischer Ausflug nach Tåsjö. Mit einer Karte und einer Tafel. *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar* 21 Afd. 3 (10): 1–64.
- Berglöv G., Asp M., Berggreen-Clausen S., Björck E., Axén Mårtensson J., Nylén L., Ohlsson A., Persson H. & Sjökvist E. 2015a. Framtidsklimat i Norrbottens län - enligt RCP-scenarier. *SMHI Klimatologi* 32: 1–75.

- Berglöv G., Asp M., Berggreen-Clausen S., Björck E., Axén Mårtensson J., Nylén L., Ohlsson A., Persson H. & Sjökvist E. 2015b. Framtidsklimat i Västerbottens län - enligt RCP-scenarier. *SMHI Klimatologi* 33: 1–75.
- Bickford D., Lohman D.J., Sodhi N.S., Ng P.K.L., Meier R., Winker K., Ingram K.K. & Das I. 2006. Cryptic species as a window on diversity and conservation. *Trends in Ecology & Evolution* 22: 148–155. <https://doi.org/10.1016/j.tree.2006.11.004>
- Braithwaite R. 1883. *The British Moss-Flora*. Vol. 1. Published by the author, London.
- Bridel S.E. von 1826. *Bryologia universa seu systematica ad novam methodum dispositio, historia et descriptio omnium muscorum frondosorum hucusque cognitorum cum synonymia ex auctoribus probatissimis*. Vol. 1. J.A. Barth, Leipzig.
- Brotherus V.F. 1901. II. Specieller Teil. Mit zahlreichen Einzelbildern in vielen Figuren. *Die Natürlichen Pflanzenfamilien* I (3): 277–1172.
- Brotherus V.F. & Saetan T. 1890. Musci Lapponiae kolaënsis. *Acta Societatis pro Fauna et Flora Fennica* 6 (4): 3–100.
- Bruch P. & Schimper W.P. 1846. *Bryologia Europaea seu genera muscorum Europaeorum monographice illustrata*. Vol. 1. Fasc. 33–36. E. Schweizerbart, Stuttgart.
- Bruch P. & Schimper W.P. 1847. *Bryologia Europaea seu genera muscorum Europaeorum monographice illustrata*. Vol. 1. Fasc. 37–40. E. Schweizerbart, Stuttgart.
- Bruch P., Schimper W.P. & Gümbel T. 1836–1851. *Bryologia Europaea seu genera muscorum Europaeorum monographice illustrata*. Vol. I. E. Schweizerbart, Stuttgart.
- Buchbender V., Hespanhol H., Krug M., Sérgio C., Séneca A., Maul K., Hedenäs L. & Quandt D. 2014. Phylogenetic reconstructions of the Hedwigiaceae reveal cryptic speciation and hybridisation in *Hedwigia*. *Bryophyte Diversity and Evolution* 1: 1–21. <https://doi.org/10.11646/bde.36.1.1>
- Carter B.E. 2012a. *Scleropodium occidentale* (Brachytheciaceae), a new moss species from western North America. *The Bryologist* 115: 222–230. <https://doi.org/10.1639/0007-2745-115.2.222>
- Carter B.E. 2012b. Species delimitation and cryptic diversity in the moss genus *Scleropodium* (Brachytheciaceae). *Molecular Phylogenetics and Evolution* 63: 891–903. <https://doi.org/10.1016/j.ympev.2012.03.002>
- Clement M., Posada D. & Crandall K.A. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657–1659. <https://doi.org/10.1046/j.1365-294x.2000.01020.x>
- Crawford D.J. & Stuessy T.F. 2016. Cryptic variation, molecular data, and the challenge of conserving plant diversity in oceanic archipelagos: the critical role of plant systematics. *Korean Journal of Plant Taxonomy* 46: 129–148. <https://doi.org/10.11110/kjpt.2016.46.2.129>
- Dixon H.N. 1926. Mosses collected in Gilgit etc., by J. Garrett and W. Lillie. *Records of the Botanical Survey of India* 9 (5): 303–313.
- Doweld A.B. 2001. *Prosyllabus tracheophytorum. Tentamen systematis plantarum vascularium (Tracheophyta)*. Geos, Moscow.
- Draper I., Hedenäs L., Stech M., Patiño J., Werner O., González-Mancebo J.M., Sim-Sim M., Lopes T. & Ros R.M. 2015. How many species of *Isoetecium* (Lembophyllaceae, Bryophyta) are there in Macaronesia? A survey using integrative taxonomy. *Botanical Journal of the Linnean Society* 177: 418–438. <https://doi.org/10.1111/boj.12250>

