

The identification and distribution of *Sphagnum balticum* (Russow) C.E.O.Jensen in Britain

Des A. Callaghan, Magni Olsen Kyrkjeide, Kristian Hassel

**QUERY SHEET**

This page lists questions we have about your paper. The numbers displayed at left are hyperlinked to the location of the query in your paper.

The title and author names are listed on this sheet as they will be published, both on your paper and on the Table of Contents. Please review and ensure the information is correct and advise us if any changes need to be made. In addition, please review your paper as a whole for typographical and essential corrections.

Your PDF proof has been enabled so that you can comment on the proof directly using Adobe Acrobat. For further information on marking corrections using Acrobat, please visit <https://authorservices.taylorandfrancis.com/how-to-correct-proofs-with-adobe/>



The CrossRef database ([www.crossref.org/](http://www.crossref.org/)) has been used to validate the references. Changes resulting from mismatches are tracked in red font.

**AUTHOR QUERIES**

<b>QUERY NO.</b>	<b>QUERY DETAILS</b>
	No Queries



## The identification and distribution of *Sphagnum balticum* (Russow) C.E.O.Jensen in Britain

Des A. Callaghan <sup>a</sup>, Magni Olsen Kyrkjeide <sup>b</sup> and Kristian Hassel <sup>c</sup>

<sup>a</sup>Bryophyte Surveys Ltd, Almondsbury, South Gloucestershire BS32 4DU, UK; <sup>b</sup>Norwegian Institute for Nature Research (NINA), Trondheim, Norway; <sup>c</sup>Department of Natural History, Norwegian University of Science and Technology, Trondheim, Norway

### ABSTRACT

**Introduction.** The aim of this study is to help clarify the identification of *Sphagnum balticum* in Britain, to review its distribution, and to investigate the possible presence of hybrids between it and either *S. cuspidatum* or *S. fallax*.

**Methods.** All sites from where *Sphagnum balticum* has been recorded recently in Britain were visited in 2020, and a search was undertaken for it and other species with which it could be confused, plus possible hybrids. Samples were collected when suitable material was found. DNA was extracted from 31 shoots, each representing one field sample. Fifteen microsatellites that have been developed for *Sphagnum* species were amplified and genotyped. The genetic structure of the data was investigated using principal coordinate analysis and cluster analysis.

**Results.** The genetic analysis results support the recognition of four taxa, which correspond to four morphologically identified taxa: *Sphagnum angustifolium*, *S. balticum*, *S. cuspidatum* and *S. fallax*. There is no evidence of hybrids. Over-recording of *S. balticum* has occurred in Britain due to confusion with some forms of *S. cuspidatum* and *S. fallax*, which can exhibit some morphological characters usually used to identify *S. balticum*. An illustrated identification key is provided to help solve this problem.

**Conclusions.** *Sphagnum balticum* is a very rare species in Britain that has undergone a decline due to habitat destruction and alteration. It is presently known to survive at only three sites, of which two are within protected areas.

### KEYWORDS

Microsatellites; *Sphagnum cuspidatum*; *Sphagnum fallax*

### Introduction

*Sphagnum balticum* (Russow) C.E.O.Jensen exhibits a broad Boreo-arctic Montane Circumpolar range, mainly occurring in the tundra and northern boreal zone, and widespread in continental interiors (Hill and Preston 1998; Blockeel et al. 2014). Located towards the southern edge of its distribution, it is very rare in Britain and is a high-profile species of conservation concern, being specially protected under Schedule 8 of the Wildlife and Countryside Act 1981 (as amended) and the subject of a national conservation action plan. It is also a designated feature of some of the Sites of Special Scientific Interest where it occurs, requiring conservation agencies to maintain its population at these sites in favourable condition.

Hill (2004), which is the main reference used for *Sphagnum* identification in Britain, makes the following note about *S. balticum*: "Superficially like a strongly coloured, slender form of *S. fallax*. Useful field characters are the  $\pm$  spreading stem leaves and the smaller number of branches per fascicle. Most British plants have the branches regularly in fascicles of 3, but plants from one site had branches mainly in fascicles of 4." Identification keys in modern guides that include *S. balticum*

have highlighted a wide variety of morphological features important for its identification, sometimes conflicting. The following are generally considered to be the most important features (Isoviita 1966; Daniels and Eddy 1985; Hill 2004; McQueen and Andrus 2007; Hölzer 2010; Flatberg 2013; Laine et al. 2018; Lönnell et al. 2019; Michaelis 2019): (i) stem cortex distinct from the cylinder; (ii) fascicles comprising two spreading branches and one pendent branch; (iii) stem leaves spreading at right angles from the stem; and (iv) stem leaves with fibrillose hyalocysts. All these features are exhibited by the recently designated lectotype of *S. balticum* (Callaghan and Brinda 2022). Nevertheless, identification of *S. balticum* has sometimes proved problematic in Britain. Unusual morphotypes have been noted (Maass 1965; Hill 2004), and the occurrence of plants that appear to be intermediate with *S. fallax* has caused problems when carrying out monitoring, leading to uncertainty about the population status of *S. balticum* at sites, and suggestions that hybrids between these two species may be present (Turner 2000; Hodgetts 2006, 2008, 2011; O'Reilly 2012, 2018; Turner 2002a, 2002b). Confusion with some forms of *S. cuspidatum* is also known to have caused recent identification mistakes in Britain (personal observation),

and confusion with *S. angustifolium* has also been highlighted (Laine et al. 2018).

