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Sphagnum incundum a new species in *Sphagnum* subg. *Acutifolia* (Sphagnaceae) from boreal and arctic regions of North America

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Abstract

We describe *Sphagnum incundum* in *Sphagnum* subg. *Acutifolia* (Sphagnaceae, Bryophyta). We used both molecular and morphological methods to describe the new species. Molecular relationships with closely related species were explored based on microsatellites and nuclear and plastid DNA sequences. The morphological description is based on qualitative examination of morphological characters and measurements of leaves and hyalocysts. Morphological characters are compared between closely related species. The results from Feulgen densitometry and microsatellite analysis show that *S. incundum* is gametophytically haploid. Molecular analyses show that it is a close relative to *S. flavicomans*, *S. subfulvum* and *S. subnitens*, but differs both genetically and in morphological key characters, justifying the description of *S. incundum* as a new species. The new peatmoss is found in North America along the western coast of Greenland, in Canada from Quebec and Northwest Territories, and Alaska (United States). The new species has a boreal to arctic distribution.

Introduction

Sphagnum Linnaeus (1753: 1106) has five subgenera, including subg. *Acutifolia* (Russow) A.J. Shaw (2016: 1523). There are three sections, *S.* sect. *Polyclada* Warnstorf (1890:225), *Insulosa* Isoviita (1966: 231) and *Acutifolia* (Russow) Schimper (1876: 825), within subg. *Acutifolia* (Shaw *et al.* 2016). It is mainly a boreal subgenus with approximately 28–31 species known from the northern hemisphere (Gao and Crosby 1999, Iwatsuki 2004, Hill *et al.* 2006, Ignatov *et al.* 2006, McQueen and Andrus 2007, Flatberg 2013). The subgenus also embraces a few species in the southern hemisphere (Eddy 1985, Fife 1996, Müller 2009). The most recent species described in subg. *Acutifolia* are *S. mirum* Flatberg & Thingsgaard (2003: 504), *S. beothuk* R.E. Andrus (2006: 966), and *S. venustum* Flatberg (2008: 2). Most of the species belong to sect. *Acutifolia* and gametophytes are either haploid or diploid with chromosome numbers n = 19 or 38, respectively (Fritsch 1982, 1991). All documented diploids have been shown to be gametophytically allodiploids, or likely so (e.g. Cronberg 1996, Greilhuber *et al.* 2003, Shaw *et al.* 2005, Flatberg 2007a).

The sect. *Acutifolia* embraces several groups of closely related species with intricate patterns of morphological and genetic variation (e.g., Shaw *et al.* 2005). The most clearly differentiated of these complexes, embraces the four species *S. mirum*, *S. squarrosum* Crome (1803: 24), *S. teres* (Schimp.) Ångström ex Hartman (1861: 417) and *S. tundrae* Flatberg (1994: 3), classified in sect. *Squarrosa* (Russow) Schimper (1876: 835) (Flatberg and Thingsgaard 2003). Another group is the *S. fimbriatum* Wilson (1847: 398) complex, comprising some three to five closely related species (Shaw *et al.* 2012). Species closely related to *S. capillifolium* (Ehrh.) Hedwig (1782: 86) comprise a third group (Cronberg 1998, Natcheva and Cronberg 2007). A fourth group is hereafter named the *S. subnitens* complex. This species complex consists of closely related species and intraspecific variants that are characterized by a combination of yellow-brown, pale brown, brown-red to pink-red-violet shoots with a characteristic blue-grey, metallic luster on the branches below the capitulum in dry specimens. This characteristic sheen is in *S. subnitens* Russow & Warnstorf (1888: 115) shown to be a structural colour attributed to light interference in the hyaline cell walls (Morris 1977). Capitula have inconspicuous small to indistinct terminal buds. The branch leaves are non-ranked and stem leaves are

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lingulate to lingulate-triangular, usually with acute to acuminate and ± narrowly truncate apices. Stem leaf hyalocysts are efibrillose to sometimes delicately fibrillose and aporose to sometimes with a few pores, and outer stem cortices are usually aporose. The species in the complex have a Northern Hemisphere distribution, except for *S. subnitens,* which occurs in New Zealand where humans likely introduced it (Karlin *et al.* 2011).

The number of recognized species in the *S. subnitens* complex has varied through time, but recently, *Sphagnum* taxonomists recognize three species (e.g. Crum 1984, McQueen and Andrus 2007). These are *S. subnitens*, *S. flavicomans* (Cardot.)Warnst. in H.G.A. Engler (1911: 79) and *S. subfulvum* Sjörs (1944: 404). *Sphagnum subnitens* and *S. subfulvum* are recorded to be monoicous, while *S. flavicomans* is dioicous (e.g. Crum 1984). All three species are haploid (n = 19) (Fritsch 1982, 1991). Furthermore, subspecies are described for both *S. subnitens* and *S. subfulvum* (Flatberg 1985, Flatberg 2013). How many species there actually are within the *S. subnitens* complex is still unknown. The newly described species *S. bergianum* R.E.Andrus (2006: 264) from Newfoundland and Alaska (Andrus 2006) falls within this group, but was later shown to belong to *S. subfulvum* based on genetic data (Shaw *et al.* 2009).

During field work performed by K.I. Flatberg in arctic parts of western Greenland in 2006, arctic Nunavik, Canada in 2007, and in the Anchorage area, Alaska in 2008 an *Acutifolia* morphotype within the *S. subnitens* complex was observed and collected at several locations. It had distinct morphological characteristics. The morphological distinctness observed in the field was later confirmed microscopically. This deviating morph in the *S. subnitens* complex was mentioned in Flatberg (2007b). The distinct tinge of red in the otherwise brownish capitula was highlighted, as well as the fairly narrow and acuminate stem leaves often furnished with some hyalocyst fibrils. *Sphagnum subnitens* (subsp. *subnitens*) had been reported from western Greenland (Lange 1984). However, these reports are now questioned as Greenlandic material of *S. subnitens* in herbarium C in fact belonged to the morph in question (Flatberg 2007b). Furthermore, *S. subnitens* is not reported from eastern North America (McQueen and Andrus 2007), and it seems to avoid arctic areas in general.

Here, we describe a new species in the *S. subnitens* complex of subg. *Acutifolia*, based on molecular and morphological data. We discuss its morphological characteristics in relation to other species in the *S. subnitens* complex, and describe the current geographic range and habitat of the new species.

Material and methods

Plant material of the new species was collected in Canada, Greenland, and the United States between 2006 and 2008. The new species was investigated using both genetic markers and morphological examination. In addition, the ploidy level was evaluated using Feulgen densitometry. *Sphagnum subfulvum* subsp. *subfulvum* and *S. subnitens* subsp. *subnitens* were used in the following analyses and will hereafter be called *S. subfulvum* and *S. subnitens,* respectively. Revision of selected specimens in herbarium TRH, LE and MHA was undertaken to confirm morphological concepts and to get data on the distribution of the new species.

Molecular analyses

Microsatellite data were obtained from 15 specimens of the new species, together with 13 specimens of the other three species belonging to the *S. subnitens* complex: *S. flavicomans* (n=3), *S. subfulvum* (n=5) and *S. subnitens* (n=5). All specimens are listed in Table 1. Plants were genotyped for microsatellite markers: 1, 12, 7, 17, 22, 65, 68 and 78 (names follow Shaw *et al.* 2008, Stenøien *et al.* 2011). DNA extraction, amplification in multiplexed PCR, and genotyping follow Kyrkjeeide *et al*. (2016).

Microsatellite data were analyzed using the software STRUCTURE 2.3.4. (Pritchard *et al.* 2000, Falush *et al.* 2003, 2007, Hubisz *et al.* 2009) and SPLITSTREE4 (Huson 1998, Huson and Bryant 2006). In the program STRUCTURE, a Bayesian approach estimates the number of likely genetic groups within the dataset, and then assign individuals to different genetic groups based on genetic similarity. The analyses were performed using 200,000 iterations after a burn-in period of 100,000 iterations. The maximum number of genetic clusters, K, were set to five, one more than the number of hypothetical species included in the analysis, and each K (one to five) was replicated ten times. The results were summarized and visualized using the online version of CLUMPAK (Kopelman *et al.* 2015). The Best K option implemented in CLUMPAK and Evanno's ΔK (Evanno *et al.* 2005) were used to evaluate the most likely number of genetic clusters in the dataset. A haplotype network allowing for conflicting phylogenies, was built by SPLITSTREE4. The network was based on genetic distances between individuals calculated in GENALEX 6.503 (Peakall and Smouse 2012). We also used microsatellite data to infer ploidy level of the new species, by counting number of alleles per locus. Allodiploid species may be detected this way as haploid plants usually have one allele at each locus, whereas allodiploid plants often have two at several markers (Karlin *et al.* 2014).

TABLE 1. Specimens from the *Sphagnum subnitens* complex used in microsatellite analyses. The specimens highlighted in bold were also used in morphometric analyses.

Taxon	Locality	Collector, coll. no.	TRH
S. flavicomans	U.S.A., New Jersey	K.I. Flatberg	**B-741129**
S. flavicomans	U.S.A., Maine	R.E. Andrus	B-727088
S. flavicomans	Canada, Newfoundland and Labrador	R.E. Andrus, 10-131	**B-727084**
S. incundum	U.S.A., Alaska, Anchorage area	K.I. Flatberg, 128-08	**B-9986**
S. incundum	U.S.A., Alaska, Anchorage area	K.I. Flatberg, 138-08	B-9987
S. incundum	Canada, Quebec, Ivujivik	K.I. Flatberg, 342-07	B-38501
S. incundum	Canada, Quebec, Ivujivik	K.I. Flatberg, 314-07, type	**B-9718**
S. incundum	Canada, Quebec, Ivujivik	K.I. Flatberg, 317-07	**B-38507**
S. incundum	Canada, Quebec, Ivujivik	K.I. Flatberg, 319-07	B-38510
S. incundum	Canada, Quebec, Ivujivik	K.I. Flatberg, 299-07	B-38514
S. incundum	Canada, Quebec, Inukjuak	K.I. Flatberg, 442-07	B-9988
S. incundum	Canada, Quebec, Inukjuak	K.I. Flatberg, 462-07	**B-9993**
S. incundum	Canada, Quebec, Inukjuak	K.I. Flatberg, 451-07	B-9999
S. incundum	Greenland, Qaasuitsup, Ilulissat	K.I. Flatberg, 199-06	**B-9981**
S. incundum	Greenland, Qaasuitsup, Ilulissat	K.I. Flatberg, 186-06	B-9984
S. incundum	Greenland, Qaasuitsup, Ilulissat	K.I. Flatberg, 216-06	B-9982
S. incundum	Greenland, Qaasuitsup, Ilulissat	K.I. Flatberg, 215-06, male	B-9983
S. incundum	Greenland, Sermersooq, Nuuk	K. Hassel, T. Prestø	B-693795
S. subfulvum	Norway, Troms	K.I. Flatberg, 67-02	**B-158979**
S. subfulvum	Norway, Nordland	K.I. Flatberg, 34-97	**B-157436**
S. subfulvum	Greenland, Kujalleq	K.I. Flatberg, 246-06	**B-725548**
S. subfulvum	Canada, Newfoundland and Labrador	R.E. Andrus, 37-332	**B-742145**
S. subfulvum	Canada, Quebec	K.I. Flatberg, 232-07	**B-741525**
S. subnitens	Norway, Nordland	K.I. Flatberg, M.O. Kyrkjeeide	**B-770207**
S. subnitens	Iceland	G. Gudjonsson	**B-11872**
S. subnitens	United Kingdom, Scotland, Highland	M.O. Kyrkjeeide	**B-120130**
S. subnitens	Canda, British Columbia	K.I. Flatberg, 70-00	**B-725567**
S. subnitens	Norway, Finnmark	K.I. Flatberg	**B-155847**