- Farris J.S., Källersjö M., Kluge A.G. & Bult C. 1995. Testing significance of incongruence. *Cladistics* 10: 315–319. <https://doi.org/10.1111/j.1096-0031.1994.tb00181.x>
- Feliner G.N. & Rosselló J.A. 2007. Better the devil you know? Guidelines for insightful utilization of nrDNA ITS in species-level evolutionary studies in plants. *Molecular Phylogenetics and Evolution* 44: 911–919. <https://doi.org/10.1016/j.ympev.2007.01.013>
- Fleischer M. 1920. Natürliches System der Laubmoose. *Hedwigia* 61: 390–400.
- Frahm J.-P., Buchbender V., Lachmann S., Reifenrath K. & Werner F. 1998. Revision der Gattung *Oncophorus* (Musci, Dicranaceae). *Tropical Bryology* 14: 119–131.
- Frey W. & Stech M. 2009. Division of Bryophyta Schimp. (Musci, Mosses). In: Frey W. (ed.) *Syllabus of Plant Families. Adolf Engler's Syllabus der Pflanzenfamilien*. 13th edition. Part 3. *Bryophytes and seedless vascular plants*: 116–257. Gebrüder Borntraeger, Berlin.
- Goffinet B., Buck W.R. & Shaw A.J. 2008. Morphology, anatomy, and classification of the Bryophyta. In: Goffinet B. & Shaw A.J. (eds) *Bryophyte biology*. 2nd edition: 55–138. Cambridge University Press, Cambridge.
- Goloboff P., Farris J. & Nixon K. 2003. Tree analysis using new technology. Available from <http://www.lillo.org.ar/phylogeny/> [accessed 24 Apr. 2017].
- Grout A.J. 1937. *Moss Flora of North America (North of Mexico)*. Vol. 1. Published by the Author, Newfane, Vermont.
- Hagen I. 1899. Musci norvegiae borealis. *Tromsö Museums Aarshefter* 21–22 (1): 1–112.
- Hallingbäck T., Lönnell N., Weibull H., Hedenäs L. & Knorring P. von 2006. *Nationalnyckeln till Sveriges flora och fauna. Bladmossor: Sköldmossor-blåmossor. Bryophyta: Buxbaumia-Leucobryum*. ArtDatabanken, SLU, Uppsala.
- Harris E.S.J. 2008. Paraphyly and multiple causes of phylogenetic incongruence in the moss genus *Plagiomnium* (Mniaceae). *Taxon* 57: 417–433.
- Hartman C.J. 1832. *Handbok i Skandinaviens flora, innefattande Sveriges och Norriges växter, till och med mossorna. Med en öfversigt af vextläran och botanikens studium i allmänhet. Andra upplagan, omarbetad och förökad*. 2nd edition. Z. Hæggströms, Stockholm.
- Hartman C.J. 1871. *Handbok i Skandinaviens Flora, innefattande sveriges och norges växter till och med mossorna. Utgifen mer Rättelser och tillägg af Carl Hartman. Sednare delen: Mossor*. [Part 2]. 10th edition. Z. Hæggströms, Stockholm.
- Hawksworth D.L. 2001. The magnitude of fungal diversity: the 1.5 million species estimate revisited. *Mycological Research* 105: 1422–1432. <https://doi.org/10.1017/S0953756201004725>
- Hedderson T.A. & Blockeel T.L. 2006. *Oncophorus dendrophilus*, a new moss species from Cyprus and Crete. *Journal of Bryology* 28: 357–359. <https://doi.org/10.1179/174328206X152324>
- Hedenäs L. 1989. The genera *Scorpidium* and *Hamatocaulis*, gen. nov., in Northern Europe. *Lindbergia* 15 (1): 8–36.
- Hedenäs L. 2005. *Oncophorus wahlenbergii* var. *elongatus* I. Hagen, an overlooked taxon in northern Europe. *Lindbergia* 30: 32–38.
- Hedenäs L. 2009. Relationships among arctic and non-arctic haplotypes of the moss species *Scorpidium cossonii* and *Scorpidium scorpioides* (Calliergonaceae). *Plant Systematics and Evolution* 277: 217–231. <https://doi.org/10.1007/s00606-008-0131-y>

