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

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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.

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; Gałka et al., 2017a, 2017b, 2017c). Certain species are indicators of wet habitats such as

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Sphagnum cuspidatum, Sphagnum majus and *Sphagnum balticum* (Barber et al., 2003; Valiranta et al., 2012; Gałka et al., 2017b, 2017c), whereas others are indicative of drier habitats, including peat hummocks (e.g. *Sphagnum fuscum, Sphagnum capillifolium* (Kuhry, 2008; Hölzer, 2010; Valiranta et al., 2012; Gałka 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. *Sphagnum fuscum* and *Sphagnum austinii*, they may indicate hydrological disturbance in the peatland catchment such as deforestation, moderate nutrient input from agriculture, or deposition of dust on the peatland (e.g. van Geel and Middeldorp, 1988; McClymont et al., 2008; Gałka and Lamentowicz, 2014; Gałka et al., 2015; Swindles et al., 2015a).

Detailed palaeoecological studies provide information on the past distribution of peat forming vegetation, temporal patterns of vegetation change, and likely drivers of change (Overbeck, 1975; Barber, 1981; Zoltai, 1993; Halsey et al., 2000; Gajewski et al., 2001; Swindles et al., 2015a). This information is useful for environmental protection efforts as it provides insight into present ecosystem states and can be used to define restoration targets and trajectories of change following disturbance (Chambers et al., 2013; McCarroll et al., 2016; Swindles et al., 2016; Gałka et al., 2017a). Moreover, data on the past occurrence of *Sphagnum* species can potentially contribute to our understanding of *Sphagnum* refugia during the Quaternary which is currently based mostly on DNA analysis (e.g. Szövenyi et al., 2006; Kyrkjeeide et al., 2012, 2014).

Sphagnum riparium (Ångström) is a very rare subfossil in peat archives and is also a rare constituent in modern plant communities. This species belongs to section Cuspidata and its distribution is described as circumpolar, sub-arctic to northern with slightly continental tendencies (Daniels and Eddy, 1985; Crum, 1992; Smith, 2004; McQueen and Andrus, 2007; Hölzer, 2010; Laine et al., 2011). It occurs as far north as 77°04′N in the Wedel Jarlsberg Land, Spitsbergen, in the Arctic Svalbard Archipelago (Wojtuń, 2007), is found mostly in minerotrophic conditions, and forms loose carpets in moist conditions, such as lake margins, open hollows in poor-fens, and among rushes on moderately-nutrient rich ground (Daniels and Eddy, 1985; Smith, 2004; McQueen and Andrus, 2007; Hölzer, 2010; Laine et al., 2011; Graham et al., 2016).

Our high-resolution plant macrofossil data supported by the results of testate amoeba analysis presented here fills a knowledge gap on the palaeoecology of *Sphagnum riparium* in the Northern Hemisphere. We provide three new palaeoecological records containing the presence of *Sphagnum riparium* and review all published subfossil data for this species (to the best of our knowledge). The main aims of our study are: (i) to study the past occurrence of *Sphagnum riparium* in three new peat records from contrasting climatic settings in the Northern Hemisphere (Yellowknife, NW Canada; Abisko, N Sweden, and Northern Ural Mountains, NW Russia); and (ii) to compare the current and past ecology of *Sphagnum riparium* to better determine the causal factor for its rarity and hence provide baseline data for its conservation.

2. Study sites

Handle Lake peatland (62°29′26.44″N, 114°23′18.23″W) is a degrading permafrost 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 intact palsa mire containing permafrost 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 uliginosum, 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 subzero 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 cm^3, 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; Mauquoy and van Geel, 2007) and recent collection materials in the Department of Biogeography and Paleoecology at Adam Mickiewicz University in Poznan. Percentage 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

