



Subfossil oribatid mite communities indicate Holocene permafrost dynamics in Canadian mires

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Permafrost thaw in peatlands is one of the most widespread and worrying consequences of climate warming in the sub-Arctic area. To predict future climate feedbacks, it is important to study the history of permafrost aggradation and thaw. Plant macrofossil analysis with radiocarbon dating has been widely used in detecting past permafrost dynamics in peatlands, however, due to a lack of permafrost-specific plant indicator species, determining the exact timing of permafrost aggradation remains a challenge. In this study, we investigated if oribatid mites can be used to determine Holocene permafrost aggradation and degradation in Canadian mires. Based on analyses of subfossil oribatid mite assemblages of Holocene peat profiles from two mires in the Hudson Bay Lowlands area, our results suggest that two species, *Carabodes labyrinthicus* and *Neoribates aurantiacus*, are useful bioindicators, which can be used in palaeoecological studies determining permafrost histories. Moreover, our results show that subfossil oribatid mite remains can reveal periods of permafrost, which cannot be determined with certainty based on plant macrofossils alone.

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Subfossil oribatid mites (Acari: Oribatida) have proven to be valuable bioindicators of ecological conditions in the geological past. Previously, oribatid mite subfossil remains found in lake sediments (e.g. Solhøy & Solhøy 2000; Presthus Heggen *et al.* 2010; Słowiński *et al.* 2018), river floodplains, peatlands (Golosova *et al.* 1985; Markkula 1986; Krivolutskii & Sidorchuk 2003; Sidorchuk 2004; Salisch *et al.* 2017; Markkula *et al.* 2018) and volcanic areas (Klinger *et al.* 1990) have been used to reconstruct past ecosystems and detect ecosystem change.

Oribatid mites are microscopic (0.1–1 mm) soil-dwelling invertebrates, which are abundant in most terrestrial ecosystems and among the most important decomposer groups of organic matter in peatlands (Behan-Pelletier & Bissett 1994; Mumladze *et al.* 2013). A characteristic feature of oribatid mite communities is a high coexistence of species: Up to 100 species can be found at one location (Behan-Pelletier & Newton 1999; Schatz & Behan-Pelletier 2008). There are both ecological and life-history characteristics associated with oribatid mites that make this soil faunal group suitable bioindicators. Unlike many other members of the soil fauna, oribatid mites often have low reproductive capacity and long life cycles, i.e. they are K-strategists (Behan-Pelletier 1999). Slow development, low fecundity and long larval stage of oribatid mites are characteristics that can help to indicate long-term disturbances in ecosystems (Gergocs & Hufnagel 2009). The distribution of oribatid mites is connected to different environmental factors, including water table levels, moisture conditions, food resources, vegetation composition and pH (e.g. Gao *et al.* 2016; Minor *et al.*

2016). Thus, species composition of oribatid mite communities can reflect prevailing environmental conditions and vegetation. Moreover, species compositions of oribatid mite communities usually differ between microhabitats in forest (Erdmann *et al.* 2012; Wehner *et al.* 2016) and peatland ecosystems (Sidorchuk 2008; Markkula 2014), and species that show high microhabitat specificity can be particularly valuable bioindicators.

In this era of climate warming, the need for bioindicator species that can be used to detect long-term environmental change in Arctic and sub-Arctic ecosystems is perhaps greater than ever. Amongst the ecosystems most vulnerable to warming are permafrost peatlands, which are found in northern Fennoscandia, Siberia, Canada and Alaska (Luoto *et al.* 2004). In recent decades, regional warming has caused accelerated thawing of permafrost in peatlands in different parts of the sub-Arctic area (Camill 2005; Aalto *et al.* 2017; Borge *et al.* 2017), which have led to changes in ecosystem structure, hydrological conditions and carbon cycling (Camill *et al.* 2001, 2009; Bosjö *et al.* 2012). In order to predict how sub-Arctic peatlands will react to increasing temperatures in the future, it is pivotal to understand their history of permafrost aggradation and degradation (Treat *et al.* 2016). Plant macrofossil analysis with radiocarbon dating is the most widely used method in studying past permafrost dynamics in peatlands. Permafrost dynamics can be reconstructed based on macrofossil plant assemblages and succession (e.g. Kuhry 2008; Gałka *et al.* 2018), and on the absence of certain species, which never occur in permafrost peatland habitats (Oksanen 2005). However, a lack of permafrost-specific plant indicator species can make it challenging to