Sequence data include sampling of a selection of sequences from subg. *Acutifolia* available in Genbank and from other unpublished projects, as well as a limited number of sequences from other subgenera of *Sphagnum* (see Table 2 for voucher information). The genes included in the analyses were one nuclear gene (*atgc*89) and two plastid genes (*trn*G and *trn*L). Laboratory protocols for DNA extraction, PCR amplification, sequencing, and sequence editing were as described by Shaw *et al.* (2003). Nucleotide sequences were aligned manually and nuclear and plastid genes analyzed separately. PARTITIONFINDER v.1.1.1 (Lanfear *et al.* 2012) was used to confirm that *trn*G and *trn*L could be run together without partition. The best-fit models of nucleotide substitution evolution were assessed using MRMODELTEST v. 2.3 (Nylander 2004) executed in PAUP* version 4.0a152 (Swofford 1998). Phylogenetic analyses for both the nuclear and plastid genes were run in MRBAYES 3.2.6 (Ronquist *et al.* 2012). The GRT+I model was selected for the nuclear gene and HKY+G for chloroplast genes. The following parameters were used for the Bayesian analysis: mcmc ngen=20000000, samplefreq=5000, printfreq=5000, nchains=4, nruns=2, sumt relburnin=yes, burninfrac=0.25. Maximum likelihood analyses were run using the program RAXML (Stamatakis 2006) with the GTR+G model for both nuclear and plastid genes. Both MRBAYES and RAXML were executed on CIPRES Science Gateway (Miller 2010). The results were checked in TRACER and visualized in FIGTREE v1.3.1 (Rambaut 2012).

Morphological analyses

To explore relative differences in leaf and cell morphology among the four species of the *S. subnitens* complex, morphometric measurements of stem and branch leaves, and of leaf hyalocysts were performed. We selected five specimens of each species (the specimens marked in bold in Table 1, in addition to *S. flavicomans* specimens TRH B-14851, 14852, 14853, not listed in Table 1) and selected one *Sphagnum* shoot of each specimen for the study. From each plant shoot, stem leaves from the upper two centimeters of the stem and branch leaves from the middle part of divergent branches were semi-permanently mounted in glycerol on microscopic slides. Five typical leaves from each slide were selected to explore stem and branch leaf size and shape. The following variables were measured for both stem and branch leaves: length, width at the middle part and at the distal 3/4 length. To study the leaf hyalocysts, we selected cells from the distal median convex portion of the stem and branch leaves. Length and maximum width measurements were made on three typical shaped cells in all leaves measured from each shoot. All measurements were taken using the Leica DM6000 B transmission microscope, and photomicrographs were made applying the Leica Application Suite LASD V2.6 for stacking.

We performed a principal component analysis (PCA) to explore the morphometric clustering of stem and branch leaves and hyalocysts in the multidimensional space relative to axes at the species level. Analyses were conducted in the R statistical environment (R Development Core Team 2015), using the R package 'ggfortify' (Horikoshi and Tang 2016, Tang *et al.* 2016) and visualized using R package 'ggplot2' (Wickham 2009).

TABLE 2. Voucher information for *Sphagnum* specimens used in phylogenetic analyses, including GenBank sequence ID.

Taxon	Locality	Collector, coll. no.	Herbarium	trng	trnl	atgc89
S. aciphyllum	Brazil	D. Costa 5146	DUKE			MG586048
S. angermanicum	USA: New York	W.R. Town 2253	DUKE	MF362500	AF192618	MG586049
S. aongstroemii	Norway	R.E. Andrus & K.I. Flatberg 7531	DUKE	AY309757	AF192619	MG586050
S. arcticum	Norway	K.I. Flatberg, S. Sastad, & K. Thingsgaard 270-00	DUKE	MF362502	AY298012	
S. arcticum	Norway	K.I. Flatberg *et al.* 158200	TRH	MG586072	MG586080	
S. arcticum	USA: Alaska	K.I. Flatberg 507-01	TRH	MG586073	MG586081	
S. bartlettianum	USA: South Carolina	J. Shaw 9279	DUKE	MF362508	AF192600	MG586051
S. beothuk	Canada: Newfoundland	R.E. Andrus 10687	DUKE	MF362509	MF362355	MG586047
S. capillifolium	Norway	J. Shaw 9650	DUKE	MG586074	AY298038	MG586052
S. concinnum	USA: Alaska	R.E. Andrus 11360	BING	JN000153	JN000081	
S. diskoense	Greenland	K.I. Flatberg *et al.* 177-06	DUKE	JN000177	JN000107	
S. fimbriatum	USA: Vermont	B. Shaw 7153	DUKE	MG586075	MG586079	MG586053
S. flavicomans	Canada: Newfoundland	W.B. Schofield 101051	DUKE	MF362530	AF192571	
S. fuscum	Greenland	K.I. Flatberg 134-06	TRH	JN000191	JN000121	
S. girgensohnii	USA: New York	J. Shaw 11553	DUKE	MF362532	AY298113	MG586054
S. girgensohnii	China	D.G. Long 34478	DUKE	MG586076	MG586082	MG586055
S. incundum	Canada: Nunavik	B. & K.I. Flatberg 442-07	TRH	MG586077	MG586083	
S. incundum	Canada: Quebec	K.I, Flatberg *et al.* 282-07	DUKE	MG586071	MG586084	
S. incundum	Greenland	K.I. Flatberg 199-06	TRH	MF362536	MF362361	MG586056
S. itatiaiae	Brazil	D.M. Vital & W. Buck 11780	NYBG			MG586057
S. junghuhnianum	China	J. Shevock 14370	MO	MF362539	AF192630	MG586058
S. molle	USA: Alabama	J.R. MacDonald 3923	DUKE	MF362551	AY298182	
S. obscurum	Greenland	K.I. Flatberg 208-06	TRH	JN000207	JN000135	
S. olafii	Greenland	K.I. Flatberg 177b-06-2	TRH	MG586078	MG586085	
S. priceae	Bolivia	M.J. Price, S.P. Churchill & Z. Mogambo 1268	MICH	MF362562	AY298220	MG586059
S. quinquefarium	Norway	J. Shaw 9682	DUKE	AY309769	AF192608	MG586060
S. rubellum	Norway	J. Shaw 1268	DUKE	KU725473	KU725473	
S. rubellum	Norway	J. Shaw 9679	DUKE			MG586061
S. rubiginosum	Norway	J. Shaw 9630	DUKE	MF362568	AF192609	MG586062
S. russowii	Finland	J. Shaw 9739	DUKE	MF362570	AY298036	MG586063
S. sitchense	USA: Alaska	R.E. Andrus 10097	DUKE			MG586064
S. skyense	United Kingdom	K.I. Flatberg s.n.	H	MF362573	AF192611	
S. subfulvum	USA: Alaska	R.E. Andrus 8878	DUKE	MF362584	AY298296	MG586065
S. subnitens	Norway	J. Shaw 9723	DUKE	AY309775	AY298303	MG586066
S. subtile	USA: New Jersey	J. Shaw 10266	DUKE	MF362587	AY298318	MG586067
S. tenerum	USA: North Carolina	J. Shaw 9335	DUKE	AY309776	AF192588	MG586068
S. tescorum	USA: Alaska	R.E. Andrus 11073	BING	JN000211	JN000141	
S. violascens	Isle Amsterdam			MF362591	MF362371	
S. warnstorfii	Finland	J. Shaw 9818	DUKE	MF362592	AY347102	
S. wulfianum	Estonia	B. Shaw 16497	DUKE	KU725459	KU725459	
S. wulfianum	Finland	J. Shaw 9855	DUKE			MG586070

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TABLE 2. (Continued)

Taxon	Locality	Collector, coll. no.	Herbarium	trng	trnl	atgc89
Outgroups:						
S. fallax	Estonia	J. Shaw 17084	DUKE	KR067370	KR06739	
S. compactum	USA: North Carolina	J. Shaw 16945	DUKE	KU725453	KU725453	
S. palustre	USA: Connecticut	B. Goffinet 10575	CONN	KU726621	KU726621	
S. teres	Norway	K.I. Flatberg, S. Sastad & K. Thingsgaard 309-00	DUKE			MG586069
S. subsecundum	USA: Alaska	J. Shaw 14226	DUKE	EU431443	EU431664	

Feulgen densitometry

Flow cytometry was not possible to perform because of old age of all the herbarium specimen. Therefore, Feulgen densitometry was used to evaluate the ploidy level of the new species. This method reliably determine ploidy levels for *Sphagnum* herbarium specimens (Temsch *et al.* 2004). The quantitative application of the method followed Feulgen and Rossenbeck (1924) and especially Greilhuber and Temsch (2001). Meristematic tissue of four representative herbarium specimens of *S. incundum* and one of *S. warnstorfii* (reference sample, see below) was fixed in a mixture of methanol and acetic acid (MA3:1) overnight in the refrigerator, transferred to ethanol (96%) and stored at–18°C until use. Primary root tips of *Pisum sativum* ´Kleine Rheinländerin´, which were also fixed in MA3:1 served as the internal standard. The plant material was hydrated and subsequently hydrolyzed in 5N HCl for 60 min at 20.0°C. Then, it was rinsed three times in water and stained in Schiff´s reagent at least 2.5h at room temperature or overnight in the refrigerator. The stained meristems were then washed six times in SO_2-water and squashed on slides in 45% acetic acid. From each preparation, two *Sphagnum* sp. and two *Pisum sativum* slides were prepared. The slides were frozen on a cold plate in order to remove the coverslip, fixed in 96% ethanol and air-dried.

Measurements were conducted on the Cell Image Retrieval and Evaluation System (CIRES, Kontron, Munich, Germany) using 63x magnification and a Sony CCD camera (Sony Electronics Inc. NY, USA) on a Zeiss Axioscope microscope (Carl Zeiss, Vienna, Austria). Ten telophase and 10 prophase nuclei were measured per resulting slide. For ploidy evaluation, the ratio between the mean *Sphagnum* sp. / mean *Pisum sativum* 2C IODs (IODR) were calculated and compared with those of a known reference. Here we used one *Sphagnum warnstorfii* herbarium sample of the same age as the *S. incundum* samples. *Sphagnum warnstorfii* is known to be haploid (n=x, Temsch *et al.* 1998).