Cross-breeding between *Sphagnum balticum* and *S. angustifolium*, *S. cuspidatum* or *S. fallax* has not been documented, but molecular evidence shows that hybridisation occurs frequently within *Sphagnum* and that allopolyploid species are common (Shaw and Goffinet 2000; Shaw et al. 2005; Flatberg et al. 2006; Natcheva and Cronberg 2007; Karlin et al. 2009, 2010; Ricca and Shaw 2010; Ricca et al. 2011; Shaw et al. 2012; Meleshko et al. 2018). For example, *S. troendelagicum* is of allopolyploid origin, arising from hybridisation between female *S. tenellum* and male *S. balticum* (Såstad et al. 2001; Stenøien et al. 2011b). Likewise, *S. jensenii* appears to be of allopolyploid origin, with *S. annulatum* and *S. balticum* as progenitors (Såstad et al. 1999).

The aim of the present study was to help clarify the identification of *Sphagnum balticum* in Britain, to review its occurrence at sites from where it has been recorded, and to investigate the possible presence of hybrids between it and *S. angustifolium*, *S. cuspidatum* or *S. fallax*.

## Materials and methods

### Taxonomy

Taxonomy follows Blockeel et al. (2021).

### Sampling

All sites from where *Sphagnum balticum* has been recorded relatively recently in Britain ( $n=6$ ) were visited during July to August 2020, including Abernethy Forest (v.-c. 96, Easternness), Black Burn (v.-c. 92, South Aberdeenshire), Cors Caron (v.-c. 46, Cardiganshire), Cors Craig y Bwlch (v.-c. 46), Muckle Moss (v.-c. 67, South Northumberland) and Thorne Moors (v.-c. 63, Southwest Yorkshire). A search was undertaken at each site for *S. balticum* and other species with which it could be confused, plus possible hybrids. *Sphagnum balticum* was provisionally determined in the field when plants were found that had fascicles comprising two spreading branches and one pendent branch, plus stem leaves spreading at right angles from the stem. Samples of such plants were collected, checked microscopically and named as *S. balticum* if they also possessed a stem cortex distinct from the cylinder and stem leaves with fibrillose hyalocysts, which amounted to 11 samples. A further 18 samples were collected of possible confusion species, plus seemingly intermediate plants. Two recent collections made by D. K. Reed that had been identified as *S. balticum* from Cors Caron were also included in the study.

### Genetic analysis

Details of the 31 field samples included in the genetic analysis are provided in Table 1. DNA was extracted from a single shoot from each sample, using the middle part of the capitulum. We used the NucleoSpin Plant II 'mini kit for DNA from plants' from Macherey-

**Table 1.** Details of specimens included within the genetic analysis.<sup>a</sup>

<i>Sphagnum</i> species	Site	Region	GR	Date
<i>S. balticum</i>	Abernethy Forest	Easternness	NJ0053612784	7 August 2020
<i>S. cuspidatum</i>	Abernethy Forest	Easternness	NJ0052112763	7 August 2020
<i>S. fallax</i>	Abernethy Forest	Easternness	NJ0054712698	7 August 2020
<i>S. angustifolium</i>	Black Burn, head of	South Aberdeenshire	NO2767781148	6 August 2020
<i>S. balticum</i>	Black Burn, head of	South Aberdeenshire	NO2756381330	6 August 2020
<i>S. balticum</i>	Black Burn, head of	South Aberdeenshire	NO2756381330	6 August 2020
<i>S. cuspidatum</i>	Black Burn, head of	South Aberdeenshire	NO2759481442	6 August 2020
<i>S. fallax</i>	Black Burn, head of	South Aberdeenshire	NO2758781213	6 August 2020
<i>S. cuspidatum</i>	Cors Caron	Cardiganshire	SN6823061934	9 October 2019
<i>S. cuspidatum</i>	Cors Caron	Cardiganshire	SN6961463581	8 November 2019
<i>S. cuspidatum</i>	Cors Caron	Cardiganshire	SN6987064008	21 July 2020
<i>S. cuspidatum</i>	Cors Caron	Cardiganshire	SN6961963573	21 July 2020
<i>S. cuspidatum</i>	Cors Caron	Cardiganshire	SN6872261980	21 July 2020
<i>S. fallax</i>	Cors Caron	Cardiganshire	SN6989263997	21 July 2020
<i>S. fallax</i>	Cors Caron	Cardiganshire	SN6987064008	21 July 2020
<i>S. cuspidatum</i>	Cors Craig y Bwlch	Cardiganshire	SN7136069768	24 July 2020
<i>S. fallax</i>	Cors Craig y Bwlch	Cardiganshire	SN7136069768	24 July 2020
<i>S. fallax</i>	Cors Craig y Bwlch	Cardiganshire	SN7136069768	24 July 2020
<i>S. fallax</i>	Cors Craig y Bwlch	Cardiganshire	SN7136069768	24 July 2020
<i>S. balticum</i>	Muckle Moss	South Northumberland	NY7998467011	5 August 2020
<i>S. cuspidatum</i>	Muckle Moss	South Northumberland	NY8020867108	5 August 2020
<i>S. fallax</i>	Muckle Moss	South Northumberland	NY8030767149	5 August 2020
<i>S. fallax</i>	Muckle Moss	South Northumberland	NY7996467065	5 August 2020
<i>S. fallax</i>	Muckle Moss	South Northumberland	NY7996467065	5 August 2020
<i>S. fallax</i>	Muckle Moss	South Northumberland	NY8016967083	5 August 2020
<i>S. fallax</i>	Muckle Moss	South Northumberland	NY8030167133	5 August 2020
<i>S. cuspidatum</i>	Thorne Moor	Southwest Yorkshire	SE7240715633	3 August 2020
<i>S. fallax</i>	Thorne Moor	Southwest Yorkshire	SE7190415811	3 August 2020
<i>S. fallax</i>	Thorne Moor	Southwest Yorkshire	SE7245215603	3 August 2020
<i>S. fallax</i>	Thorne Moor	Southwest Yorkshire	SE7245215603	3 August 2020
<i>S. fallax</i>	Thorne Moor	Southwest Yorkshire	SE7190215814	3 August 2020

