Palaeoecology of *Sphagnum riparium* (Ångström) in Northern Hemisphere peatlands: Implications for peatland conservation and palaeoecological research

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A R T I C L E   I N F O

Article history:
Received 7 October 2017
Received in revised form 5 April 2018
Accepted 25 April 2018
Available online 26 April 2018

Keywords:
Plant macrofossils
Testate amoebae
Plant succession
Palaeoecology
Peat-forming species
Biodiversity conservation

A B S T R A C T

*Sphagnum riparium* (Ångström) is a rare constituent of modern peatland plant communities and is also very rarely found as a subfossil in peat archives. We present new data on the occurrence of *Sphagnum riparium* macrofossils in three Northern Hemisphere peatlands from Yellowknife (NW Canada), Abisko (N Sweden), and the Northern Ural Mountains (NW Russia). *Sphagnum riparium* macrofossils were present in transitional phases between rich fen and oligotrophic bog. *Sphagnum riparium* was a dominant species in the three sites and was found in combination with *Sphagnum angustifolium*, *Drepanocladus sp.*, and vascular plants including *Andromeda polifolia*, *Chamedaphne calyculata* and *Oxycoccus palustris*. Testate amoebae indicate that the species occurred in wet to moderately wet conditions (water-table depth inferred from a testate amoeba transfer function model ranged between 25 and 0 cm under the peatland surface). The wet-indicator taxa *Archerella flavum* and *Hyalosphenia papilio* dominated the testate amoeba communities in peat horizons containing *Sphagnum riparium*. The presence of *Sphagnum riparium* macrofossils in peat profiles in the Northern Hemisphere can be interpreted as an indication of wet minerotrophic conditions, often corresponding to a rise in water-level and establishment of a wet habitat. *Sphagnum riparium* is a transient species in these peatlands and is replaced by communities dominated by more acidophilic species such as *Sphagnum angustifolium*, *Sphagnum russowii*, and *Sphagnum fuscum.* Our data show that although *Sphagnum riparium* is a transient peat-forming species, it is widespread in sub-arctic and boreal environments. The subfossil occurrence of *Sphagnum riparium* in the Northern Hemisphere may indicate that its range has increased during the Late Holocene. The conservation of *Sphagnum riparium* in peatlands depends on the existence of relatively short-lived transitional communities which potentially can be artificially created.

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1. Introduction

*Sphagnum* mosses are among the most common plant species in northern bogs and poor fens where they are commonly the main contributors to peat-formation (Crum, 1992; Halsey et al., 2000; University of Leeds Peat Club, 2017). Peatlands represent an important archive of past environmental conditions enabling reconstructions of local vegetation communities over millennia (Overbeck, 1975; Barber, 1981). *Sphagnum* mosses are particularly common in oligotrophic peatlands and their fossil remains can be identified to the species level due to their distinctive morphological features (Hölzer, 2010; Lange, 1982; Mauquoy and van Geel, 2007). The present-day ecological preferences of *Sphagnum* mosses (e.g. water-table depth, pH) are used to infer past climatic and environmental changes (Mauquoy et al., 2008; Valiranta et al., 2012; Lamentowicz et al., 2015; Galka et al., 2017a, 2017b, 2017c). Certain species are indicators of wet habitats such as

https://doi.org/10.1016/j.revpalbo.2018.04.006
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Sphagnum cuspidatum, Sphagnum magus and Sphagnum balticum (Barber et al., 2003; Valiarrta et al., 2012; Galka et al., 2017b, 2017c), whereas others are indicative of drier habitats, including peat hummocks (e.g. *Sphagnum fuscum, Sphagnum capillifolium* (Kuhry, 2008; Höller, 2010; Valiarrta et al., 2012; Galka et al., 2017b, 2017c)). Furthermore, some more minerotrophic *Sphagnum* species and/or species with broad ecological tolerances e.g. *Sphagnum papillosum, Sphagnum fallax* and *Sphagnum magellanicum* can occur in various habitats; where they are found above peat layers formed by typical oligotrophic species e.g. *Valiranta et al., 2012; Ga. Sphagnum fuscum, Sphagnum capillifolium* van Geel and Middeldorp, 1988; McClymont et al., 2008; Ga. input from agriculture, or deposition of dust on the peatland (e.g. distribution of peat forming vegetation, temporal patterns of vegetation de...2015a). This information is useful for environmental protection efforts Zoltai, 1993; Halsey et al., 2000; Gajewski et al., 2001; Swindles et al., 2012, 2014). 