Results

Morphological variation, combined with molecular data, supports the interpretation that the new *Acutifolia* morph is morphologically and genetically distinct. We hereafter call it *Sphagnum incundum* (see description/typification below).

Molecular analyses-microsatellites

Only one allele was identified for each microsatellite marker in all four species in the *S. subnitens* complex, suggesting that the gametophytes of these species are haploid. All eight microsatellites amplified in all four species, except marker 17 that had missing data for most samples of *S. incundum*. Thus, we excluded marker 17 from the haplotype analysis in SPLITSTREE4, as missing data affect estimates of genetic distances. However, this marker was included in the STRUCTURE analysis. For the other markers, amplification failed in one *S. subnitens* sample for marker 12 (only one allele was otherwise observed across the four species), and in two samples of *S. flavicomans* for marker 68.

Evanno's ΔK indicates that there is likely two genetic clusters in the microsatellite dataset of the *S. subnitens* complex, while the Best K option implemented in CLUMPAK indicates K=4 (Probability of 0.84). The STRUCTURE analysis shows that *Sphagnum incundum* plants form a genetic group distinct from *S. subnitens* and *S. subfulvum* (Figure 1). The same genetic group (blue) is also present in *S. flavicomans* when the number of genetic clusters is set at two (K = 2). *Sphagnum flavicomans* does not share any haplotypes with *S. incundum*, but markers 1 and 12 have identical alleles in the two species across all specimens. In addition, marker 68 with missing data in two out of three samples of *S. flavicomans* has the same allele as in *S. incundum*. When K = 3, *S. subnitens* and *S. subfulvum* are separated in different genetic groups. Increasing the number of genetic groups to four does not improve the resolution among species. The SPLITSTREE4 haplotype network corroborates inferences from STRUCTURE; the four species in the *S. subnitens* complex occur on different branches in the network (Figure 2). Five haplotypes were recognized in *S. incundum*, and these are highlighted in Figure 2. Four of the *S. incundum* haplotypes are only found once in the dataset, while 11 specimens belong to one common haplotype that was found at all locations in eastern North America and western Greenland, but not in western North America. Three of the haplotypes are found in Inukjuak, Quebec, and two haplotypes are found in Anchorage, Alaska.

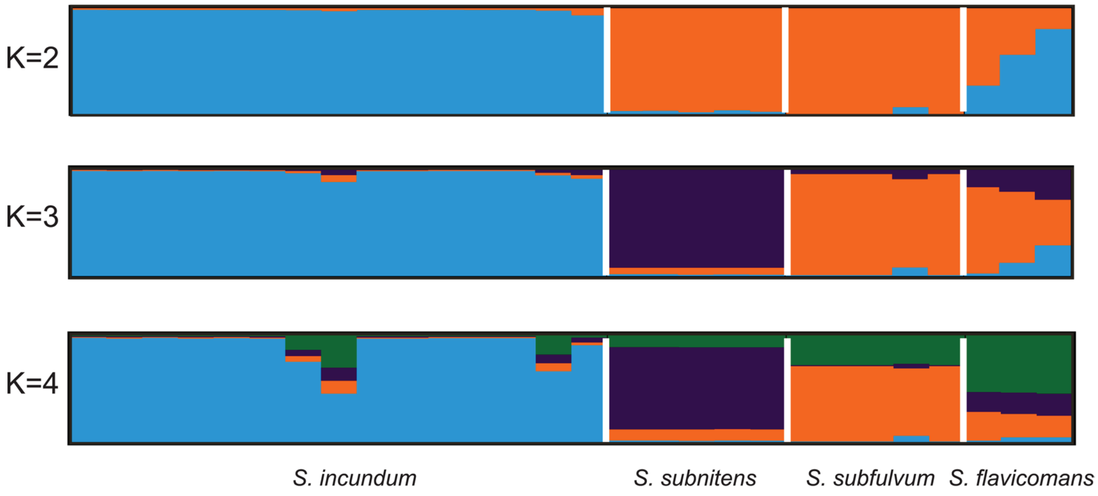

FIGURE 1. STRUCTURE analysis using microsatellite data shows that *Sphagnum incundum* form a separate genetic group from *S. subnitens* and *S. subfulvum*. *Sphagnum flavicomans* seems to be a mixture of the recognized genetic groups. The upper panel shows data separated in two genetic groups, the middel panel shows the data separated in three genetic groups, and the lower one show the data separated in four genetic groups.

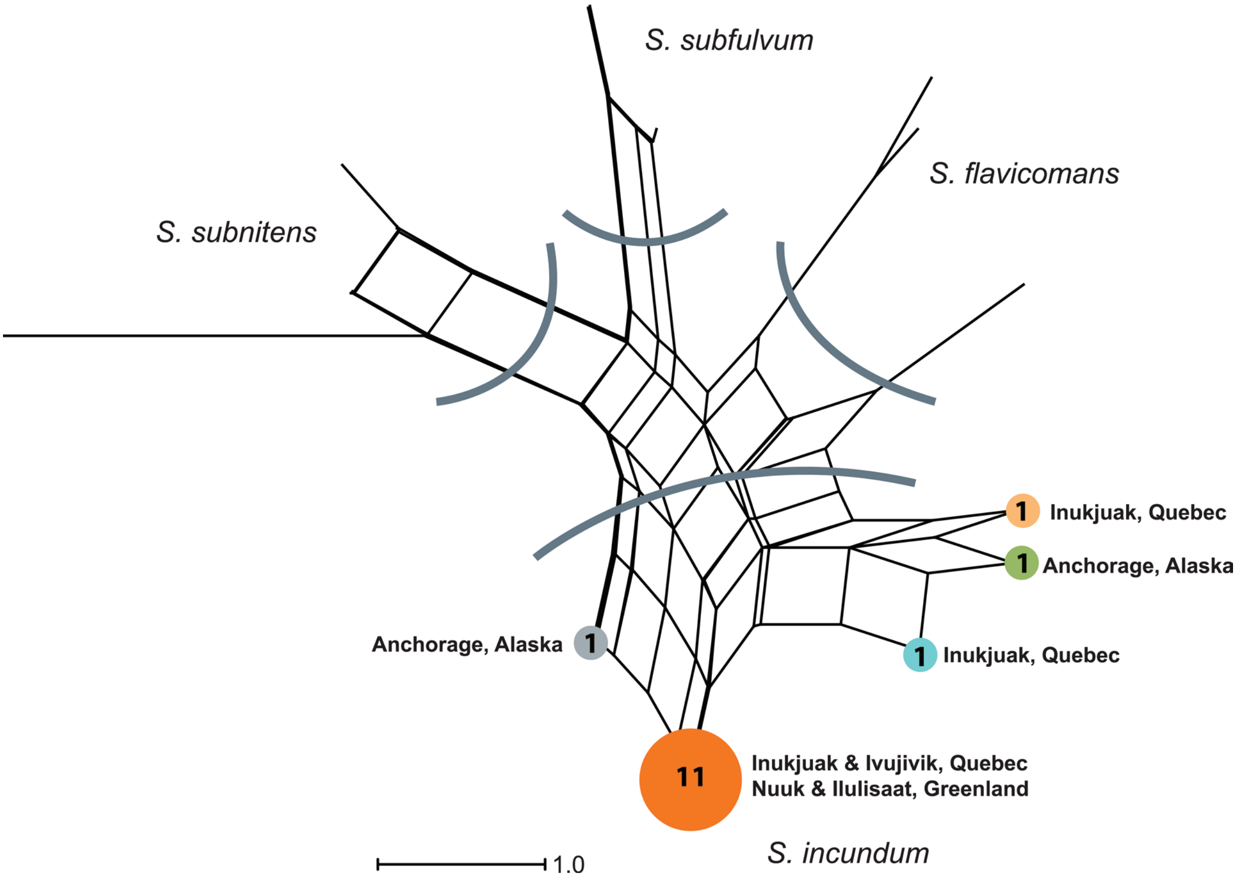

FIGURE 2. Haplotype network constructed in SPLITSTREE4 based on genetic distances calculated between all specimens using microsatellite data. The network shows that the four species in the *S. subnitens* complex are separated into individual branches. The five haplotypes recognized in *S. incundum* are highlighted in different colors. The number of individuals for each haplotype are given in the circles and the sizes of the circles corresponds to sample size. The geographical location are given for each haplotype of *S. incundum*.

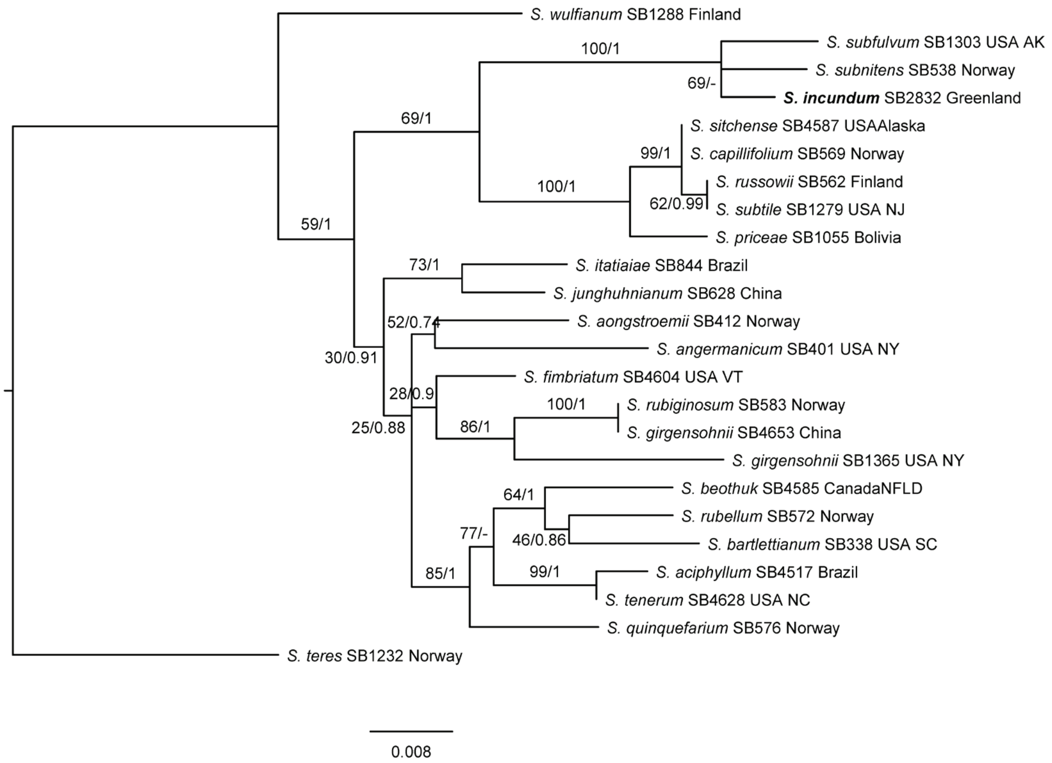

FIGURE 3. ML reconstruction of phylogenetic relationships among *Acutifolia* species based on the nuclear gene *atgc*89. Maximum likelihood support are shown above branches.