<sup>a</sup>D. K. Reed collected the samples in 2019 and D. A. Callaghan collected the samples in 2020.

Nagel (Düren, Germany), following the manufacturer's protocol. Fifteen microsatellites (1, 7, 9, 12, 17, 19, 20, 22, 29, 30, 56, 65, 68, 78 and 93) that were developed for *Sphagnum* species (Shaw et al. 2008; Stenøien et al. 2011a; Shaw et al. 2013) were amplified in four multiplex reactions (Qiagen Multiplex PCR Kit; Qiagen, Venlo, The Netherlands) and genotyped using GENEMAPPER software (Applied Biosystems, Carlsbad, CA, USA). For details regarding multiplex reactions and thermocycling regimens, see Kyrkjeeide et al. (2016).

The genetic structure of the data was investigated using principal coordinate analysis (PCoA) in GenALEX 6.503 (Peakall and Smouse 2012) and clustering analysis in Structure v.2.3.4 (Falush et al. 2007; Pritchard et al. 2000). The latter was used to explore if the number of genetic groups identified corresponded to the morphologically defined taxa, and if there were any admixture between these taxa. We ran the analyses using  $K=2-4$ , with an expectation that the number of genetic clusters equals the four morphologically identified species (*sensu van Hengstum et al. 2012; Meirmans 2015*). The admixture ( $\alpha = 1/4$ , Wang 2017) and correlated allele frequency models were applied, with 10 replicates per number of  $k$ , each with 500,000 iterations and a burn-in of 100,000, without specifying any a priori population membership information. The results from Structure were visualised using StructureSelector including Clumpak (Li and Liu 2018).

#### Identification

Informed by the results of the genetic analysis, the morphology and identification of the specimens was reviewed, and an illustrated key was compiled to allow for the discrimination of *Sphagnum balticum* and similar forms of *S. cuspidatum* and *S. fallax* in Britain. *Sphagnum angustifolium* was excluded from this key because the sample size in this study was small ( $n = 1$ ), and it appears to be simple to discriminate from *S. balticum* using established criteria (Hill 2004).

#### Distribution

Vouchers labelled as *Sphagnum balticum* in BBSUK, BM, MANCH, NMW and various private herbaria were reviewed, and an updated distribution map of the species in Britain was compiled.

## Results

#### Genetic analysis

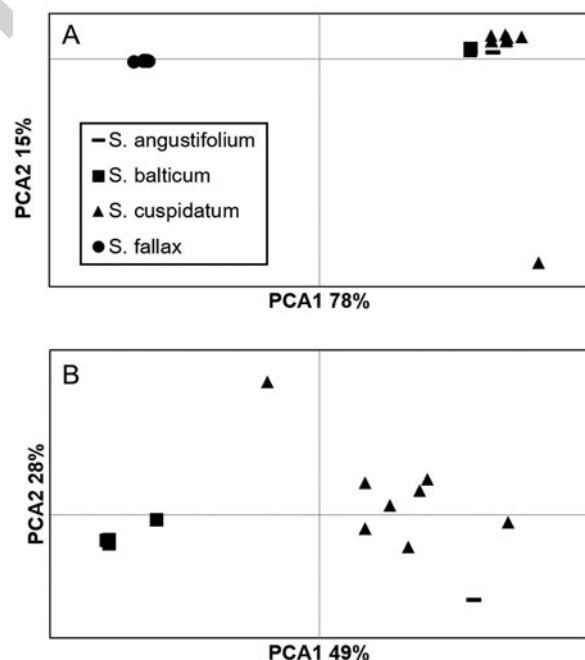
All 31 samples were genotyped for all microsatellites, except *Sphagnum fallax*, which did not have any alleles in microsatellite 9, seemingly lacking this locus. Otherwise, data were missing at only four loci

in three specimens. The samples missing two alleles were excluded from the PCoA analysis of all four taxa.