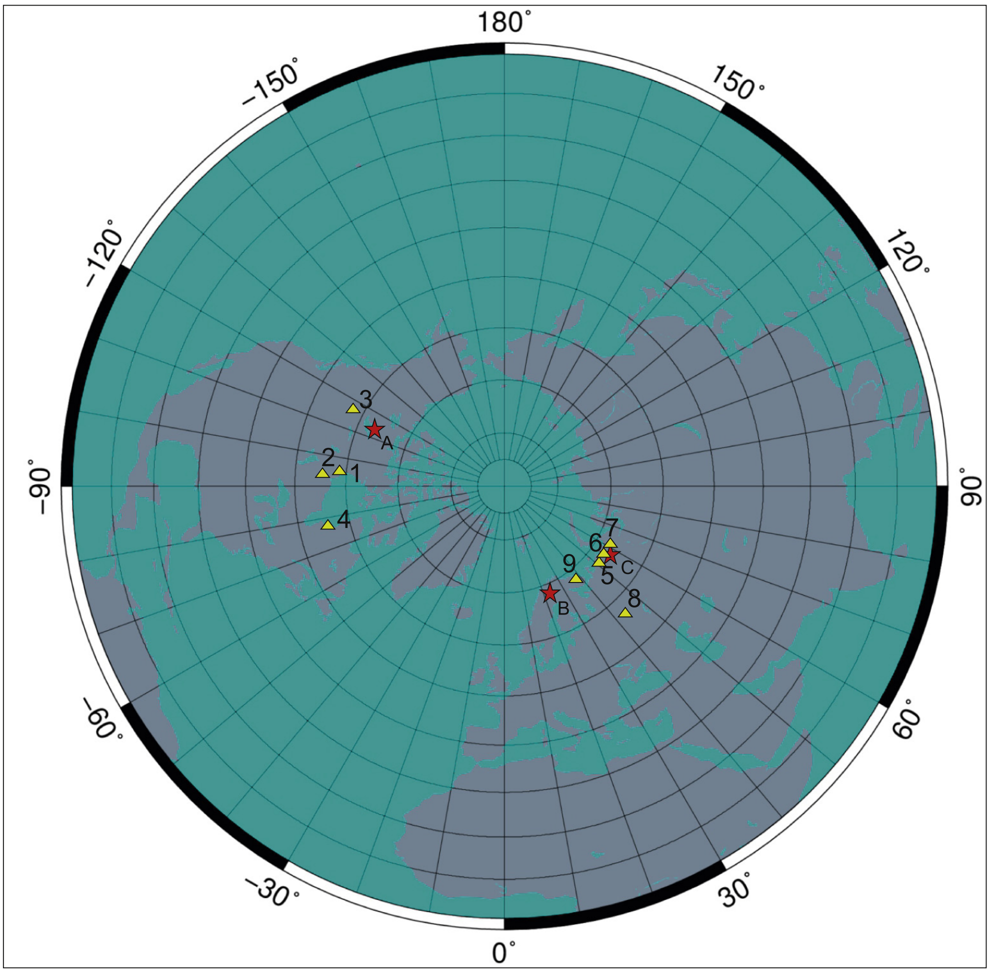

Fig. 1. Map of sites where subfossil *Sphagnum riparium* remains were discovered in the Northern Hemisphere. New findings presented in this paper (stars): A) Canada, Handle Lake peatland, B) Sweden, Crater Pool, C) Russia, Banana bog. Published data (triangles): 1. Kuhry (2008), 2. Sannel and Kuhry (2008), 3. Zoltai (1993), 4. Arlen-Pouliot and Bhiry (2005), Roy (2007), Fillion et al. (2014), 5. Oksanen et al. (2001), 6. Kultti et al. (2004), 7. Routh et al. (2014), 8. Novenko et al. (2009), 9. Oleg Kuznetsov (pers. comm.). Further data are shown in Table 2.
Map source: https://placeandthings.wordpress.com/africa/the-earths-hemispheres/northern-hemisphere.