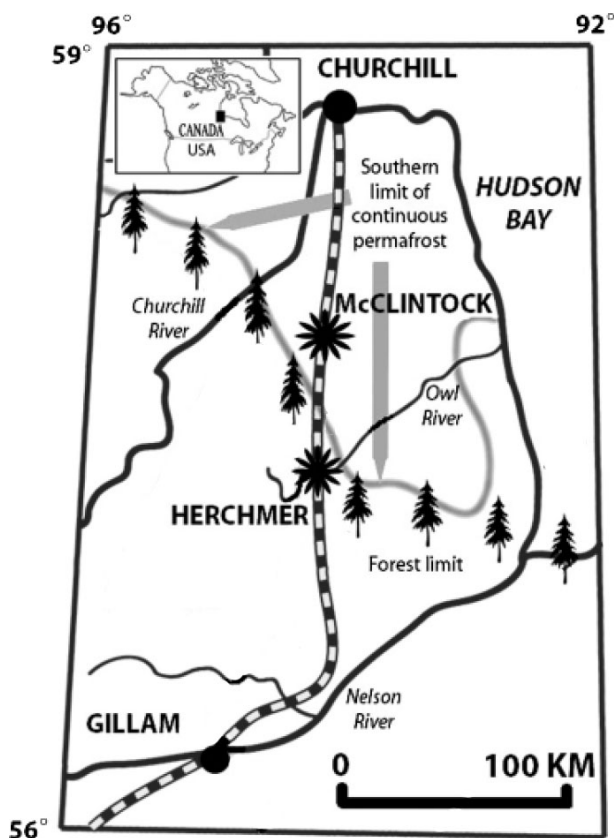


Fig. 1. Location of the Herchmer palsa and McClintock peat plateau sites along the railroad between Gillam and Churchill in Northeastern Manitoba. Map modified from Kuhry (2008).

determine the history and exact timing of permafrost aggradation within peatlands (Oksanen & Väliranta 2006; Sannel & Kuhry 2008; Camill *et al.* 2009; Treat *et al.* 2016).

Previous studies have pointed out that there is a need to develop and test new proxy methods to examine past and present environmental changes, in particular in sub-Arctic peatlands, which are undergoing rapid alterations in hydrology, vegetation and C-dynamics (Swindles *et al.* 2015; Gałka *et al.* 2018). Oribatid mites can be a promising new proxy. In a recent study, we found that three oribatid species, *Carabodes labyrinthicus*, *Neoribates aurantiacus* and *Chamobates borealis*, are promising bioindicators to detect past permafrost occurrence in northern European peatlands (Markkula *et al.* 2018). However, no studies have so far been conducted on the indicator potential of oribatid mites in Canadian permafrost mires. In this study, we analyzed subfossil oribatid mite assemblages in Holocene peat profiles from two mires in the permafrost region of northern Canada, and compared the results with earlier plant macrofossil records from the same sites. We aim to investigate if oribatid mite subfossil assemblages are able to identify stages of permafrost aggradation and search for specific oribatid species, which could indicate permafrost history and dynamics in Canadian mire ecosystems.

Material and methods

Research sites and peat profiles

The two investigated peatlands are situated in the Hudson Bay Lowlands of northeastern Manitoba, along the railroad between the towns of Gillam and Churchill (Fig. 1). The area belongs to the low to high sub-arctic ecoregions (Ecoregions Working Group 1989) and is situated at the border of the discontinuous and continuous permafrost zones (National Atlas of Canada 1995). Mean annual temperatures at Churchill Airport and Gillam Airport are -7.1 and -4.4 °C, respectively; annual precipitation is 412 mm for Churchill and 494 mm for Gillam (period 1961–1990, Canadian climate stations data, <https://climate.weather.gc.ca>).