Sphagnum refugia during the Quaternary which is currently based... distribution of peat forming vegetation, temporal patterns of vegetation degrading permafrost peatland in NW Canada near the City of Yellow-
Picea mariana, Betula papyrifera, Betula nana

**2. Study sites**

Handle Lake peatland (62°29'26.44"N, 114°23'18.23"W) is a degrading peatfrost peatland in NW Canada near the City of Yellowknife (Fig. 1). Arboreal vegetation surrounding the peatland includes Picea mariana, Betula papyrifera, Betula nana, Rhododendron groenlandicum and Pinus banksiana. The mean annual air temperature in the area (1981–2010) is −4.1 °C and mean annual precipitation is 291 mm, of which 40% falls as snow (Environment Canada, 2017).

Crater Pool, Abisko, N Sweden (68°19'10.1"N, 19°51'27.2"E) is an in-tact palsa mire containing peatfrost in the Abisko region of sub-arctic northern Sweden (Fig. 1). Within the site, water-table depth varies from −5 to 45 cm and pH varies from 3.76–4.77. Common plants include Sphagnum fuscum, Rubus chamaemorus, Eriophorum vaginatum, Eriophorum angustifolium and Betula nana. In addition, Sphagnum balticum, Drepanocladus sp. and Carex rostrata are also present. The climate of Abisko is considerably milder and drier than other locations at similar latitudes (Yang et al., 2012). Mean annual precipitation is 332 mm (1981–2010) (Callaghan et al., 2010). For this time period, mean winter and summer temperatures were -9.3 °C and 10.1 °C, respectively.

Banana bog, Northern Ural Mountains, Russia is located on the eastern bank of the Bolshaya Porozhnyaya river (60°02' N 58°59' E) at an altitude of 270–280 m a.s.l. in the Pechora-Ilych Nature Reserve (Fig. 1). The peatland covers an area of 8.9 ha (ca. 600 × 180 m), is banana-shaped and slightly sloping. It is best classified as an upland Sphagnum-dominated bog with clear hummock-ridge topography. Scattered trees are found throughout the mire in low density (10–20%). These include mostly Betula pubescens, occasional Picea obovata and a small number of Pinus sylvestris and Pinus sibirica. The herbaceous and low-shrub layer consists of typical oligotrophic taxa and covers about 20–40% of the mire surface. The layer is dominated by Eriophorum vaginatum and Carex spp. (Carex globularis, Carex pauciflora, and Carex rariflora) with other species including Andromeda polifolia, Vaccinium alpinum, Empetrum nigrum, Rubus chamaemorus, Baeothryon (Trichophorum) alpinum, Dactylorhiza traunsteineri, and Oxycoccus palustris. The climate of the study area is temperate continental; mean annual air temperature = −0.4 °C, mean air temperature for January = −15.0 to −17.5 °C, and July 15.5 to 16.5 °C; 175–185 days with sub-zero temperatures and ground snow cover form late October to early November = 180–190 days; length of the growing season = 140–150 days; average total annual precipitation = 627 mm.

### 3. Material and methods

#### 3.1. Coring, subsampling, and chronology

The Handle Lake peatland core (BH-HL-15-01) was sampled in September, 2015. A 65-cm deep monolith was extracted. The Crater Pool (CP) peat profiles were sampled with a Waardenaar peat extractor (100 cm long, 10 cm × 10 cm) and peat core was recovered at Banana bog, Ural site, by using a Russian peat corer (50 cm long, 5 cm wide).