- Hedenäs L. 2016. Intraspecific diversity matters in bryophyte conservation – internal transcribed spacer and *rpl16* G2 intron variation in European mosses. *Journal of Bryology*: 173–182. <https://doi.org/10.1080/03736687.2016.1145522>
- Hedenäs L., Désamoré A., Laenen B., Papp B., Quandt D., González-Mancebo J.M., Patiño J., Vanderpoorten A. & Stech M. 2014. Three species for the price of one within the moss *Homalothecium sericeum* s.l. *Taxon* 63: 249–257. <https://doi.org/10.12705/632.16>
- Hedwig J. 1801. *Species muscorum frondosorum: descriptae et tabulis aeneis lxxvii coloratis illustratae*. J.A. Barthii, Leipzig; A. Koenig, Paris.
- Heinrichs J., Hentschel J., Bombosch A., Fiebig A., Reise J., Edelmann M., Kreier H.-P., Schäfer-Verwimp A., Caspari S., Schmidt A.R., Zhu R.-L., Konrat M. von, Shaw B. & Shaw A.J. 2010. One species or at least eight? Delimitation and distribution of *Frullania tamarisci* (L.) Dumort. s. l. (Jungermanniopsida, Porellales) inferred from nuclear and chloroplast DNA markers. *Molecular Phylogenetics and Evolution* 56: 1105–1114. <https://doi.org/10.1016/j.ympev.2010.05.004>
- Herzog T. 1910. Kritische u. neue Arten der europäischen Laubmoosflora. *Allgemeine Botanische Zeitschrift für Systematik, Floristik, Pflanzengeographie* 16: 81–85.
- Howis S., Barker N.P. & Mucina L. 2009. Globally grown, but poorly known: species limits and biogeography of *Gazania* Gaertn. (Asteraceae) inferred from chloroplast and nuclear DNA sequence data. *Taxon* 58: 871–882.
- Hübener J.W.P. 1833. *Muscologia Germanica, oder beschreibung der Deutschen Laubmoose*. F. Hofmeister, Leipzig.
- Huson D.H. & Bryant D. 2006. Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution* 23: 254–267. <https://doi.org/10.1093/molbev/msj030>
- Ignatov M.S. & Afonina O.M. 1992. Check-list of mosses of the former USSR. *Arctoa* 1: 1–85.
- Košnar J., Herbstová M., Kolář F., Koutecký P. & Kučera J. 2012. A case of intragenomic ITS variation in bryophytes: Assessment of gene flow and role of ploidy in the origin of European taxa of the *Tortula muralis* (Musci: Pottiaceae) complex. *Taxon* 61: 709–720.
- Limpricht K.G. 1886. *Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. I. Abtheilung. Lieferung 5*. Verlag von Eduard Kummer, Leipzig.
- Lindberg S.O. 1864. De Tortulis et ceteris Trichostomeis europæis. *Öfversigt af Kongelige Vetenskaps-Akademiens Förhandlingar* 21: 213–254.
- Lindberg S.O. 1872. *Contributio ad Floram Cryptogamam Asiae Boreali-Orientalis*. Societatis Litterariæ Fennicæ, Helsingfors.
- Mönkemeyer W. 1927. *Die Laubmoose Europas. IV. Band, Ergänzungsband. Andreaeales-Bryales*. Akademische Verlagsgesellschaft m.b.H, Leipzig.
- Müller C. 1851. *Synopsis muscorum frondosorum omnium hucusque cognitorum*. Vol. 2. A. Foerstner, Berlin.
- Müller C. 1898. Bryologia provinciae Schen-Si sinensis ex collectione Giraladiana III. *Nuovo Giornale Botanico Italiano, n.s.* 5 (2): 158–209.
- Müller K. 2005. SeqState. *Applied Bioinformatics* 4: 65–69. <https://doi.org/10.2165/00822942-200504010-00008>
- Nadot S., Bajon R. & Lejeune B. 1994. The chloroplast gene *rps4* as a tool for the study of Poaceae phylogeny. *Plant Systematics and Evolution* 191: 27–38. <https://doi.org/10.1007/BF00985340>