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 cm^3 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 *Drepanocladus* sp. was also present. The peat layer containing *Sphagnum riparium*

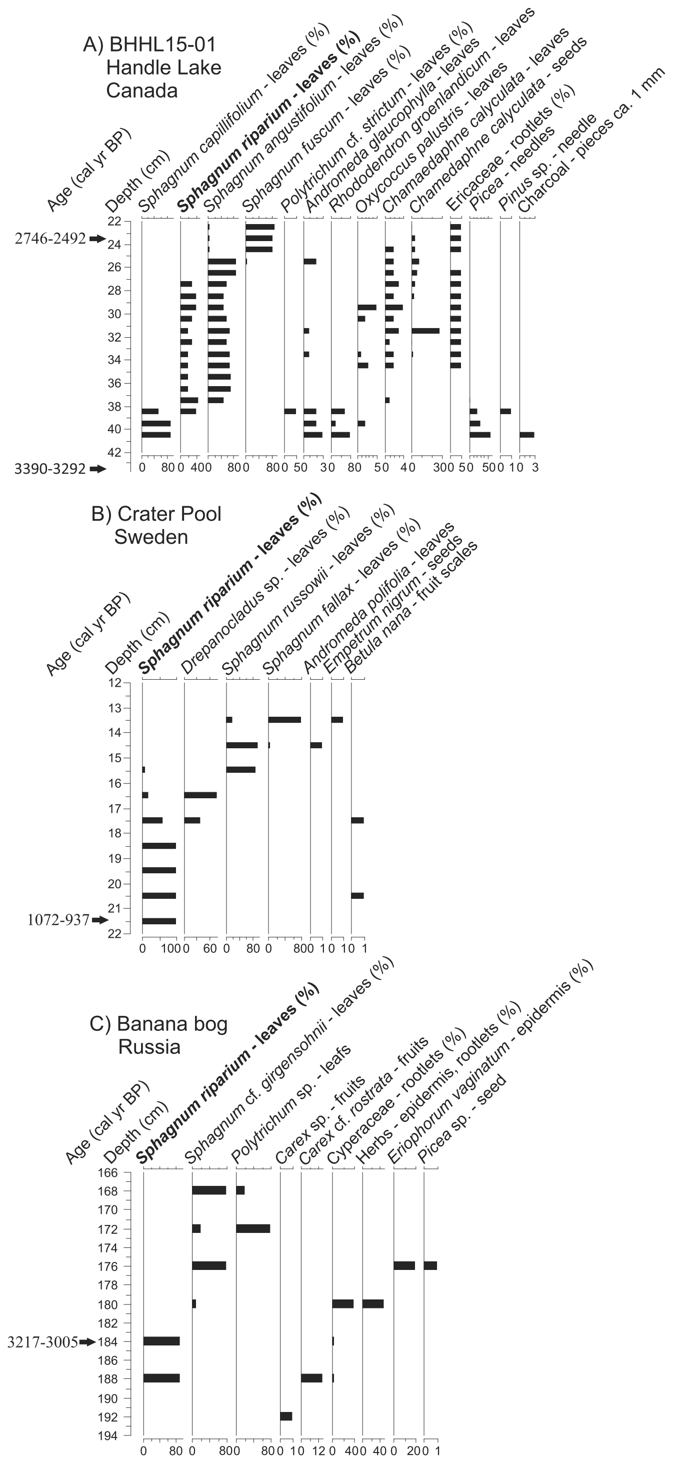

Fig. 2. Percentage plant macrofossil diagram presenting local vegetation development in the three peatlands: A) Handle Lake, Canada, B) Crater Pool, Sweden, C) Banana bog, Russia.

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 Ural 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. Hölzer, 2010; Smith, 2004; Melosik, 2006; Wojtuń 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 *Warnstorfia fluitans*

Table 1
Radiocarbon dates from analysed sites.