Four AMS (Accelerator Mass Spectrometry) radiocarbon dates, on hand-picked plant macrofossils, were used to determine the time of *Sphagnum riparium* occurrence. Radiocarbon dating was undertaken at the Poznań Radiocarbon Laboratory and the A.E. Lalonde AMS Laboratory, University of Ottawa. Radiocarbon dates were calibrated using OxCal 4.1 (Bronk Ramsey, 2009) and the IntCal13 curve (Reimer et al., 2013).

#### 3.2. Plant macrofossils

Plant macrofossils were analysed in samples of approximately 5–10 cm³, at 1-cm contiguous intervals in the Canadian and Swedish peat profiles and in 4-cm intervals in the Russian samples. In total, 35 samples were analysed. The samples were washed and sieved under warm-water using a 0.20-mm mesh screen. Initially, the entire sample was analysed with a stereoscopic microscope and the proportion of individual fossils of vascular plants and mosses to the total number of plant macrofossils counted was obtained. The fossil carpological remains and vegetative fragments (leaves, rootlets, epidermis) were identified using identification keys (Smith, 2004; Maquoy and van Geel, 2007) and recent collection materials in the Department of Biogeography and Paleoecology at Adam Mickiewicz University in Poznan. Per centage volumes of the different vegetative remains and *Sphagnum* sections were estimated to the nearest 5%. The numbers of seeds, fruits, needles, bud scales and leaves were counted separately. The relative proportions of taxonomic groups of *Sphagnum* were estimated on the basis of the branch leaves, which were investigated under the...
microscope on two 22 × 22-mm cover glasses. The identification of Sphagnum taxa to the species level was performed separately on the basis of the stem leaves and cross-sections using specialist keys (Hölzer, 2010; Laine et al., 2011), and compared to modern reference material. We use the nomenclature of Mirek et al. (2002) for vascular plants and Ochyra et al. (2003) for bryophytes. Plant macrofossil diagrams were drafted using C2 software (Juggins, 2003).

3.3. Testate amoebae

Testate amoebae were used to reconstruct the palaeohydrological conditions of the peatlands (e.g. Booth et al., 2008; Swindles et al., 2015a, 2015b). Testate amoebae were extracted using a modified version of Booth et al. (2010). Peat samples, 2 cm³ in volume from 1-cm thick slices, were boiled in water for 15 min to disaggregate the peat. The peat-water mix was filtered using a 300 μm sieve, the filtrate was back-sieved at 15 μm and then allowed to settle. The 15–300 μm fraction was then observed under the microscope (200–400 × magnification). A total of 100 to 200 amoebae per sample were counted and identified to species level or “type”. The transfer function of Swindles et al. (2015b) developed for permafrost peatlands in Northern Sweden was used to reconstruct past water-table depths (WTD).

4. Results

4.1. Handle Lake, Canada

Sphagnum riparium macrofossils (branch and stems leaves) were recorded in an 11-cm thick peat layer together with Sphagnum angustifolium (Fig. 2A). The peat layer with Sphagnum riparium was developed between the layers formed by Sphagnum capillifolium and Sphagnum fuscum. A peat layer at 43 cm depth in the monolith was dated to be 3390–3239 cal yr BP. The reduction in their proportion relative to other plant macrofossils at ~25 cm occurs at about 2755–2378 cal yr BP (Table 1). The most common testate amoebae immediately above this level were the hydrophilous species Archerella flavum, Hyalosphenia papilio, and Difflugia globulosa. Reconstructed WTD ranged between about 4 to 0 cm under the peatland surface (Fig. 3A). The WTD shift from dry to wet and to dry again was documented.

4.2. Crater Pool, N Sweden

Sphagnum riparium macrofossils (branch and stems leaves) were found in a 7-cm thick layer (Fig. 2B). In the upper part Drepanocladius sp. was also present. The peat layer containing Sphagnum riparium...
accumulated about 1000 cal yr BP (Table 1). The most common testate amoebae were hydrophilous *Archerella flavum*, *Hyalosphenia papilio* alongside the xerophilous *Nebela militaris*. Reconstructed WTD ranged between about 25 to 12 cm under the peatland surface (Fig. 3B).