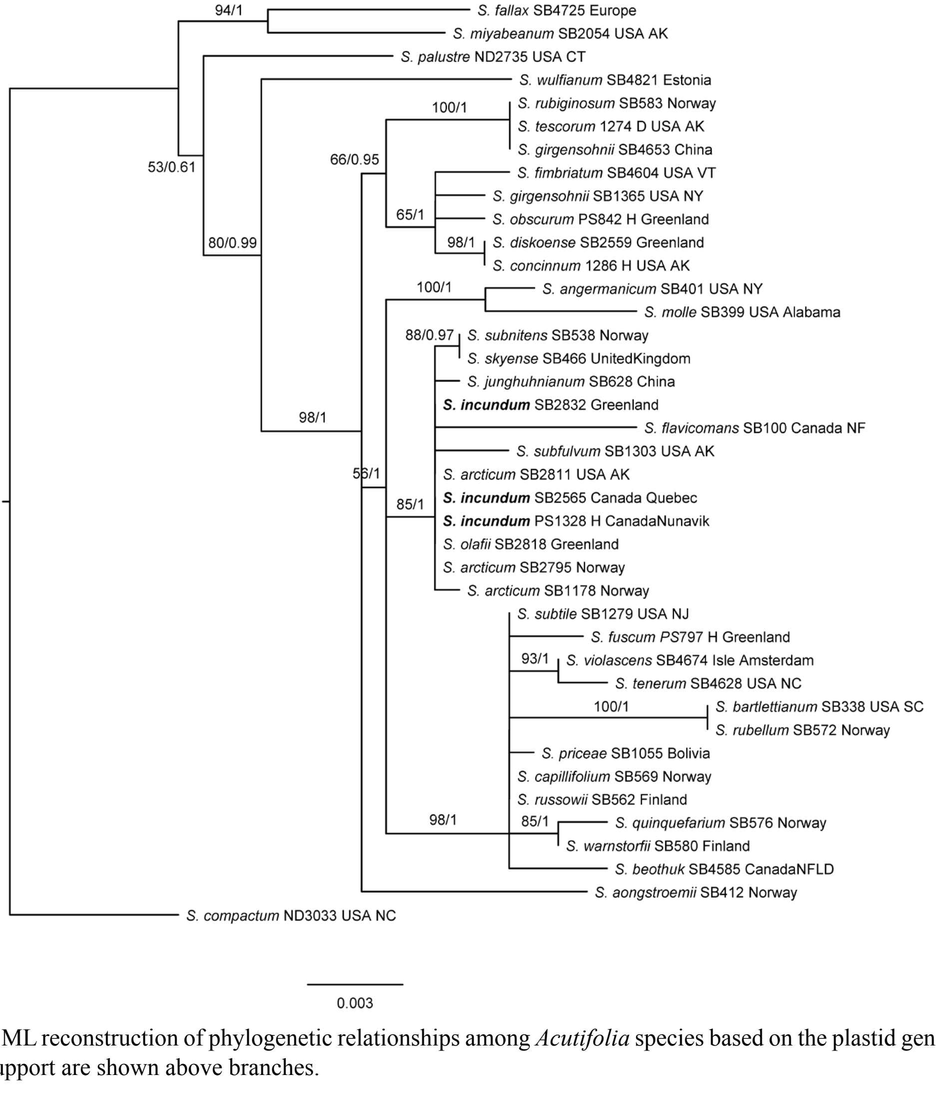

FIGURE 4. ML reconstruction of phylogenetic relationships among *Acutifolia* species based on the plastid gene *trn*G and *trn*L. Maximum likelihood support are shown above branches.

Molecular analyses-sequences

The ML reconstruction of relationships among *S. subnitens* complex species within subg. *Acutifolia* show that *S. flavicomans, S. incundum, S. subfulvum* and *S. subnitens* group together and are close relatives, both for nuclear DNA (Figure 3) and plastid DNA (Figure 4). Unfortunately, no nuclear sequences from *S. flavicomans* were obtained. We present maximum likelihood trees from RAXML with ML boostrap support/Bayesian posterior probabilities above branches. *Sphagnum incundum* has identical plastid sequences as the allodiploids *S.* × *arcticum* Flatberg & Frisvoll (1984: 143) and *S.* × *olafii* Flatberg (1993: 613).

Morphological analyses

In the field, *S. incundum* is recognized by (1) the slender habit of the shoots with tightly arranged and crowded branch fascicles with fairly short divergent branches covered by non-ranked leaves, (2) pale brown to brown-orange capitula usually with a distinct tinge of purple-red, and (3) a pale brownish stem. Microscopic examinations reveal (4) narrowly lingulate stem leaves with narrowly acute to acute-obtuse, and varyingly truncate apices, narrowly to moderately expanded proximal end bordered, common occurrence of delicate fibrils in their distal part, and narrow and S-shaped distal hyalocysts, (5) lanceolate-ovate to elliptic-ovate branch leaves evenly tapering above, with fairly long and rather narrow hyalocysts in distal leaf part with elliptic, semi-circular to ± circular pores on the convex surface, occupying between 1/3 and 1/2 of cell width. In dry herbarium plants, the leaves of the innermost capitulum branches are straight in their distal part.

Differences in stem and branch leaf size and shape (Figure 5) and differences in hyalocyst sizes (Figure 6) were explored by PCA (results not shown). Outliers were removed and the mean of each specimen (shoot) were used in the analysis. The result showed that the four species are somewhat separated, but also overlap in morphometric characters. Stem leaves are longest in *S. flavicomans* and shortest in *S. subfulvum* (Figure 5, Table 3), while stem leaf length in *S. subnitens* and *S. incundum* are in between. For branch leaves, *S. flavicomans* and *S. subnitens* have the longest leaves, while *S. incundum S. subfulvum* have shorter leaves (Table 3). The largest branch leaf hyalocysts (Figure 6, Table 3) are found in *S. flavicomans*, while *S. incundum* and *S. subfulvum* have the shortest branch leaf hyalocysts. Among the four species, *S. subfulvum* seemingly has the shortest and widest stem leaf hyalocysts (Figure 6) on the distal part surface of the leaves. *Sphagnum incundum* can be separated from *S. subnitens* and *S. flavicomans* by narrower and shorter stem leaf hyalocysts (Figure 6), even though hyalocyst sizes may vary within all four species (Table 3). Most importantly, *S. incundum* has clearly more S-shaped chlorocysts and hyalocysts than the three other species. Morphological differences comparing the four species in the *S. subnitens* complex are listed in Table 3.

Pore structure of the hyalocysts on the convex surface of the branch leaves can also be used to separate the four species. This is easiest to see in the median distal leaf part. *Sphagnum flavicomans* has more narrow-elliptic pores than the other species. The pores in *S. incundum* and *S. subfulvum* are more widely elliptic to elliptic-semicircular in shape. However, the pores of *S. incundum* are relatively smaller. *Sphagnum subnitens* is most similar to *S. incundum*, but has fewer, somewhat smaller and more circular-shaped pores.

Sphagnum flavicomans is the only species in the *S. subnitens* complex with stem leaves ordinarily furnished with hyalocyst fibrils. These are confined to the distal part of the leaves, and are conspicuously delicate. Similarly, *S. incundum* has frequent occurrence of leaves with similar delicate fibrils in the distal parts of the leaves. Such fibrils are usually absent in stem leaves of *S. subnitens* and *S. subfulvum*, but occasionally a few fibrils can be seen near the distal leaf end. Usually, *S. flavicomans* has some hyalocysts with a few and often irregularly shaped pores in the distal part of the leaves. Such pores occur only occasionally close to the distal leaf ends in the other three species.

Spore sizes within the *S. subnitens* complex seems to be very similar. The spores investigated in one capsule of *S. incundum* from the Anchorage area, Alaska (TRH B-741567) have a diameter of (24–)26–27(–29) µm. Sjörs (1944) reports the diameter of mature spores in *S. subfulvum* to be 28–31 µm, and about 27 µm in *S. subnitens*, while Daniels and Eddy (1990) give diameters of 28–29 and 26–32 µm, respectively. Cao and Vitt (1986) report the spore diameter of *S. subfulvum* to 26–30 µm and to 25–29 µm in *S. subnitens*. McQueen and Andrus (2007) give a spore diameter of 27–32 µm in *S. flavicomans*.

Feulgen densitometry

The mean IODR of *Sphagnum incundum* was 0.100 compared to *S. warnstorfii* with a mean IODR of 0.107. Both species vary only 1.07-fold. Therefore, the ploidy levels were unequivocally determinable as DNA-haploid ($n=x$) in all four samples (Figure 7). Notably, the stainability of the 10-year-old herbarium samples seem to be almost as in freshly prepared fixations. The IODR from the herbarium sample of *S. warnstorfii* varied only 0.985-fold from freshly fixed material (IODR=0.109, Temsch *et al.* 1998).