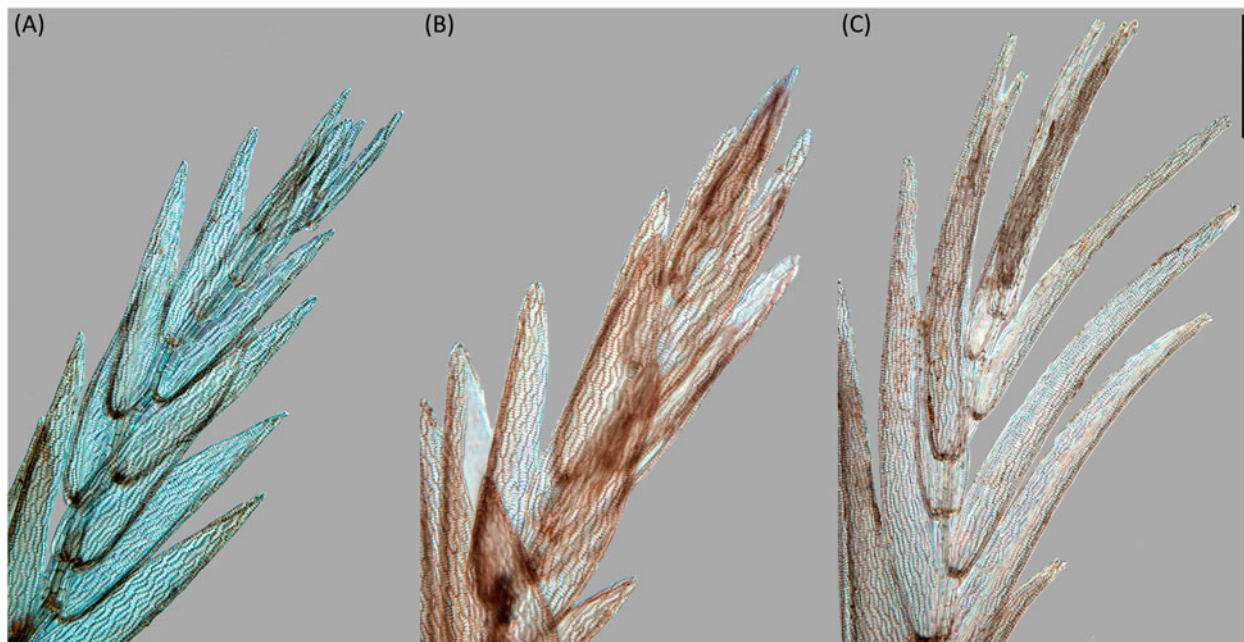
The PCoA plot shows that *Sphagnum fallax* is well separated from *S. angustifolium*, *S. balticum* and *S. cuspidatum* (Figure 1A). One sample identified as *S. cuspidatum* is separated from the other samples at the y-axis. This is probably due to one missing allele. The plot generated by PCoA excluding *S. fallax* show that the three other taxa are separated from each other, and although *S. angustifolium* clusters close to *S. cuspidatum*, it is represented by only a single specimen (Figure 1B). Like the PCoA plots, the results of clustering analysis support four taxa, with one genetic group identified for each morphologically identified taxon.

#### Identification

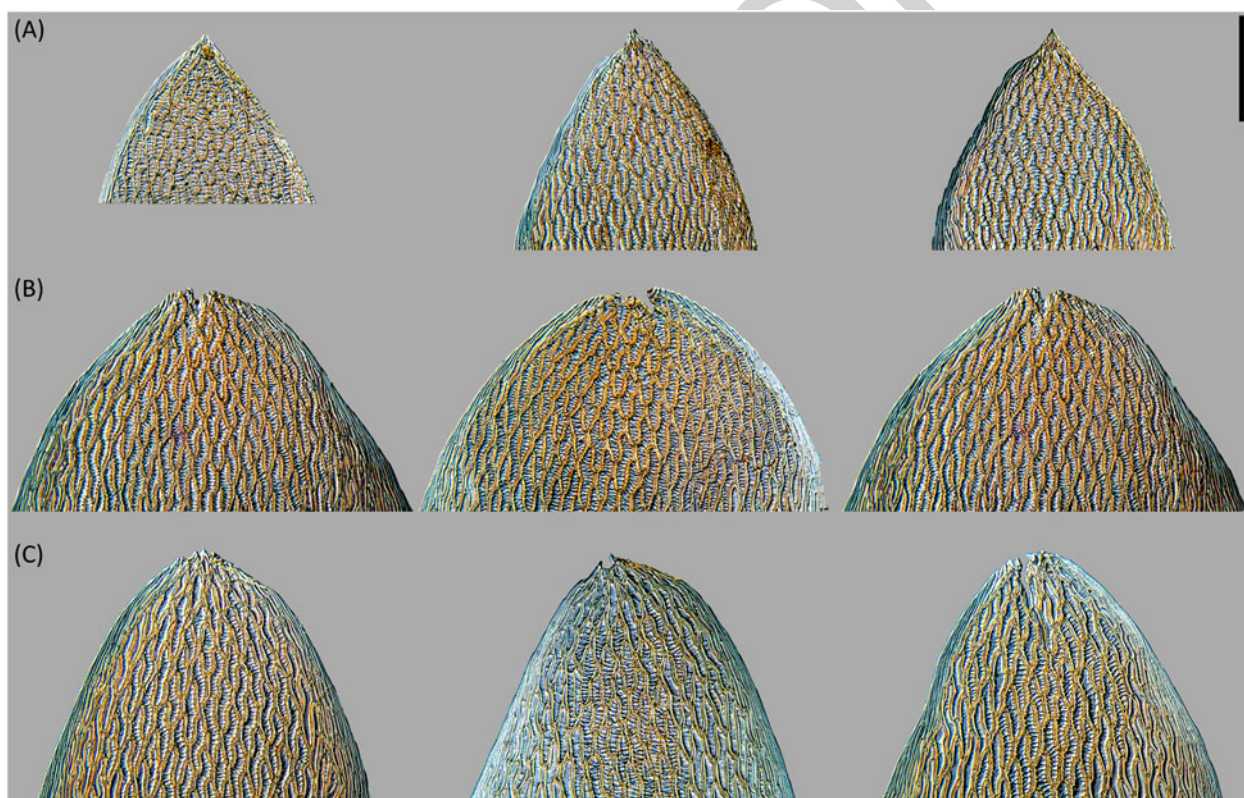
The morphological review, informed by the genetic analysis results, showed that some terrestrial forms of *Sphagnum cuspidatum* and some reduced forms of *S. fallax* can be misidentified as *S. balticum* because they can have a combination of characters usually considered to be characteristic of *S. balticum*, including (i) stem cortex distinct from the cylinder, (ii) fascicles comprising two spreading branches and one pendent branch, (iii) stem leaves spreading at right angles from the stem, and (iv) stem leaves with fibrillose hyalocysts. No other species that could be confused easily with *S. balticum* were found at the sites