4.3. “Banana” bog, Northern Urals, Mountains, Russia

*Sphagnum riparium* macrofossils (only branch leaves) were found in a 10-cm thick peat layer (Fig. 2C), which accumulated about 3000 cal yr BP in the lower part of the profile (Table 1). The most common testate amoebae encountered there were hydrophilous *Archerella flavum*, *Hyalosphenia papilio* and *Difflugia globulosa*. Reconstructed WTD ranged between about 11 to 1 cm under the peatland surface (Fig. 3C).

5. Discussion

5.1. *Sphagnum riparium* macrofossils in Holocene records

*Sphagnum riparium* is one of the rarest *Sphagnum* mosses reported from fossil records. In fact, to our knowledge, there is no record on the distribution of *Sphagnum riparium* in peat layers older than the Holocene. The oldest known *Sphagnum riparium* macrofossil has been dated to ca. 5900 cal yr BP and was found in the tundra zone in Russia, Arkhangelsk Region (Kultti et al., 2004, Table 2). The species has also been found in SW Nunavut, Canada at about 5700 cal yr BP (Sannel and Kuhry, 2008, Table 2). However, according to Oleg Kuznetsov (pers. comm.) peat layers containing *Sphagnum riparium* from the Preboreal period have been observed in Karelia, Russia. The data we present here may suggest that the range of *S. riparium* increased during the Late Holocene. It can be partly linked to peatland development processes (succession from rich fen to oligotrophic bog) that would have favoured the spread of *Sphagnum riparium*.

*Sphagnum riparium* can be considered to be a peat forming species. However, peat layers formed by this species are usually less than 50 cm thick (e.g. Novenko et al., 2009; Kultti et al., 2004; Kuhry, 2008; Oksanen et al., 2001; Fillion et al., 2014; Routh et al., 2014). Until now almost all sites with *Sphagnum riparium* are located in the sub-arctic zone; although it is present in contemporary temperate Europe, but has not been found in the peat archive there (e.g. Hölder, 2010; Smith, 2004; Melosik, 2006; Wojtun et al., 2013).

5.2. *Sphagnum riparium* in palaeoecological interpretations and implications for conservation

*Sphagnum riparium* can be considered to be an indicator of wet and minerotrophic habitats in palaeoecological records. According to the testate amoeba-based water-table reconstructions, *Sphagnum riparium* grew in moderately wet to wet habitats, with a water-table ranging between 25 and 0 cm under the surface, but mostly in those with a water-table ranging between 10 and 0 cm (Fig. 3). Our results and previously published work show that *Sphagnum riparium* macrofossils were usually found in peat profiles indicating transition phases between rich fen and bog (Table 2). The wet and minerotrophic habitat of *Sphagnum riparium* in the past is supported by the common presence of *Sphagnum riparium* macrofossils alongside *Sphagnum angustifolium*, *Sphagnum lindbergii*, *Sphagnum jensenii/balticum*, and *Warnstorfa fluviatilis*.
These moss species usually grow in wet and relatively minerotrophic habitats (Crum, 1992; Daniels and Eddy, 1985; Hölzer, 2010; Laine et al., 2011; Smith, 2004). In some sites, the peatland development pathway followed a gradual succession from wet fen to relatively dry bog (hummocks) conditions with a shift in dominance towards Sphagnum species such as Sphagnum fuscum (e.g. Kuhry, 2008, Sannel & Kuhry, 2008; our site in Canada). The disappearance of Sphagnum riparium at our study sites and at other sites described in the literature were thus likely caused by an autogenic trophic shift and succession towards more acidophilic conditions favourable to species such as Sphagnum fuscum, Sphagnum angustifolium and Sphagnum russowii. Once the peatlands reach the ombrotrophic phase in their development, the growth of S. riparium is likely limited by the increasing nutrient-limitation to which other species are better adapted. Furthermore, in the sub-arctic region, Sphagnum riparium is considered to be a typical collapse scar species (Zoltai, 1993; Oksanen et al., 2001; Kuhry, 2008) that can appear in the wet (and relatively nutrient-rich) depressions after permafrost degradation. According to Zoltai (1993)

![Fig. 3. Percentage testate amoeba diagrams alongside Sphagnum riparium abundance and reconstructed water tables in the three peatlands: A) Handle Lake, Canada, B) Crater Pool, Sweden, C) Banana bog, Russia.](image-url)
Table 2
Subfossil Sphagnum riparium in the Northern Hemisphere.