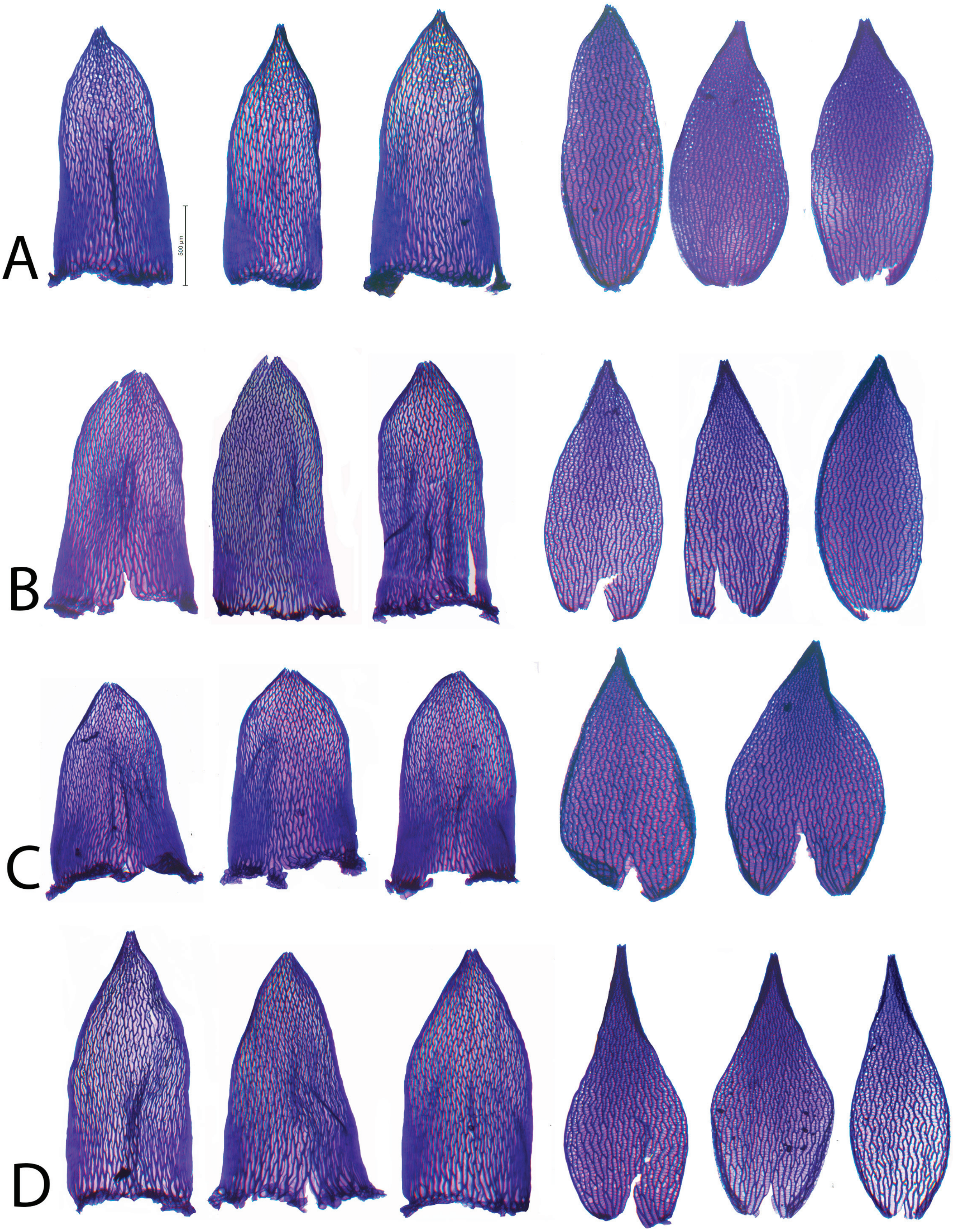

FIGURE 5. Stem (left) and branch leaf (right) shapes in the *Sphagnum subnitens* complex. A: *S. flavicomans* (TRH B-727084). B: *S. incundum* (TRH B-9718). C: *S. subfulvum* (TRH B-158979). D. *S. subnitens* (TRH B-155847).

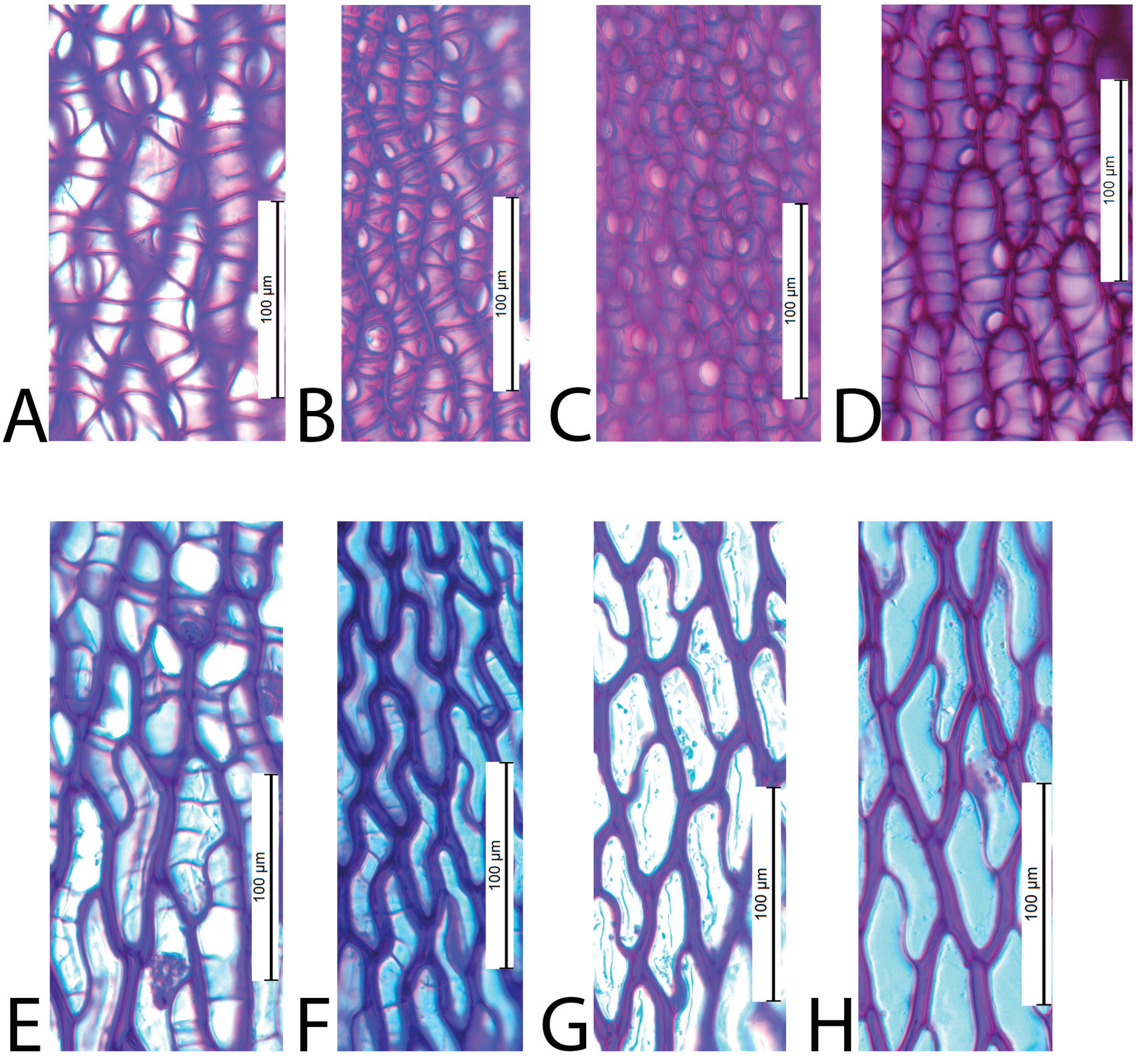

FIGURE 6. Hyalocyst shapes and pore structure on distal end convex surface of divergent branch leaves (above) and stem leaves (below) in the *Sphagnum subnitens* complex. A,E: *S. flavicomans* (TRH B-727084). B,F: *S. incundum* (TRH B-9718). C,G: *S. subfulvum* (TRH B-158979). D,H. *S. subnitens* (TRH B-155847).

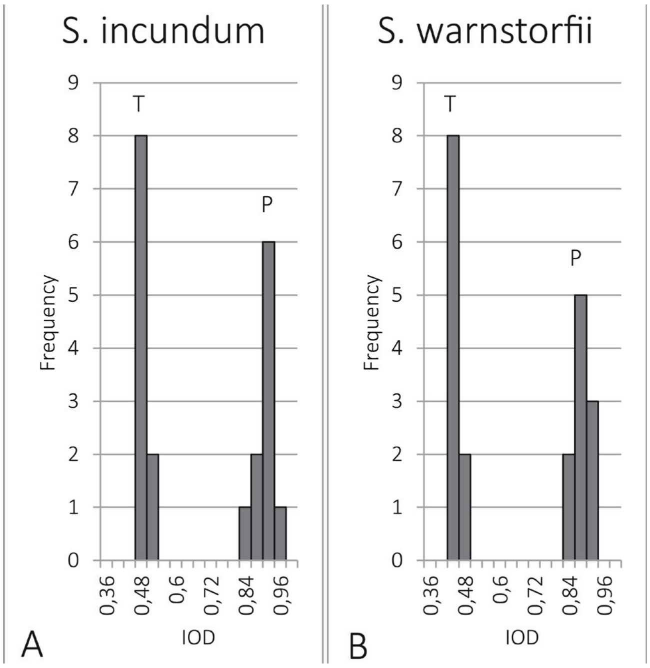

FIGURE 7 The histograms show the nuclear integrated density values (IOD) of *Sphagnum incundum* (A) and *S. warnstorii* (B, with ploidy level known to be haploid). T = nuclei in telophase (1C), P = nuclei in prophase (2C).

TABLE 3. Comparison of morphological characters of four species in the *Sphagnum subnitens* complex.

Character	*S. flavicomans*	*S. incundum*	*S. subfulvum* subs. *subfulvum*	*S. subnitens* subsp. *subnitens*
Shoots	coarse	slender and rather small-sized	slender to moderate-sized	slender to moderate-sized
Capitulum				
colour	brown	pale brown, brown-orange to purple-red	pale brown to yellowish brown	pink-purple-red to brown-red
shape	domed-shaped	rather flat	rather flat	flat to somewhat dome-shaped
dry leaves of innermost branches	straight, non-recurved in distal part	straight, non-recurved in distal part	straight, non-recurved in distal part	markedly recurved in distal part
Stem colour	dark brown to deep blood-red	pale brown	pale to most commonly dark brown	pale to most commonly dark purple-red to brown-red
Outer stem cortical pores	aporose to occasionally present	aporose	aporose	aporose
Stem leaves				
length mm (mean ± SD; n=25)	1.70 ± 0.10	1.53 ± 0.08	1.33 ± 0.10	1.58 ± 0.04
shape	narrowly elongate-lingulate	narrowly lingulate	broadly lingulate to lingulate-triangular	moderate broadly lingulate-triangular
apex	acuminate and often tubularly inrolled	narrowly acute to acute-obtuse	broadly acute to acute-obtuse	broadly acuminate
proximal end cell border expansions	moderately expanded, occupying about 0,30–0,60 of proximal end leaf breadth	narrowly to moderately expanded, occupying about 0,25–0,40 of proximal end leaf breadth	markedly expanded occupying about 0,50–0,60 of proximal end leaf breadth	narrowly expanded, occupying about 0,20–0,30 of proximal end leaf breadth
fibrillosity cv surface	usually delicately fibrillose in distal part of leaf	efibrilloe to common delicately fibrillose in distal part of leaf	efibrillose	efibrillose to occasionally delicately fibrillose in distal end part of leaf
porosity cv surface	usually with some circular to irregularly shaped pores in distal part of leaf	aporose to occasionally with a very few ± circular pores near distal end of leaf	aporose	aporose to rarely with a ver few ± circular pores near distal end of leaf
hyalocyst shape in distal end median surface	long and wide	fairly short and narrow, strongly S-shaped	short and narrow	long and wide
approx. size of hyalocysts in distal end median surface	66–179 µm long and 15–53 µm wide	49–130 µm long and 9–30 µm wide	57–121 µm long and 14–38 µm wide	58–134 µm long and 15–39 µm wide
Branch leaves				
length mm (mean ± SD; n=25)	1.62 ± 0.11	1.46 ± 0.14	1.42 ± 0.11	1.64 ± 0.21
shape	elliptic-ovate	lanceolate-ovate to elliptic-ovate	ovate	lanceolate-ovate
apex	evenly tapering, often distinctly dentate	evenly tapering, obscurely dentate	evenly tapering, obscurely dentate	markedly tapering , obscurely dentate
hyalocyst shape in distal end median surface	long and wide	fairly long and rather narrow	rather short and narrow to fairly wide	fairly long and narrow