Herchmer mire site ($57^{\circ}23'N$; $94^{\circ}11'W$; 106 m a.p.s.l.) is characterized by a mosaic of habitats: treed palsa bogs, permafrost-free fens and ponds. From the Herchmer site, one peat core from a palsa hummock was subsampled and analyzed for subfossil oribatid mites. Palsa hummocks in Herchmer raise about 1.5 m above the fen surface, and vegetation consists of sparse *Picea mariana*, *Rhododendron* and other ericaceous dwarf shrubs, *Rubus chamaemorus*, and lichens or *Sphagnum fuscum* in the ground layer.

McClintock mire site ($57^{\circ}50'N$; $94^{\circ}12'W$; 85 m a.p.s.l.) is an extensive peat plateau with scattered thermokarst lakes. From McClintock, two peat cores were subsampled and analyzed for oribatid mites, one from a peat plateau site and one from a fen site along the margin of a thermokarst pond at approximately 3 m distance from the peat plateau edge. The peat plateau is elevated by about 1 m relative to the adjacent thermokarst lake and is characterized by dry and acidic surface conditions. Vegetation consists of sparse and dwarfed *Picea mariana*, *Rhododendron palustre* and lichens in the more extensive, drier surfaces. In slightly wetter sites, *Larix laricina*, *Chamaedaphne calyculata*, *Rhododendron groenlandicum*, *Rubus chamaemorus* and *Sphagnum fuscum* are found. At present, the fen site is permafrost-free and dominant vegetation includes *Carex* spp., *Eriophorum* sp. and *Sphagnum riparium*.

Peat profile excavation and plant macrofossil analyses

Subfossil oribatid mites were analyzed from peat profiles, which were originally collected to reconstruct peat plateau and palsa development and to study Late Holocene permafrost dynamics in the Hudson Bay Lowlands area, based on plant macrofossil analyses and radiocarbon dating (Kuhry 1998, 2008). Peat profiles were excavated in August 1992, from cleaned edges of a palsa at Herchmer and a peat plateau at McClintock sites. Several large blocks of material ($\sim 60 \times 15 \times 15$ cm) were cut out along the length of the profile to the mineral subsoil and wrapped for transportation. Sam-

ples from the adjacent fen site at McClintock were taken with a modified Macaulay peat sampler (half cylinder, 5 cm diameter). Coring was continued until mineral soil was reached. The material was stored in a half section of a PVC-pipe (1 m in length), which was wrapped for transportation. It should be noted, therefore, that the amount of material available for analysis is much more limited at the McClintock fen site, compared to the Herchmer palsa and McClintock peat plateau sites.

In the laboratory, a gross-stratigraphic description of each succession was made based on a visual scale of peat humification and the presence of wood, gyttja and minerogenic materials. Bulk organic samples for conventional and AMS-radiocarbon (accelerator mass spectrometry) dating were analyzed at the Alberta Environmental Centre in Vegreville (Canada) and the University of Helsinki (Finland), respectively. Radiocarbon ages were calibrated with the OxCal3 program (Bronk Ramsey 2001). The conventional radiocarbon analysis performed at the Alberta Environmental Centre in Vegreville (Canada) required large sample sizes. Particularly for the McClintock fen site, which was collected using the modified Macaulay peat sampler, large peat sections (6–8 cm in depth interval) had to be submitted for dating (Kuhry 1998). As a consequence, the quality of the chronological control at this site is much lower than that for the Herchmer palsa and McClintock peat plateau sites, where peat sections only 2–6 cm thick could be dated (Kuhry 2008).

Known volumes of material were taken for analyses of macrofossil remains (in general ~5 cm³, range 4–9 cm³). Samples were treated with a gently boiling 5% aqueous KOH -solution for deflocculation, and subsequently cleaned of fine debris by rinsing through a 150 µm sieve. Macrofossils were counted and recalculated as numbers per 5 cm³ of material (e.g. needles), or alternatively assessed as volume percentages of the sample used (e.g. mosses).