<table>
<thead>
<tr>
<th>Site description (location, please look at Fig. 1)</th>
<th>Age of the peat layer with Sphagnum riparium</th>
<th>Plant composition</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>A) Canada, Handle Lake, BHHL-01, NW Canada near the City of Yellowknife</td>
<td>Between 2500 and 3200 cal yr BP</td>
<td>Sphagnum angustifolium, S. capillifolium, Chamedaphne calyculata, Andromeda glaucophyta, Oxycoccus palustris</td>
<td>This study</td>
</tr>
<tr>
<td>B) Sweden, Crater Pool, Abisko region</td>
<td>ca. 1000 cal yr BP</td>
<td>Sphagnum russowii, Drepanoclados sp., Betula nana</td>
<td>This study</td>
</tr>
<tr>
<td>C) Russia, the upper Pezoria River region, Banana bog</td>
<td>ca. 3100 cal yr BP</td>
<td>Sphagnum cf. girgensohni</td>
<td>This study</td>
</tr>
<tr>
<td>1. Canada, The Hercherm palsa, the Hudson Bay Lowlands of northeastern Manitoba along the railroad between Gills and Churchill</td>
<td>ca. 2250–800 cal yr BP and ca. 500 cal yr BP to AD 1960</td>
<td>Sphagnum jenseni/balticum, Sphagnum lindbergii, Sphagnum magellanicum, Picea and Larix (needles) and Ericaceae (including Oxycoccus and Chamaedaphne (leaves))</td>
<td>Kuhry, 2008</td>
</tr>
<tr>
<td>2. Canada, Nunavut and Saskatchewan, peatlands located close to Ennadai Lake and Selwyn Lake</td>
<td>ca. 5700–4800 cal yr BP</td>
<td>Sphagnum lindbergii, Sphagnum cuspidatum, Sphagnum teres, Sphagnum balticum, Calliergon stramineum</td>
<td>Sannel and Kuhry, 2008</td>
</tr>
<tr>
<td>4. Canada, northern Québec, peatland located near Whapmagoostui-Kuujjuarapik</td>
<td>ca. 500 cal yr BP to present</td>
<td>Sphagnum lindbergii, Calliergon stramineum, Drepanoclados euanulatus/fluitans</td>
<td>Roy, 2007; Arlen-Pouliot and Bhiry, 2005; Fillion et al., 2014</td>
</tr>
<tr>
<td>5. Russia, Rogovaya River peat plateau</td>
<td>ca. 3400 to ca. 2300 cal yr BP</td>
<td>Sphagnum lindbergii, Sphagnum balticum, Warnstorfia cf. fluitans, Warnstorfia cf. examinulatum, Carex sp.</td>
<td>Oksanen et al., 2001</td>
</tr>
<tr>
<td>6. Russia, district of the Arkhangelsk Region</td>
<td>ca. 5900–4500 cal yr BP</td>
<td>Sphagnum lindbergii, Sphagnum annulatum, Warnstorfia fluitans, Scheuchzeria palustris</td>
<td>Kulthi et al., 2004</td>
</tr>
<tr>
<td>7. Russia, west of the Ural Mountains, near the village of Seida</td>
<td>ca. 800 yr to present</td>
<td>Sphagnum lindbergii, Sphagnum jenseni, Sphagnum fallax Drepanoclados cf. fluitans, Calliergon sp.</td>
<td>Routh et al., 2014</td>
</tr>
<tr>
<td>8. Russia, the Tver’ region, Staroselsky Moch’ mire</td>
<td>Not older than 200 cal yr BP</td>
<td>Sphagnum gregensomnii, Sphagnum nemoreum, Sphagnum squarrosum</td>
<td>Novenko et al., 2009</td>
</tr>
<tr>
<td>9. Russia, Karelia</td>
<td>Preboreal period</td>
<td>Lack of data</td>
<td>Oleg Kuznetsov (pers. comm.)</td>
</tr>
</tbody>
</table>