...continued on the next page

TABLE 3. (Continued)

Character	*S. flavicomans*	*S. incundum*	*S. subfulvum* subs. *subfulvum*	*S. subnitens* subsp. *subnitens*
approx. size of hyalocysts in distal end median surface	79–178 µm long and 12–26 µm wide	65–162 µm long and 8–22 µm wide	66–148 µm long and 8–24 µm wide	98–170 µm long and 9–23 µm wide
hyalocyst pores on distal end convex surface	narrowly elliptic to semi-circular, usually occupying less than 1/2 of cell width	elliptic, semi-circular to ± circular, usually occupying between 1/3 and 1/2 of cell width	elliptic to semi-circular, often occupying 1/2 or more of cell width	semi-circular to circular, usually occupying less than 1/3 of cell width
Sexuality	dioicous	dioicous or andro-polyoicous	monoicous (or andro-polyoicous?)	monoicous

Discussion

Morphological examinations and comparisons with other species in the *S. subnitens* complex support the distinctness of the morph in question. Genetic analyses further support this. We therefore conclude that this justifies the description of *Sphagnum incundum* as a new species.

Sphagnum incundum is gametophytically haploid based on Feulgen densitometry. This is also indicated by the number of alleles found at each loci in microsatellite data (Ricca *et al.* 2008, Karlin *et al.* 2014). The new species seems to be genetically rather uniform based on microsatellite data, but this could change as more markers and specimens are genotyped. The species is well-separated from, but closely related to the other species in the *S. subnitens* complex in terms of microsatellite markers and both nuclear and chloroplast DNA sequences. The resemblance between *S. incundum* and *S. flavicomans* using microsatellite data might be an artifact of rather few markers and missing data, as the size of the alleles identified at some of the loci are quite different. We cannot determine at present if these size differences are due to flanking regions or repeat numbers per se. This pattern is not evident in the plastid genes, as *S. flavicomans* is separated from *S. incundum* by a long branch in the maximum likelihood tree. More data will likely resolve additional genetic differentiation between these two species.

Differences in leaf size measurements among the four species in the *S. subnitens* complex show large variation within species and overlap between species. These findings are not surprising as the species are closely related. In addition, our investigated plants are specimens collected from different geographical regions, and from unknown microhabitats. As shown by Flatberg (1985), *S. subfulvum* and *S. subnitens* express considerable phenoplastic variation in leaf shapes and sizes correlated to wetness and richness conditions along local mire ecogradients. These aspects are likely to influence upon and obscure interspecific leaf size relationships found between the four species. *Sphagnum incundum* has narrowly lingulate stem leaves that can be distinguished from the more broadly lingulate to lingulate-triangular, shorter and more acute-obtuse stem leaves of the two subsp. of *S. subfulvum*. *Sphagnum subfulvum* can also be separated from the three other by more widely expanded proximal end border of narrow cells. It is more problematic to separate the stem leaves of *S. incundum* and the two subsp. of *S. subnitens*, as they are more similar in size and shape. However, microscopic examination reveals that *S. subnitens* has fewer, smaller and more circular hyalocyst pores on the convex distal surface of the branch leaves than *S. incundum* (see Flatberg 1985, Figure 38) and more clearly S-shaped hyalocysts in the stem leaves. Dry plants of *S. incundum* also have straight, non-recurved branch leaves in the innermost part of the capitula. These are recurved in both subsp. of *S. subnitens*. The stem leaves of *S. incundum* and *S. flavicomans* are more narrowly lingulate in shape than in the two other species, but the leaf apices of *S. flavicomans* are more acuminate and often tubularly inrolled. The branch leaves of *S. incundum* are typically somewhat shorter than in *S. flavicomans* and *S. subnitens*, and longer than in *S. subfulvum*, but this is a variable character. The branch leaf shape in *S. incundum* varies between lanceolate-ovate and elliptic-ovate, and in this respect shows closer similarity to *S. flavicomans* than to *S. subfulvum* and *S. subnitens*. *Sphagnum subfulvum* has conspicuously wider branch leaves, and *S. subnitens* has more narrow-pointed leaf apices. Leaf apex dentations are variable in all four species, and their appearance depends on the degree of involutness of the distal end leaf margins. *Sphagnum flavicomans* shows the most distinct apex dentation.

Morphological variation within the *S. subnitens* complex (Flatberg 1985) has led to confusion among bryologists. Even though *S. flavicomans* shows fairly homogeneous morphology, both *S. subfulvum* and *S. subnitens* express considerable intraspecific morphological variation. Most confusing is probably the variation in capitulum colour, which has led to misidentifications and taxonomic disagreement among bryologists. *Sphagnum subfulvum* commonly has yellow-brown to pale brown capitula, but sometimes has shoots with distinct pink-red to purplish-brown capitula within its boreal distribution in Europe and eastern North America (subsp. *purpureum* Flatberg (1985: 50)). This variant has mistakenly been misinterpreted as *S. subnitens* in eastern North America (Crum 1984), where *S. subnitens* is unknown. In reverse, *S. subnitens*, typically with pinkish to purplish-brown capitula, may occur in a variant with pale brownish capitula lacking red colour (subsp. *ferrugineum* Flatberg (1985: 50), var. *ferrugineum* (Flatberg) M.O. Hill in Blockeel & Long (1998: 26). This variant has erroneously been recorded as *S. subfulvum* from Atlantic regions in Europe, and was cited from Wales (Sjörs 1944) and Ireland (Moen and Synnott 1983). The two above subspecific colour morphs are both well connected to their respective species by other diagnostic leaf and cell characteristics (Flatberg 1985). However, genetic data comparing these four variants are still lacking. Unpublished genetic data (Shaw *et al.*) support the interpretation that *S. subnitens* in particular has complex intraspecific genetic structure.

Sphagnum incundum varies in capitulum colour from pale brown to brown-orange with a distinct tinge of purple-red. Unfortunately, the low number of field observations of *S. incundum* are insufficient to define the variation in capitulum colour more precisely. In the field, this variation makes it difficult to separate *S. incundum* shoots from *S. subfulvum* subsp. *subfulvum* and *S. subnitens* subsp. *ferrugineum* with pale brown capitula and *S. subfulvum* subsp. *purpureum* and *S. subnitens* subsp. *subnitens* shoots with brownish pink-red capitula (Flatberg 1985).

Flatberg (1985) revised the identity of specimens with brown capitula from four herbarium collections labelled *S. subfulvum* from West Greenland, Alaska, U.S.A. and Northwest Territories, Canada to his *S. subnitens* subsp. *ferrugineum*. However, re-examination of leaf slide mountings of these herbarium specimens has shown that these in fact belong to *S. incundum*. The leaf illustrations of subsp. *ferrugineum* in Flatberg (1985, Figurs 6 and 10) from West Greenland and Umiat, Alaska also refer to *S. incundum* (see Specimen list under description below). The leaf illustration of *S. subfulvum* from Ritenbank, W Greenland in Sjörs (1944, Figure 2f) is also *S. incundum*. These findings excludes *S. subnitens* subsp. *ferrugineum* as a member of the *Sphagnum* flora of North America. Two specimens collected by K.I. Flatberg near Bethel, Alaska, and named *S. subfulvum* cf. *purpureum* (TRH B-741566 and 741567), also belong to *S. incundum* based on leaf and cell characteristics.

The distribution of species in the *S. subnitens* complex differ. The current known distribution range of *S. incundum* is from Alaska, USA, in the west to West Greenland in the east, where it is found within the boreal and arctic zones. *Sphagnum flavicomans* is found along the eastern coast of North America from New Jersey to Newfoundland and Labrador (Crum 1984, McQueen and Andrus 2007). *Sphagnum subfulvum* mainly occur in boreal regions of North America and Europe, but also in temperate and sub-meridional regions in southern Europe at higher elevations and in arctic Greenland (McQueen and Andrus 2007). *Sphagnum subnitens* is found in most European countries (Daniels and Eddy 1990), along the Pacific coast of North America from Oregon to boreal parts of Alaska including the Aleutians (McQueen and Andrus 2007), and New Zealand (Karlin *et al.* 2011). Thus, *S. incundum*, together with *S. subfulvum*, has a boreal to arctic distribution, while the other species are boreal to temperate.

The sexual status of *S. incundum* is somewhat uncertain. However, the record of pure male plants (TRH B-9983) from West Greenland, and the seemingly lack of antheridial branches in capsule-producing shoots both in field and herbarium collections, suggest that *S. incundum* is dioicous. The rather few observations of sporophyte-bearing plants in the field also points in this direction. But, antheridial branches can be rather similar to normal divergent branches in the *S. subnitens* complex and are thus easily overlooked. *Sphagnum flavicomans* is reported to be dioicous (Osvald 1940, Crum 1984, McQueen and Andrus 2007). The rarity of sporophytes in this species supports this. *Sphagnum subfulvum* and *S. subnitens* are both commonly found with sporophytes, particularly the latter. Sjörs (1944), Crum (1984), Daniels and Eddy (1990), McQueen and Andrus (2007) and Hölzer (2010) all report *S. subfulvum* to be monoicous. The same applies to *S. subnitens*, but Crum (1984), Daniels and Eddy (1990) and Hölzer (2010) mention occasional occurrences of dioicous plants in this species. It is uncertain whether these observations refer to records of separate female and male plants, or to the presence of monoicous and male plants. The latter kind of sexual diversity seems to be the rule in many if not all *Acutifolia* species recorded to be monoicous (Flatberg 2013), and such species can be termed andro-polyoicous. To sort out pure female plants without sporophytes, is practically impossible.

Sphagnum incundum seems to be very closely related to the arctic allodiploid species *S.* × *arcticum* and *S.* × *olafii*, as these three species have identical plastid DNA sequences. Of the five allodiploids known within subg. *Acutifolia*, only *S. subnitens* within the *S. subnitens* complex seems to have been involved in allopolyploid speciation. It has been hypothesized to be one of the parents of the allodiploid *S.* × *skyense* Flatberg (1988: 101) (Shaw *et al.* 2005). The same authors also indicate that *S. subnitens* is a possible parent of the two arctic allodiploid species *S.* × *arcticum* and *S.* × *olafii*. However, our data indicates that *S. incundum* rather than *S. subnitens* may be the female parent of these two species. Moreover, *S. incundum* seems to be the female parent of a new inter-subgeneric allotriploid species between subgenera *Acutifolia* and *Subsecunda* from Arctic Russia (Kyrkjeeide *et al.* in prep.). This indicates that *S. incundum* may play an important role in allopolyploid speciation in arctic areas.