Site/depth [cm]	Material	Lab. code - number	C14 date [BP]	Age [cal yr BP] (95.4%)
Canada, Handle Lake 24–25	*Sphagnum fuscum* stems	UOC-1944	2530 ± 30 BP	2755–2378
Canada, Handle Lake 44–44	*Sphagnum* cf. *capilifolium* stems + 1 needle of *Picea mariana* + 1 fragm. needle of *Pinus* sp.	UOC-1945	3113 ± 30	3390–3292
Sweden, Crater Pool 21–22	*Sphagnum riparium* stems with leaves	Poz-80223	1110 ± 30 BP	1072–937
Russia, Banana bog 184	15 fruits of *Carex* cf. *rostrata*	Poz-51259	2965 ± 30 BP	3217–3005

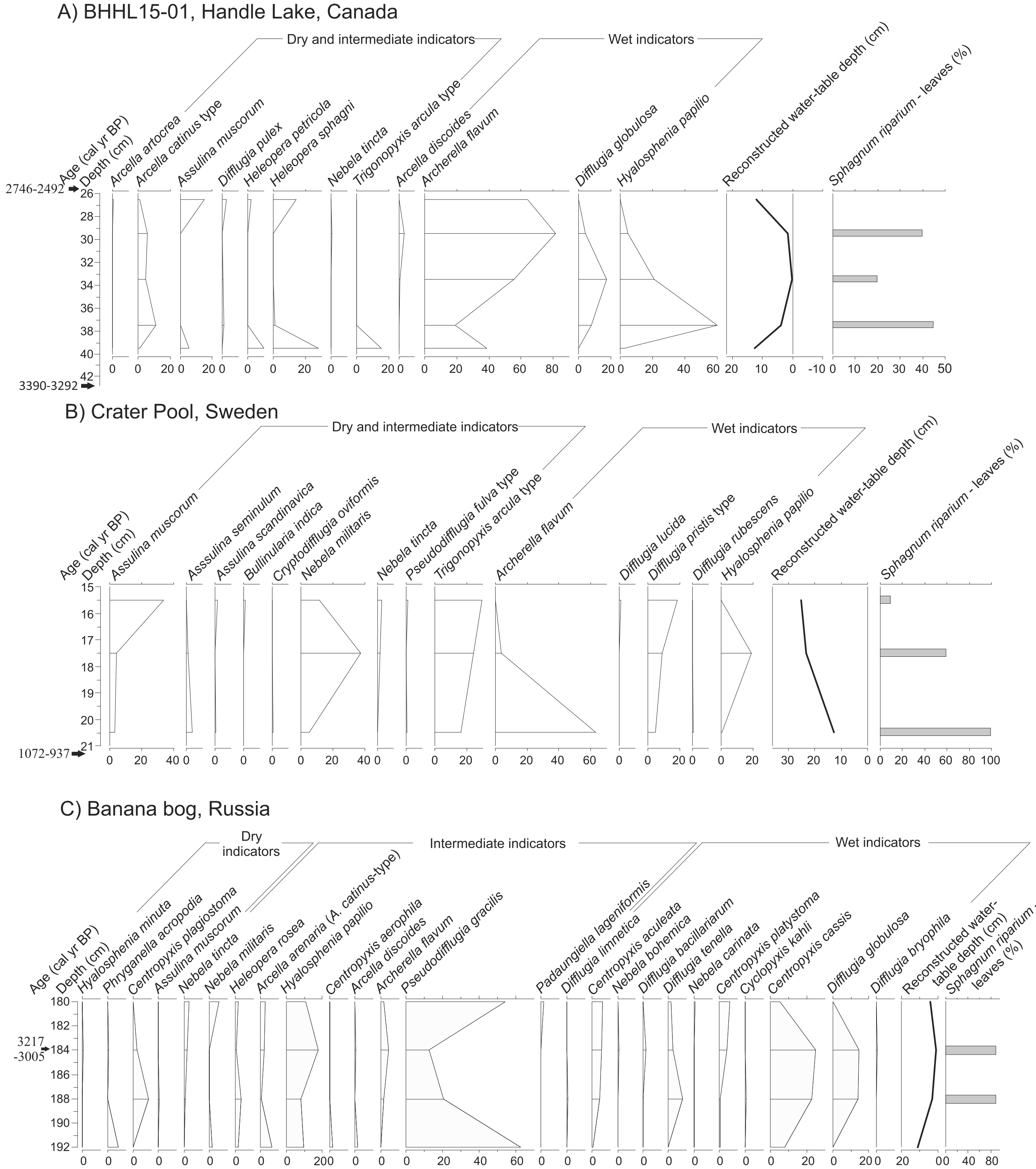

Fig. 3. Percentage testate amoeba diagrams alongside *Sphagnum riparium* abundance and reconstructed water tables in the three peatlands: A) Handle Lake, Canada, B) Crater Pool, Sweden, C) Banana bog, Russia.