Oribatid mite subfossil extraction and identification

The remaining material from the peat profiles, not used for plant macrofossil and radiocarbon analyses, was stored at –18 °C (since 1992). In May 2016 and September 2018, subsamples of 25 cm³ were cut out from three peat profiles. Results from a previous study on permafrost peatlands in northern Europe (Markkula *et al.* 2018) had suggested that in order to obtain high enough counts significantly larger volumes of material are needed for subfossil oribatid mite analysis than for plant macrofossil analysis. Samples from McClintock peat plateau core were analyzed at 2–8 cm interval. Herchmer samples were analyzed at 2–6 cm interval between depths of 3–62 cm, at 10 cm interval between depths of 62–82, and 20 cm interval between depths of 82–162 cm. The lowermost layers were not analyzed for mites, as the numbers of mite subfossils found below

150 cm were very low. Samples from McClintock fen site were analyzed at 20 cm intervals. This subsampling strategy focused on the permafrost peatland sites and upper peat deposits, in which permafrost occurrence was likely based on the plant macrofossil records. Due to the limited amount of remaining material for the McClintock fen site, subsamples for oribatid mite analysis had to be collected from a larger depth interval (5–10 cm) compared to the Herchmer palsa and McClintock peat plateau sites (2 cm), lowering the temporal resolution of the record.

Subsamples were thawed at room temperature and mixed with water. Oribatid mite subfossils were hand-picked from the solution, and then identified to genus or species level by using light microscopy. All specimens that could be identified to species or genera were included in the analyses, and no minimum count size sets were used. Species identifications were based on Weigmann (2006), and information regarding Canadian oribatid fauna was gained from Canadian Biodiversity Information Facility (2019). Nomenclature follows Weigmann (2006) and Behan-Pelletier & Lindo (2019). The material is stored at the Zoological Museum of the University of Turku. Oribatid mite subfossil data is available at a Zenodo deposit (Markkula 2019).

Results

Oribatid subfossil assemblages

All together 1909 oribatid mite subfossils were recorded from 51 samples (25 cm³ in size). Most of these, 1268 specimens, are recorded from the McClintock peat plateau profile (Table 1). Most of the specimens were identified to higher taxonomic levels, because species identifications were difficult to conduct due to poor preservation of the subfossils and the lack of fresh reference material. Species and genera identified in this study and their known habitat preferences and indicator potential are presented in Table 2.

Comparisons of plant macrofossil and oribatid subfossil records

The oribatid subfossil community compositions are compared to the originally inferred permafrost dynamics based on plant macrofossil analyses at both study sites.

Table 1. Numbers of samples analyzed and oribatid mite subfossils counts.

Site	Habitat	N of samples analysed	N of oribatids identified	Mean N of specimen/sample
Herchmer	Palsa hummock	20	410	20.5
McClintock	Peat plateau	20	1268	63.4
McClintock	Fen	11	231	21.0

Table 2. Oribatid mite species and genera found in the peat cores, and known habitat preferences in upland and wetland settings. Species that were suggested as permafrost indicator species in an earlier study by Markkula *et al.* (2018) are marked with *. Habitat preferences according to Behan-Pelletier & Lindo (2019), Markkula (2014) and Markkula *et al.* (2018).

Taxon	Habitat	
	Upland	Wetland
<i>Limnozetes ciliatus</i> (Schrank 1803)		Aquatic
<i>Limnozetes</i> sp.		
<i>Hydrozetes</i> spp.		Aquatic
<i>Tectocephus velatus</i> (Michael 1880)	Tussock tundra, moss, forests, grass prairie	Mostly in hummocks, also among <i>Carex</i>
<i>Carabodes labyrinthicus</i> * (Michael 1879)	Tussock tundra, forests, lichen	Permafrost hummocks, among lichen
<i>Carabodes</i> sp.		
<i>Neoribates aurantiacus</i> * (Oudemans 1914)	Shrub tundra, among <i>Dryas</i> , <i>Empetrum</i> , <i>Vaccinium</i> and lichen	Permafrost hummocks, among lichen
<i>Diapterobates humeralis</i> (Hermann 1804)	Arboreal species in boreal forest, tussock tundra	Found in low numbers among lichen, <i>Empetrum</i> , <i>Rubus</i> and <i>Sphagnum</i>
<i>Ceratozetes</i> spp.		
<i>Trichobates</i> sp.		
<i>Schelorbates</i> sp.		
<i>Ceratoppia</i> sp.		
<i>Galumna</i> sp.		
<i>Camisia</i> sp.		
<i>Melanozetes</i> sp.		
<i>Punctoribates</i> sp.		
<i>Oppiidae</i> spp.		