**Figure 1.** Principal coordinate analysis plots for four (A) and three (B) *Sphagnum* species, based on microsatellite data. *Sphagnum angustifolium*, *S. balticum* and *S. cuspidatum* overlap when analysed together with *S. fallax* (A), but *S. balticum* and *S. cuspidatum* are well separated when *S. fallax* is excluded from the analysis (B). *Sphagnum angustifolium* is also separated from the other species in (B), but the species is represented only by one sample.



**Figure 2.** Tips of spreading branches of (A) *Sphagnum fallax*, (B) *S. balticum* and (C) *S. cuspidatum*. Scale bar = 1 mm. Photographs: D. A. Callaghan.



**Figure 3.** Stem leaf tips (convex side) compressed beneath microscope coverslip of (A) *Sphagnum fallax*, (B) *S. balticum* and (C) *S. cuspidatum*. Scale bar = 0.2 mm. Photographs: D. A. Callaghan.

surveyed. The following provides a key for the discrimination of *S. balticum* from such confusing forms of *S. cuspidatum* and *S. fallax*.

- |  |   |
|--|---|
| <p>1. Leaves near tips of spreading branches linear aneolate and mostly &gt; 1.5 mm long (Figure 2C) ..... <b><i>S. cuspidatum</i></b></p> | <p>1. Leaves near tips of spreading branches ovate and mostly &lt; 1.5 mm long (Figure 2A, B)..... <b>2</b></p> <p>2. When compressed beneath a microscope coverslip, tips of most stem leaves with a sharp mucro (Figure 3A) ..... <b><i>S. fallax</i></b></p> |
|--|---|

■ Extant  
 □ Extinct



**Figure 4.** Occupancy of Ordnance Survey 10 km grid cells by *Sphagnum balticum* in Britain.

2. When compressed beneath a microscope coverslip, tips of stem leaves without a sharp mucro (Figure 3B) ..... ***S. balticum***

Distribution



The review of herbarium material revealed some errors in the identification of *Sphagnum balticum* in Britain, involving *S. cuspidatum* from Cors Caron (Cardiganshire; D. K. Reed priv. herb.), *S. fallax* from Carrington Moss (v.-c. 58, Cheshire; MANCH EM668947!

and EM668946!) and Cors Craig y Bwlch (Cardiganshire; NMW C.2011.013.2!), and *S. obtusum* from Netherton (v.-c. 59, South Lancashire; NMW 25.152.14848! and 15.54.78!). Based on the review of specimens and fieldwork carried out in 2020, Figure 4 shows occupancy of Ordnance Survey 10 km grid cells by *S. balticum* in Britain. It has been known from seven sites but has been lost from four due to habitat loss and degradation. It presently survives at three sites: in a small mire at the edge of Abernethy Forest (Easterness), in a mire at

445  
450  
455  
460  
465  
470  
475  
480  
485

500  
505  
510  
515  
520  
525  
530  
535  
540

PDF



the head of Black Burn (South Aberdeenshire) and at Muckle Moss (South Northumberland).

## Discussion

No evidence for the occurrence of hybrids between *Sphagnum balticum* and related species was found during this study. The genetic results agree with recent findings (Shaw et al. 2016; Duffy et al. 2020). Shaw et al. (2016) showed that *S. balticum*, *S. fallax*, *S. angustifolium* and *S. cuspidatum* are clearly separated taxonomic entities. Even though hybridisation and allopolyploidisation are common among species of *Sphagnum* (see Meleshko et al. 2018 for a review), we did not find any sign of admixture in our sampled plants. Likewise, Duffy et al. (2020) were not able to detect significant admixture among *S. balticum*, *S. fallax* and *S. angustifolium* using genomic data. The same study identified two major genetic clades within the *S. recurvum* complex, and refer to one group, including *S. balticum* and *S. angustifolium*, as having rounded stem leaves, and another group, including *S. fallax*, as having pointed stem leaves (Duffy et al. 2020).

The results of the present study show that over-recording of *Sphagnum balticum* has occurred in Britain due in particular to confusion with some forms of *S. cuspidatum* and *S. fallax*. Similarly, a voucher from East Sutherland (v.-c. 107) of *S. balticum*, which was verified by E. M. Lobleby and included in Warburg (1963), was subsequently redetermined as *S. fallax* by Maass (1965). The illustrated key provided by this study should help to alleviate the problem.