Taxonomy

Sphagnum incundum Flatberg & Hassel *sp. nov.* (Figures 8–9)

Type:—Canada. Quebec: Nunavik. Ivujivik, 27 m a.s.l., 62°24'50.2"N, 77°54'39.6"W, leg. Bergfrid & Kjell I. Flatberg 4 Aug 2007, Flatberg 314-07, TRH B-9718. Holotype TRH; isotypes: LE, DUKE, QFA. Habitat: Intermediate, slightly sloping arctic fen.

FIGURE 8. *Sphagnum incundum* in field surface view. A: The type collection including selected holotype and isotypes. Collected in Ivujivik, Quebec, Canada, in intermediate, slightly sloping arctic fen. Photo by K. I. Flatberg, 4 July 2007. Flatberg 314-07 (TRH B-9718). B: Together with *S. squarrosum*, both with young sporophytes. From Inukjuak, Quebec, Canada, in topogenous, rich fen lawn in arctic mire. Photo by K. I. Flatberg, 14 August 2007. Flatberg 451-07 (TRH B-9999).

Diagnosis:—*Sphagnum incundum* is in macro-morphology recognized by slender shoots with predominantly brown-orange to purple-red capitula and straight and non-recurved leaves on innermost capitulum branches on dry plants. In micro-morphology, it is foremost recognized by narrowly lingulate stem leaves with acute to acute-obtuse apices, strongly S-shaped stem leaf hyalocysts with common occurrence of faint fibrils in distal leaf-parts, and divergent branch leaf hyalocysts on distal end convex surfaces with pores usually occupying between 1/3 and 1/2 of cell width. The new species is gametophytic haploid and closely allied morphologically to *S. flavicomans*, *S. subfulvum*, and *S. subnitens*.

Sphagnum subg. *Acutifolia* sect. *Acutifolia*. *Gametophytic plants* haploid, varyingly medium-sized. *Capitulum* (Figure 8) rather flat, indistinctly 5-parted from above. Predominantly pale brown-orange usually with distinct tinge of purple-red (Figure 8), sometimes markedly so in exposed habitats, to more greenish brown in more shaded habitats. *Capitulum branches* rather straight to varyingly incurved with acute-obtuse ends. Leaves on innermost branches in dry capitula narrowly tapering above and non-recurved. *Terminal bud* inconspicuous and often hidden by innermost branches. *Stem* greenish in upper part, pale brownish in lower parts; in transverse sect. with markedly differentiated, (2–)3–4(–5) cells wide cortex of large cells (Figure 9C), and with a brownish sclerodermis of small, incrassate cells 3–6 cells wide, and a central medulla of large, thin-walled cells; stem cortex in superficial view (Figure 9C) non-porose. *Stem leaves* (Figure 9A) erect-patent to erect-appressed to the stem, narrowly lingulate to less commonly lingulate-triangular and sometimes somewhat involute above. Apex narrowly acute to obtuse and somewhat truncate. Border in distal half of leaf narrow, 2–4 cells wide, in proximal part widened and filling up 1/3 to 1/2 of baseline width. Mean length (n=25) 1.53 mm ± 0.08 mm (min–max: 1.14–1.67 mm), mean mid-leaf breadth 0.68 mm ± 0.06 mm (min–max: 0.54–0.68 mm): Hyalocysts in distal portion of leaves narrowly and distinctly S-shaped, in proximal portion more elongate-S-shaped, markedly larger and wider towards middle portion proximal end, efibrillose to rather commonly with some or sometimes many cells faintly fibrillose (mainly present on convex leaf surface) in distal 1/3(–1/2) of leaf, non-porose or sometimes with some cells close to distal end with one ± circular to elongate membrane gap pore, short hyalocyst close to baseline sometimes with one, large ± circular pore, with a mixture of non-septate and predominantly 2-septate cells, sometimes some cells divided in 3 to 4 parts; chlorocysts rather straight into slightly S-shaped. *Branch fascicles* moderate distantly crowded, of usually two divergent and one (rarely two) pendent branches. Divergent branches 7–12 mm long, rather straight to somewhat curved, varyingly orientated from stem dependent on growth form, shoots in dense cushions with patent-incurved branches. Pendent branch(es) about equally long as divergent ones, markedly thinner and paler and mostly covering the stem; cortex of divergent branches unistratose and dimorphic, retort cells with somewhat protruding neck. *Divergent branch leaves* non-ranked and straight to slightly secund in proximal part of branches, non-recurved when dry. Leaves from the middle of branches ovate-lancolate, evenly to rather abruptly tapering above (Figure 9E), mean length (n=25) 1.46 mm ± 0.14 mm (min–max: 1.17–1.78 mm), mean mid-leaf breadth 0.56 mm ± 0.09 mm (min–max: 0.44–0.74 mm). *Hyalocysts* in distal portion of leaf narrowly S-shaped, in proximal portion with wider outline and towards leaf base more elongate (Figure 9B). Hyalocysts on distal end convex portion of leaf 111.0 ± 20.9 µm long, 14.2 ± 3.3 µm wide (mean of 75 cells), with 3–8(–10), elliptic to semi-circular, perfect, mostly ringed pores at cell ends and along commissures. Commissural pores usually filling up less than 1/2 of cell width, pores now and then rather small, circular and free-lying; in mid-median portion with 2–4(–6) elongate-elliptic, perfect and ringed pores along the commissures. Towards leaf margins more widely elliptic to semi-circular, and towards proximal leaf end with 1–2, ± circular and large pores filling out half or more of cell width. Hyalocysts on concave surface in median leaf portions non-porose to some cells with 1(–2), large, circular, perfect and ringed, mostly somewhat free-lying pores filling out 1/2–2/3 of cell width, increasing in number towards leaf margins with usually (3–)4–6 similar pores; hyalocysts in transverse section markedly bulging on convex surface. Branch leaf chlorocysts in superficial view varyingly straight to somewhat S-shaped; in transverse sect. isosceles triangular to triangular-rectangular, in lumen shape with apical end mostly reaching convex surface. Border of leaves narrow, 2–4 cells wide, without resorption furrow. Leaves of pendant branches smaller and narrower than on divergent branches, with more elliptic shape of the commissural pores on distal convex surface (Figure 9O), and with several large circular pores in median portions of the concave leaf surface.

Sexual status: Uncertain, but seemingly dioicous or andro-polyoicous. Female plants with sporophytes and without observed antheridial branches (Canada. Inukjuak, TRH B-9993, B9994, B9998, B9999; Greenland. Ilulissat, TRH B-9981; USA. Alaska, Flatberg TRH B-9986). Male plants with antheridial branches, without sporophytes (Greenland. Ilulissat, TRH B-9983).

Male plants with short divergent antheridial branches with brownish clavate ends. Perigonial leaves ovate (Figure 9P), smaller than ordinary leaves; hyalocysts with pore structure similar to that of divergent branch leaves, but with more circular pores on their concave leaf surface, and with only weakly fibrillose cells towards proximal leaf end. Stem leaves more lingulate in shape and with more obtuse apices than in female plants.

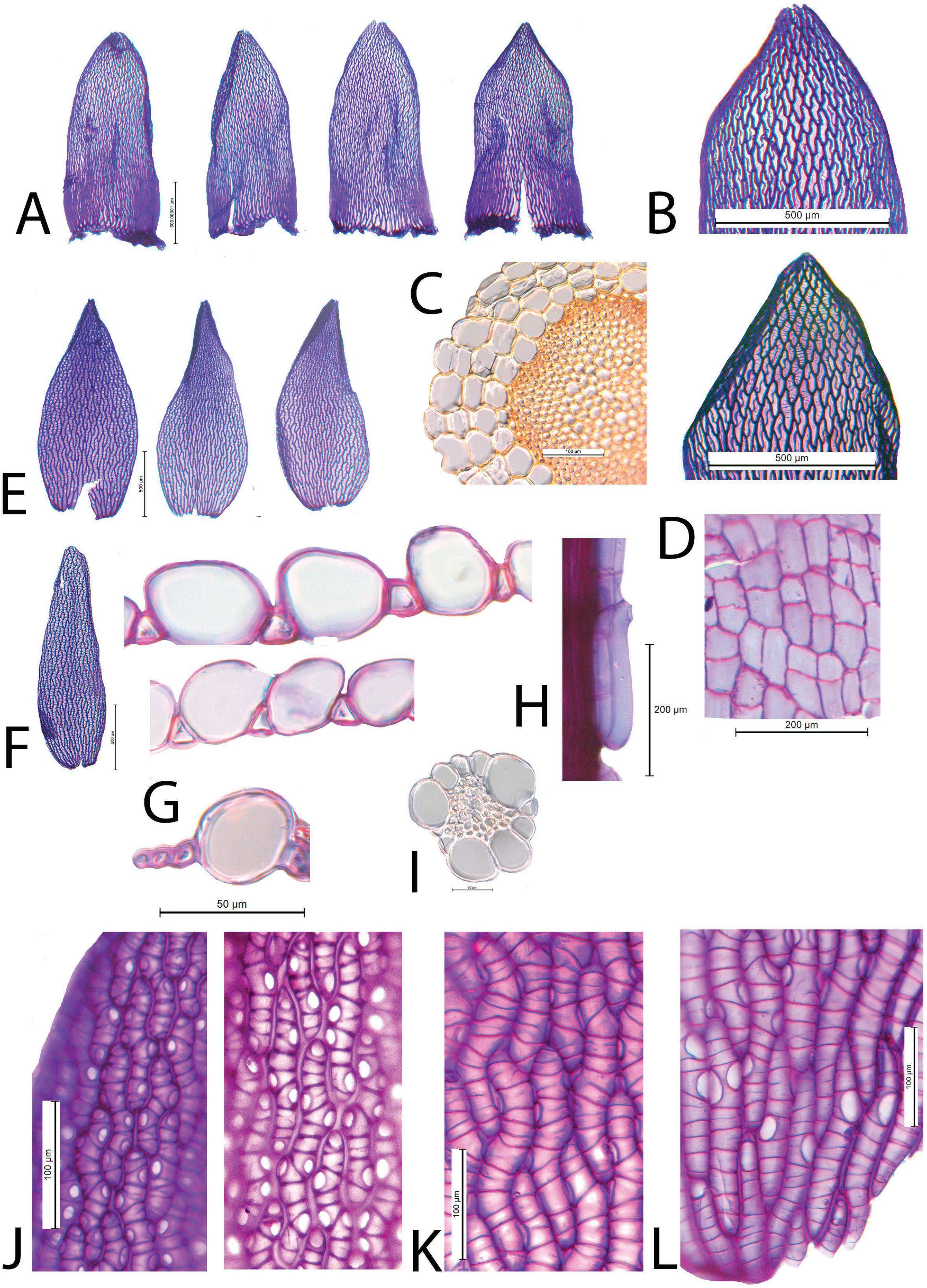

FIGURE 9 (part 1). Microscopic pictures of different morphological characters in *Sphagnum incundum*. A: Stem leaf shapes, B: Stem leaves distal part, C: Stem in transverse sect., D: Stem cortex in superficial view, E: Leaves from middle part of divergent branches, F: Pendent branch leaf, G: Branch leaves in transverse sect., H: Retort cell of branch cortex in superficial view, I: Branch in transverse sect., J–L: Cell structure on convex surface of divergent branch leaves.–J: Distal end portions.–K: Mid-median portion.–L: Proximal end portion.