- Newmaster S.G. 2007. *Oncophorus* (Bridel) Bridel, Muscol. Recent., suppl. 4:53. 1819. In: Committee FoNAE (ed.) *Flora of North America North of Mexico*. Vol. 27: 423–424. Oxford University Press, New York, Oxford.
- Nyholm E. 1987. *Illustrated Flora of Nordic Mosses*. Fasc. 1. *Fissidentaceae-Seligeriaceae*. Nordic Bryological Society, Copenhagen, Lund.
- Nylén L., Asp M., Berggreen-Clausen S., Berglöv G., Björck E., Axén Mårtensson J., Ohlsson A., Persson H. & Sjökvist E. 2015. Framtidsklimat i Jämtlands län - enligt RCP-scenarier. *SMHI Klimatologi* 34: 1–75.
- Nylinder S., Cronholm B., Lange P.J. de, Walsh N. & Anderberg A.A. 2013. Species tree phylogeny and character evolution in the genus *Centipeda* (Asteraceae): evidence from DNA sequences from coding and non-coding loci from the plastid and nuclear genomes. *Molecular Phylogenetics and Evolution* 68: 239–250. <https://doi.org/10.1016/j.ympev.2013.03.020>
- Pacak A. & Szweykowska-Kulińska Z. 2000. Molecular data concerning allopolyploid character and the origin of chloroplast and mitochondrial genomes in the liverwort species *Pellia borealis*. *Journal of Plant Biotechnology* 2: 101–108.
- Paris E.G. 1900. *Index Bryologicus sive enumeratio muscorum hucusque cognitorum. Supplementum Primum*. Georg & Cie, Geneva, Basel.
- Pax F.A. 1900. *Prantl's Lehrbuch der Botanik*. 11th edition. Wilhelm Engelmann, Leipzig.
- Rydin C., Pedersen K.R. & Friis E.M. 2004. On the evolutionary history of *Ephedra*: Cretaceous fossils and extant molecules. *Proceedings of the National Academy of Sciences of the United States of America* 101: 16571–16576. <https://doi.org/10.1073/pnas.0407588101>
- Schimper W.P. 1856. *Corollarium Bryologiae Europaeae, conspectum diagnosticum familiarum, generum et specierum, adnotationes novas atque emendationes complectens*. E. Schweizerbart, Stuttgart.
- Schultz C.F. 1828. Observationes Bryologicae. Particula prima. In: Hornschuch C.F. (ed.) *Sylloge plantarum novarum itemque minus cognitarum*. Vol. 2: 119–154. C.E. Brenck, Regensburg.
- Shaw A.J., McDaniel S.F., Werner O. & Ros R.M. 2002. New frontiers in bryology and lichenology. Phylogeography and phylodemography. *The Bryologist* 105: 373–383.
- Simmons M.P. & Ochoterena H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369–381. <https://doi.org/10.1093/sysbio/49.2.369>
- Souza-Chies T.T., Bittar G., Nadot S., Carter L., Besin E. & Lejeune B. 1997. Phylogenetic analysis of Iridaceae with parsimony and distance methods using the plastid gene *rps4*. *Plant Systematics and Evolution* 204: 109–123. <https://doi.org/10.1007/BF00982535>
- StatSoft I. 2013. *STATISTICA (data analysis software system), version 12*. Available from <http://www.statsoft.com> [accessed 1 May 2013].
- Stech M. & Frey W. 2008. A morpho-molecular classification of the mosses. *Nova Hedwigia* 86: 1–21. <https://doi.org/10.1127/0029-5035/2008/0086-0001>
- Stech M., McDaniel S.F., Hernández-Maqueda R., Ros R.M., Werner O., Muñoz J. & Quandt D. 2012. Phylogeny of haplolepideous mosses – challenges and perspectives. *Journal of Bryology* 34: 173–186. <https://doi.org/10.1179/1743282012Y.0000000014>
- Thiers B. Continuously updated. *Index Herbariorum: a global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available from <http://sweetgum.nybg.org/science/ih/> [accessed 21 Mar. 2017].

Wendel J.F. & Doyle J.J. 1998. Phylogenetic incongruence: window into genome history and molecular evolution. *In*: Soltis D.E., Soltis P.S. & Doyle J.J. (eds) *Molecular systematics of plants II. DNA sequencing*: 265–296. Chapman and Hall, New York. https://doi.org/10.1007/978-1-4615-5419-6_10

Manuscript received: 2 June 2016

Manuscript accepted: 23 August 2016

Published on: 2 May 2017

Topic editor: Koen Martens

Desk editor: Natacha Beau

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France; Botanic Garden Meise, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Natural History Museum, London, United Kingdom; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Real Jardín Botánico de Madrid CSIC, Spain.