*Sphagnum balticum* is a very rare species in Britain and has undergone a decline due to habitat destruction and alteration. It is presently known to survive at only three sites. Two of these sites, at Abernethy Forest and Muckle Moss, are within protected areas, where the species receives specific conservation attention. The third site, a mire at the head of Black Burn, has no statutory conservation protection and the *S. balticum* population receives no conservation attention. There is a clear need to safeguard the Black Burn population, and to carry out surveys of other potential sites to try to locate any further populations that may exist. Significant habitat restoration measures have recently been carried out at two of the sites where *S. balticum* once occurred, at Cors Caron and Thorne Moors. The potential reintroduction of the species to these sites should be assessed if favourable habitat for the species ultimately redevelops. Populations at both Abernethy Forest and Muckle Moss are reasonably large and could potentially provide source material for trial conservation translocations, as has begun recently in England in efforts to conserve

another nationally rare boreal peatland moss, *Dicranum undulatum* (Callaghan 2021).

Efforts to assess, monitor and conserve threatened species fundamentally depend on the accurate determination of species. Even in a region such as Britain, which has a long history of bryological study, much work remains to be done to better understand the relationships between similar species and their identification characters. For example, 11 species are categorised at 'Data Deficient (Taxonomic Uncertainty)' in the new IUCN Red List of the bryophytes of Britain because data are so uncertain that both Critically Endangered and Least Concern are plausible categories, and this is mainly because of taxonomic uncertainty (Callaghan 2023). Integrative taxonomic studies, such as those reported here, are crucial to resolving this problem.

## Acknowledgements

Many thanks to Martin Furness (Natural England) for managing the project contract. For various help and support, many thanks to Tom Blockeel (Sheffield, UK), Sam Bosanquet (Natural Resources Wales), Dave Genney (NatureScot), Steven Heathcote (JBA Consulting), Niklas Lönnell (Swedish University of Agricultural Sciences), John O'Reilly (Ptyxis Ecology), Dave Reed (Natural Resources Wales), Chris Tilbury (Royal Society for the Protection of Birds) and Rachel Webster (MANCH). Thanks also to NINA Genlab for assistance in the laboratory, and to reviewers for reviewing the manuscript.

## Disclosure statement

No potential conflicts of interest were reported by the author.

## Funding

Funding for this study was provided by Natural England and the British Bryological Society.

## Notes on contributors

**Des A. Callaghan** is a consultant bryologist operating under Bryophyte Surveys Ltd, working throughout Britain and further afield. His research is focused on threatened species, taxonomy and conservation ecology.

**Magni O. Kyrkjeide** is a researcher at Norwegian Institute for Nature Research (NINA), working on *Sphagnum* systematics, mire restoration, monitoring and conservation of threatened species.

**Kristian Hassel** is a professor at Norwegian University of Science and Technology, where he is head of the botanical collections at NTNU University Museum. His research focuses on bryophyte biosystematics with a special emphasis on speciation processes and biogeography of northern species, but also including questions related to applied conservation biology.

## ORCID

Des A. Callaghan  <http://orcid.org/0000-0002-0415-1493>  
Magni Olsen Kyrkjeide  <http://orcid.org/0000-0002-7454-3652>  
Kristian Hassel  <http://orcid.org/0000-0002-1906-8166>