Sphagnum riparium is commonly a pioneer species in peatlands that experience a rise in water-table. The present-day habitat of Sphagnum riparium confirms our palaeoecological reconstructions. This species has been documented in the Northern Hemisphere habitats where water tables were shallow. Gignac et al. (1991) found that in western Canada, its maximum abundance was when the water-table was near the surface and pH was about 5.6. In the western Siberian arctic zone (Yamal Peninsula), it forms loose mats in hummocky sedge-Sphagnum mires, and is often associated with Sphagnum fimbriatum and Sphagnum girgensohnii (Czernyadyeva, 2001). In the Białowieża Forest (Poland), it is found in mesotrophic spruce forest within hollows containing stagnant water (Melosik, 2006). In Scandinavia, it forms loose carpets in moist conditions such as fens and along streams, ditches and lake shores and with Sphagnum lindbergii, Sphagnum teres, Sphagnum angustifolium (Laine et al., 2011). In Schwarzwald (SW Germany), it grows in the wet edges of oligotrophic peatlands alongside Sphagnum squarrosum, Sphagnum fallax and Sphagnum girgensohnii (Hölzer, 2010). Sphagnum riparium is considered to be a highly productive species, and can accelerate the terrestrialisation of fens in drained sites, creating suitable microhabitats for other species to colonise (Kangas et al., 2014). Sphagnum riparium may thus represent a key species for recolonising disturbed peatlands. It may be favoured in northern regions experiencing rapid climate warming leading to permafrost degradation and elsewhere in places where formerly ombrotrophic peatlands are transforming into wetter, more minerotrophic ecosystems due to peat extraction or hydrological changes (Vitt et al., 1994; Jorgenson et al., 2001; Swindles et al, 2015c).

6. Summary

1. The presence of Sphagnum riparium macrofossils in peat profiles can be interpreted as an indication of wet minerotrophic conditions, often corresponding to an increase in water level and establishment of a wet habitat.

2. Sphagnum riparium is a peat forming species in the sub-arctic and boreal zone, however peat layers dominated by its macrofossils are not thick (usually <50 cm).

3. The subfossil occurrence of Sphagnum riparium in the Northern Hemisphere may indicate that the range of this species increased during the Late Holocene.

4. The reconstructed environment of Sphagnum riparium in the Holocene is consistent with the modern ecology of this species in the Northern Hemisphere.

Acknowledgements

AMS dating of one sample was funded by the National Science Centre in Poland (project: DEC-2013/09/B/ST10/01589, primary investigator M.G.). Funding was provided by the Geological Survey of Canada (Environmental Geoscience Program; activity lead J.M.G.) and Polar Knowledge Canada (Project 1516–149, primary investigators J.M.G., R.T.P.). G.T.S. acknowledges the Worldwide University Network (WUN) for funding fieldwork in Abisko (Project: Arctic Environments, Vulnerabilities and Opportunities). The work was partly supported by the Russian Science Foundation (grant 14-50-00029 for Yu.M.) and Russian Foundation for Basic Research (grant 17-04-00320 for A.N.T.). E.A.D.M. acknowledges funding by the Scientific & Technological Cooperation Program Switzerland-Russia–federal exchange project (grant IZLR Z3 128338 Q4655). We thank Adam Hölzer for help in the identification of mosses species and the valuable review, that allowed us improve manuscript. We are grateful for the support of Nicole Couture (Geological Survey of Canada) for providing comments to improve the paper and of Clare Miller (Queen’s University) and Lisa Neville (Geological Survey of Canada) for assistance in collection of the Handle Lake peatland material.

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