Material (TRH): A: B-9998, 9981, 9718, 693715, B: B-9981, 9998, C: B-38507, D: B-9987, E: B-9998, 9718, F–I: B-9718, J: B-38515, K–L: B-9981.

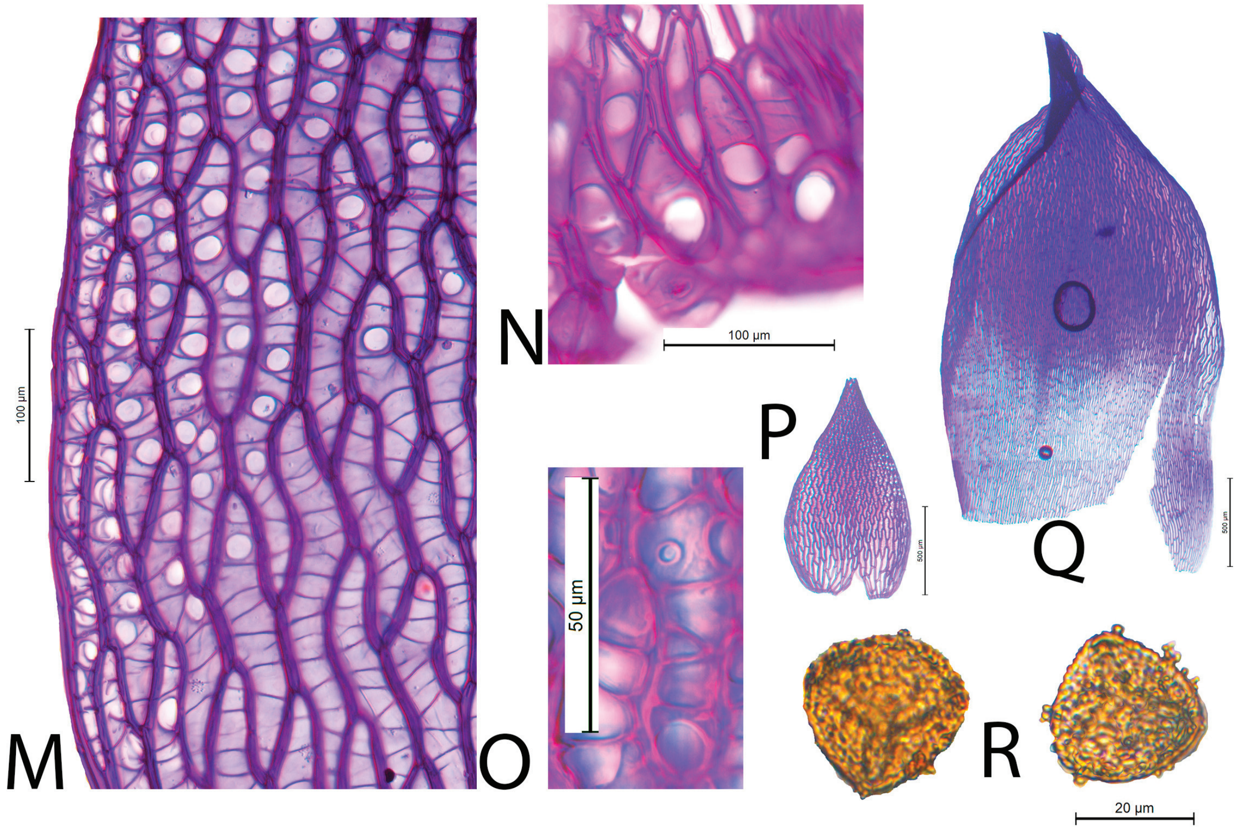

FIGURE 9 (part 2). M–N: cell structure on concave surface of divergent branch leaves.–M: Middle portion.–N: Proximal end portion, O: Distal end convex surface of divergent branch leaf with one circular, ringed, perfect and free-lying hyalocyst pore, P: Perigonial leaf from male plant, Q: Perichaetial leaf, R: Spores.
Material (TRH): M–N: B-9998, O: B-9987, P: B-9983, Q–R: B-9986.

Perichaetial leaves (Figure 9Q) varyingly broadly ovate-elliptic to lingulate along the pseudopodium, with broadly obtuse to ± tubularly innrolled apex; hyalocysts narrowly S-shaped to elongate, non-porose and efibrillose, with some cells septate in 2–3 parts.

Capsules dark brown and ± globose. Spores (Figure 9R) yellowish brown to golden brown in mass, (24–)26–27(–29) µm in diameter; on the outer surface coarsely granulate-verrucose with sometimes markedly protruding verrucae.

Etymology:—The specific epithet is derived from the Latin adjective *incundus* = pleasant, agreeable, delightful.

Distribution:—West Greenland, Canada in Quebec, Nunavut and North West territories, and U.S.A in Alaska. Currently known from the northern boreal to middle arctic vegetation zone.

Ecology:—*Sphagnum incundum* in arctic localities in West Greenland, and Nunavik, Quebec, occurs in arctic mires on shallow peat in intermediate and rich fens, partly forming small mats and low cushions on gently sloping, soligenous mire, partly growing in small patches on lawn and carpet mire. The most commonly associated sphagna in both regions were *S. concinnum* (Berggr.) Flatberg (2007: 88), *S. squarrosum, S. teres* and *S. warnstorfii* Russow (1886: 315). In the boreal Anchorage area, Alaska, it was found growing in a large fen mire on high lawn patches in topogenous, varyingly intermediate to rich fen vegetation, associated with *S. papillosum* Lind. (1872: 280), *S. subfulvum* and *S. miyabeanum* Warnstorf (1911: 321). In Bethel area, Alaska, it occurred scattered on intermediate fen lawns in tundra mire.

Specimen list:—W GREENLAND: Qaasuitsup. Ilulissat, Typilak Island, Egedesminne [= Tupilak Island, Aasiaat], [68.70000°N 52.93333°W], Holmen 16975 (S); id. Christianshåb [= Qasigiannguit], [68.820144°N 51.193242°W], Holmen 15450 (S); id. Jakobshavn [= Ilulissat], [69.216667°N 51.10000°W], 1870 Berggren (S, UPS), Holmen 12120 (S), 16986 (UPS); id. Ilulissat, S of the village, along the track to Seqinniarfik, 69.206°N 51.1205°W, ca. 70 m, 17 Jul 2006 Flatberg 186-06 (TRH B-9984), 190-06 (TRH B-9981); id. Ilulissat, S of the village, 69.2078°N 51.129°W, ca. 60 m, 17 Jul 2006 Flatberg 199-06 (with sporophytes (TRH B-9981); id. NE of the village, 69.2111°N 51.0701°W ca. 90 m, 17 Jul 2006 Flatberg 215-06 (male plants) (TRH B-9983), 216-06 (TRH B-9982); id. Sermersooq, Nuuk, E of the church yard N of Grønlands Naturinstitutt, 64°11’31,78”N 51°41’44,83”W, 1–25 m, 15 Aug 2010 K. Hassel, T. Prestø (TRH B-693795); id. Ritenbenk, 69.767°N 51.317°W, 1870 Berggren (S, UPS).

CANADA: Quebec. Nouveau-Quebéc, Rivère aux feuilles, 58°15’N 72°W. 16 Jul 1978, L. Couillard 658 (TRH B-35435); id. Lac Minto, Péninsule, 57°16’13”N 75°01’28”W, 600 ft, 23 Jul 1975, R. Gauthier 5239, A. Légère (TRH B-35430); id. Nunavik, 300 m à l’est de la rivière Kimber et 9 km au nord-ouest du lac Charlery, 61°3’27”N 72°26’48”W, 340 m, 28 Jul 2011, L. Couillard, D. Bérubé (TRH B-773451); id. Inukjuak, 58°27.109’N 78°07.173’W, 10 m, 14 Aug 2007 B. Flatberg, K.I. Flatberg 441-07 (TRH B-9989, 9990), 442-07 (TRH B-9988, 9991), 451-07 (TRH B-9998, 9999), 452-07 TRH B-9996, 9997), 460-07 (with sporophytes) (TRH B-9992, 9995), 462-07 (with sporophytes) (TRH B-9993, 9994); id. Ivujivik, 62°24.321’N 77°54.855’W, 77 m, 3 Aug 2007 B. Flatberg, K.I. Flatberg 299-07 (TRH B-38513, 38514); 62°24.837’N 77°54.660’W, 27 m, 4 Aug 2007 B. Flatberg, K.I. Flatberg 314-07 (TRH B-9718 (type), 317-07 (TRH B-38509), 319-07 (TRH B-38510, 38511), 320-07 (TRH B-38508, 38512), 339-07 (TRH B-38503, 38506, 10000), 340-07 (TRH B-38504, 38505), 342-07 (TRH B-38501, 38502); 62°23.273’N 77°52.646’W, 5 Aug 2007 B. Flatberg, K.I. Flatberg 343-07 (TRH B-38515, 38516); id. Nunavut. Baker Lake, 64.318056°N 96.0175°W, Duitilly 478 (MICH, NY); id. Northwest Territories. Mackenzie District, Virginia Falls, South Nahani River, 61°38’N 125°42’W [= 61.633333°N 125.700000°W], Marsh 4557 (NY).

U.S.A.: Alaska. Alaska Peninsula, Marsh, Naknek, Lepage 22642, 22663 (MICH), [58.739722°N 156.971667°W]; id. Anchorage area. Baxter Bog Park between Baxter Rd. and Patterson St., 61°11’30.3”N 149°45’28.7”W, 70 m, 5 Aug 2008 Flatberg 128-08 (with sporophytes) (TRH B-9986), 138-08 (TRH B-9987), id., near surroundings of the village Bethel, 60°47’N 161°49’W, ca. 20–25 m, 18 Aug 2001 Flatberg 652-01 (TRH B-741566, 741567); id. Colville River, Umiat, 69°22’N 152°08’W [69.366944°N 152.144167°W], 2 Aug 1960 Steere, Holmen, Mårtensson (Bryoph. Arctica Exsicc. 30) (H, MICH, S).

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