## References

- 670 Blockeel TL, Bell NE, Hill MO, Hodgetts NG, Long DG, Pilkington SL, Rothero GP. 2021. A new checklist of the bryophytes of Britain and Ireland, 2020. *Journal of Bryology*. 43(1):1–51. <https://doi.org/10.1080/03736687.2020.1860866>.
- 675 Blockeel TL, Bosanquet SDS, Hill MO, Preston CD. 2014. Atlas of British and Irish bryophytes. Vol. 1. Newbury: Pisces Publications.
- Callaghan DA. 2021. Trial reintroduction of *Dicranum undulatum*. *Field Bryology*. 126:56.
- Callaghan DA. 2023. A new IUCN Red List of the bryophytes of Britain, 2023. *Journal of Bryology*. 44(4):271–389. <https://doi.org/10.1080/03736687.2023.2185393>.
- 680 Callaghan DA, Brinda JC. 2022. Typification of *Sphagnum balticum* (Russow) C.E.O. Jensen. *Journal of Bryology*. 44(2):149–155. <https://doi.org/10.1080/03736687.2022.2047546>.
- 685 Daniels RE, Eddy A. 1985. *Handbook of European Sphagna*. Huntingdon: Institute of Terrestrial Ecology.
- Duffy AM, Agüero B, Stenøien HK, Flatberg KI, Ignatov MS, Hassel K, Shaw AJ. 2020. Phylogenetic structure in the *Sphagnum recurvum* complex (Bryophyta) in relation to taxonomy and geography. *American Journal of Botany*. 107(9):1283–1295. <https://doi.org/10.1002/ajb2.1525>.
- 690 Falush D, Stephens M, Pritchard JK. 2007. Inference of population structure using multilocus genotype data: dominant markers and null alleles. *Molecular Ecology Notes*. 7(4):574–578. <https://doi.org/10.1111/j.1471-8286.2007.01758.x>.
- 695 Flatberg KI. 2013. *Norges torvmoser*. Trondheim: Akademika forlag.
- Flatberg KI, Thinggaard K, Sæstad SM. 2006. Interploidal gene flow and introgression in bryophytes: *Sphagnum girgensohnii* × *S. russowii*, a case of spontaneous neotriploidy. *Journal of Bryology*. 28(1):27–37. <https://doi.org/10.1179/174328206X90459>.
- 700 Hill MO. 2004. Class Sphagnopsida. In: Smith AJE. *The moss flora of Britain and Ireland*. 2nd ed. Cambridge: Cambridge University Press; p.43–102.
- Hill MO, Preston CD. 1998. The geographical relationships of British and Irish bryophytes. *Journal of Bryology*. 20(1):127–226. <https://doi.org/10.1179/jbr.1998.20.1.127>.
- 705 Hodgetts NG. 2006. Monitoring Baltic bog-moss (*Sphagnum balticum*) at Muckle Moss, Northumberland, 2006. Unpublished report to Plantlife.
- Hodgetts NG. 2008. *Sphagnum balticum* species dossier. Salisbury: Plantlife.
- 710 Hodgetts NG. 2011. Surveillance of priority bryophytes in Scotland 2010–2013: *Sphagnum balticum*. Unpublished report to Scottish Natural Heritage.
- Hölzer A. 2010. Die Torfmoose Südwestdeutschlands und der Nachbargebiete. Jena: Weissdorn-Verlag Jena.
- Isoviita. 1966. Studies on *Sphagnum* L. I. Nomenclatural revision of the European taxa. *Annales Botanici Fennici*. 3:199–264.
- 715 Karlin EF, Boles SB, Ricca M, Temsch EM, Greilhuber J, Shaw AJ. 2009. Three-genome mosses: complex double allopolyploid origins for triploid gametophytes in *Sphagnum*. *Molecular Ecology*. 18:1439–1454. <https://doi.org/10.1111/j.1365-294X.2009.04113.x>.
- Karlin EF, Gardner GP, Lukshis K, Boles S, Shaw AJ. 2010. Allopolyploidy in *Sphagnum mendocinum* and *S. papillosum* (Sphagnaceae). *The Bryologist*. 113(1):114–119. <https://doi.org/10.1639/0007-2745-113.1.114>.
- Kyrkjeide MO, Hassel K, Flatberg KI, Shaw AJ, Brochmann C, Stenøien HK. 2016. Long-distance dispersal and barriers shape genetic structure of peatmosses (*Sphagnum*) across the Northern Hemisphere. *Journal of Biogeography*. 43(6):1215–1226. <https://doi.org/10.1111/jbi.12716>.
- Laine J, Flatberg KI, Harju P, Timonen T, Minkkinen K, Laine A, Tuittila ES, Vasander H. 2018. *Sphagnum* mosses – the stars of European mires. Helsinki: University of Helsinki.
- Li YL, Liu JX. 2018. StructureSelector: a web-based software to select and visualize the optimal number of clusters using multiple methods. *Molecular Ecology Resources*. 18(1):176–177. <https://doi.org/10.1111/1755-0998.12719>.
- Lönnell N, Hallingbäck T, Hedenäs L, Reisborg C. 2019. Nationalnyckeln till Sveriges flora och fauna. Vitmossor – knappålsmossor. Bryophyta: *Sphagnum–Tetradontium*. Uppsala: SLU ArtDatabanken.
- Maass WSG. 1965. *Sphagnum dusenii* and *Sphagnum balticum* in Britain. *The Bryologist*. 68(2):211–217. <https://doi.org/10.2307/3241016>.
- McQueen CB, Andrus RE. 2007. Sphagnaceae Dumortier. In: *Flora of North America Editorial Committee, editors. Flora of North America. Vol. 27, Bryophytes: mosses, Part 1*. New York (NY): Oxford University Press; p. 45–101.
- Meirmans PG. 2015. Seven common mistakes in population genetics and how to avoid them. *Molecular Ecology*. 24(13):3223–3231. <https://doi.org/10.1111/mec.13243>.
- 745 Meleshko O, Stenøien HK, Speed JD, Flatberg KI, Kyrkjeide MO, Hassel K. 2018. Is interspecific gene flow and speciation in peatmosses (*Sphagnum*) constrained by phylogenetic relationship and life-history traits? *Lindbergia*. 41(1):1–14. <https://doi.org/10.25227/linbg.01107>.
- Michaelis D. 2019. *The Sphagnum species of the world*. *Bibliotheca Botanica*. 162:1–435.
- 750 Natcheva R, Cronberg N. 2007. Recombination and introgression of nuclear and chloroplast genomes between the peat mosses, *Sphagnum capillifolium* and *Sphagnum quinquefarium*. *Molecular Ecology*. 16(4):811–818. <https://doi.org/10.1111/j.1365-294X.2006.03163.x>.
- O'Reilly J. 2012. Muckle Moss NNR: NVC survey and bryophyte survey. Unpublished report to Natural England.
- O'Reilly J. 2018. *Sphagnum balticum*: an update on its status at Muckle Moss NNR. Unpublished report to Natural England.
- 760 Peakall R, Smouse PE. 2012. GenA1Ex 6.5: genetic analysis in Excel. Population genetic software for teaching and research – an update. *Bioinformatics*. 28(19):2537–2539. <https://doi.org/10.1093/bioinformatics/bts460>.
- Pritchard JK, Stephens M, Donnelly P. 2000. Inference of population structure using multilocus genotype data. *Genetics*. 155(2):945–959. <https://doi.org/10.1093/genetics/155.2.945>.
- 765 Ricca M, Shaw AJ. 2010. Allopolyploidy and homoploid hybridization in the *Sphagnum subsecundum* complex (Sphagnaceae: Bryophyta). *Biological Journal of the Linnean Society*. 99(1):135–151. <https://doi.org/10.1111/j.1095-8312.2009.01340.x>.
- Ricca M, Szövényi P, Temsch EM, Johnson MG, Shaw AJ. 2011. Interploidal hybridization and mating patterns in the *Sphagnum subsecundum* complex. *Molecular Ecology*. 20