(Table 2). 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)

Table 2
Subfossil *Sphagnum riparium* in the Northern Hemisphere.

Site description (location, please look at Fig. 1)	Age of the peat layer with *Sphagnum riparium*	Plant composition	Reference
A) Canada, Handle Lake, BHHL-01, NW Canada near the City of Yellowknife	Between 2500 and 3200 cal yr BP	*Sphagnum angustifolium, S. capillifolium, Chamedaphne calyculata, Andromeda glaucophyla, Oxycoccus palustris*	This study
B) Sweden, Crater Pool, Abisko region	ca. 1000 cal yr BP	*Sphagnum russowii, Drepanocladus* sp., *Betula nana*	This study
C) Russia, the upper Peczora River region, Banana bog	ca. 3100 cal yr BP	*Sphagnum* cf. *girgensohnii*	This study
1. Canada, The Herchmer palsa, the Hudson Bay Lowlands of northeastern Manitoba along the railroad between Gillam and Churchill	ca. 2250–800 cal yr BP and ca. 500 cal yr BP to AD 1960	*Sphagnum jensenii/balticum, Sphagnum lindbergii, Sphagnum magellanicum, Picea and Larix* (needles) and *Ericaceous* (including *Oxycoccus* and *Chamaedaphne* (leaves))	Kuhry, 2008
2. Canada, Nunavut and Saskatchewan, peatlands located close to Ennadai Lake and Selwyn Lake	ca. 5700–4800 cal yr BP	*Sphagnum lindbergii, Sphagnum cuspidatum, Sphagnum teres, Sphagnum balticum, Calliergon stramineum*	Sannel and Kuhry, 2008
3. Canada, northwestern Alberta	ca. 4440–3800 cal yr BP, ca. 1530–1180 cal yr BP, ca. 1230–790 cal yr BP	*Sphagnum angustifolium, Chamaedaphne calyculata, Eriophorum brachyantherum*	Zoltai, 1993
4. Canada, northern Québec, peatland located near Whapmagoostui-Kuujjuarapik	ca. 500 cal yr BP to present	*Sphagnum lindbergii, Calliergon stramineum, Drepanocladus exannulatus/fluitans*	Roy, 2007; Arlen-Pouliot and Bhiry, 2005; Fillion et al., 2014
5. Russia, Rogovaya River peat plateau	ca. 3400 to ca. 2300 cal yr BP	*Sphagnum lindbergii, Sphagnum balticum, Warnstorfia* cf. *fluitans, Warnstorfia* cf. *exannulata, Carex* sp.	Oksanen et al., 2001
6. Russia, district of the Arkhangelsk Region	ca. 5900–4500 cal yr BP	*Sphagnum balticum, Sphagnum annulatum, Warnstorfia fluitans, Scheuchzeria palustris*	Kultti et al., 2004
7. Russia, west of the Ural Mountains, near the village of Seida	ca. 800 cal yr to present	*Sphagnum lindbergii, Sphagnum jensenii, Sphagnum fallax Drepanocladus* cf. *fluitans, Calliergon* sp.	Routh et al., 2014
8. Russia, the Tver' region, Staroselsky Moch' mire	Not older than 200 cal yr BP	*Sphagnum girgensohnii, Sphagnum nemoreum, Sphagnum squarrosum*	Novenko et al., 2009
9. Russia, Karelia	Preboreal period	Lack of data	Oleg Kuznetsov (pers. comm.)

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 hollows in hummocky sedge-*Sphagnum* mires, and is often associated with *Sphagnum fimbriatum* and *Sphagnum girgensohnii* (Czernyadjeva, 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 ditches 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 cases 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.

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