(15):3202–3218. <https://doi.org/10.1111/j.1365-294X.2011.05170.x>.

Såstad SM, Flatberg KI, Cronberg N. 1999. Electrophoretic evidence supporting a theory of allopolyploid origin of the peatmoss *Sphagnum jensenii*. *Nordic Journal of Botany*. 19(3):355–362. <https://doi.org/10.1111/j.1756-1051.1999.tb01127.x>.

Såstad SM, Stenøien HK, Flatberg KI, Bakken S. 2001. The narrow endemic *Sphagnum troendelagicum* is an allopolyploid derivative of the widespread *S. balticum* and *S. tenellum*. *Systematic Botany*. 26(1):66–74.

Shaw AJ, Cao T, Wang LS, Flatberg KI, Flatberg B, Shaw B, Zhou P, Boles S, Terracciano S. 2008. Genetic variation in three Chinese peat mosses (*Sphagnum*) based on microsatellite markers, with primer information and analysis of ascertainment bias. *The Bryologist*. 111(2):271–281. <https://www.jstor.org/stable/20110940>.

Shaw AJ, Cox CJ, Boles SB. 2005. Phylogeny, species delimitation, and recombination in *Sphagnum* section *Acutifolia*. *Systematic Botany*. 30(1):16–33. <https://www.jstor.org/stable/25064038>.

Shaw AJ, Devos N, Liu Y, Cox CJ, Goffinet B, Flatberg KI, Shaw B. 2016. Organellar phylogenomics of an emerging model system: *Sphagnum* (peatmoss). *Annals of Botany*. 118(2):185–196. <https://doi.org/10.1093/aob/mcw086>.

Shaw AJ, Flatberg KI, Szövényi P, Ricca M, Johnson MG, Stenøien HK, Shaw B. 2012. Systematics of the *Sphagnum fimbriatum* complex: phylogenetic relationships, morphological variation, and allopolyploidy. *Systematic Botany*. 37(1):15–30. <https://www.jstor.org/stable/41416932>.

Shaw AJ, Goffinet B. 2000. Molecular evidence of reticulate evolution in the peatmosses (*Sphagnum*), including *S. ehyalinum* sp. nov. *The Bryologist*. 103(2):357–374. <https://www.jstor.org/stable/3244163>.

Shaw AJ, Shaw B, Johnson MG, Higuchi M, Arikawa T, Ueno T, Devos N. 2013. Origins, genetic structure, and systematics of the narrow endemic peatmosses (*Sphagnum*): *S. guwassanense* and *S. triseriporum* (Sphagnaceae). *American Journal of Botany*. 100(6):1202–1220. <https://www.jstor.org/stable/23435186>.

Stenøien HK, Shaw AJ, Shaw B, Hassel K, Gunnarsson U. 2011a. North American origin and recent European establishment of the amphi-Atlantic peat moss *Sphagnum angermanicum*. *Evolution*. 65(4):1181–1194. <https://doi.org/10.1111/j.1558-5646.2010.01191.x>.

Stenøien HK, Shaw AJ, Stengrundet K, Flatberg KI. 2011b. The narrow endemic Norwegian peat moss *Sphagnum troendelagicum* originated before the last glacial maximum. *Heredity*. 106:370–382. <https://doi.org/10.1038/hdy.2010.96>.

Turner JM. 2000. Baltic Bog Moss *Sphagnum balticum* in England. *Plantlife Report no. 163*. London: Plantlife.

Turner JM. 2002a. Baltic Bog Moss *Sphagnum balticum* in England and Wales. *Plantlife Report no. 201*. London: Plantlife.

Turner JM. 2002b. Baltic Bog Moss *Sphagnum balticum* in England 2002. *Plantlife Report no. 223*. London: Plantlife.

van Hengstum T, Lachmuth S, Oostermeijer JGB, den Nijs HCM, Meirmans PG, van Tienderen PH. 2012. Human-induced hybridization among congeneric endemic plants on Tenerife, Canary Islands. *Plant Systematics and Evolution*. 298:1119–1131. <https://doi.org/10.1007/s00606-012-0624-6>.

Wang J. 2017. The computer program STRUCTURE for assigning individuals to populations: easy to use but easier to misuse. *Molecular Ecology Resources*. 17(5):981–990. <https://doi.org/10.1111/1755-0998.12650>.

Warburg EF. 1963. *Census catalogue of British mosses*. 3rd ed. London: British Bryological Society.

775

780

785

790

795

800

805

810

815

820

825

830

835

840

845

850

855

860

865

870

875

880