Herchmer palsa site. – According to the plant macrofossil record, Herchmer palsa site remained permafrost-free until very recently (Fig. 2). The site developed from a treed wet rich fen (Zone A, 171–60 cm, ~6900–2100 cal. a BP) into an open wet rich fen (Zone B, 60–33 cm, ~2100–500 cal. a BP) and then into a treed wet poor fen (Zone C, 33–15 cm, ~500 cal. a BP to AD 1960) under permafrost-free conditions (Kuhry 2008; Fig. 2). Throughout these periods, aquatic and hygrophilous oribatid mites, including *Limnozetes ciliatus* and *Limnozetes* sp. and *Hydrozetes* spp. (Weigmann 2006) are found in abundance. Also, *Ceratozetes* spp. are common, and *Diapterobates humeralis* is present in low numbers (Fig. 2).

At depths between 0–15 cm (Zone D, ~AD 1960 to AD 1993), a rapid succession from *Sphagnum* Sect. *Acutifolia* (*S.* cf. *fuscum*) through *Polytrichum* to lichen remains occurs in the plant macrofossil record (Fig. 2). This

indicates palsa (permafrost hummock) formation, which took place at the Herchmer site after ~AD 1958±3 (Kuhry 2008). This succession is also reflected in oribatid mite assemblages. Aquatic oribatid mites, which dominated the subfossil assemblages in lower layers, disappear from the record, and *Carabodes labyrinthicus* and *Tectocephus velatus* become dominant (Fig. 2).

McClintock peat plateau site. – In the McClintock peat plateau site, Holocene permafrost conditions were dynamic and two former periods of permafrost aggradation and degradation were indicated based on plant macrofossils (Fig. 3).

In the lowermost part (zone A, until 111 cm, ~6700–5000 cal. a BP) the plant macrofossil record, dominated by detritus with *Calliergon* and *Drepanocladus* remains, indicates that the site was a shrubby wet rich fen under permafrost-free conditions (Kuhry 2008; Fig. 3). Only twelve oribatid specimen was found from this zone (from five samples between depths 112–154 cm), of which four *Limnozetes ciliatus*, one *Schelorbates* sp., one *Carabodes labyrinthicus* and two *Diapterobates humeralis* could be identified to species or genus level. Because oribatid subfossil counts were very low, we did not conduct comparisons with plant macrofossils for these peat layers.

The first permafrost phase characterized by treed bog vegetation in the McClintock peat plateau is dated to >2250 cal. a BP. In the depths between 111–71 cm (zone B, ~5000–2250 cal. a BP), *Larix* needles are abundant in the lower part, *Picea* needles and *Sphagnum* sect. *Acutifolia* remains are found throughout the zone, and *Polytrichum* occurs in the upper part (Fig. 3). *Polytrichum* is a characteristic moss of a permafrost environment, and this together with the rootlet peat found in the upper layers suggests that the site developed into a dry treed bog most likely underlain by permafrost (Kuhry 2008). However, it is difficult to assess the exact timing of permafrost aggradation based on plant macrofossils. In the oribatid record, hygrophilous oribatid mites (*Limnozetes ciliatus*, *Limnozetes* sp. and *Hydrozetes* sp.) are found throughout the zone, and are most abundant in the upper part. *Tectocephus velatus* is the dominant species in layers between 82–84 and 72–74 cm, but is absent in the layer between 74–76 cm. *Carabodes labyrinthicus* appears at a depth of 82–84 cm and increases in abundance towards the upper parts of the zone. Also, *Neoribates aurantiacus* is present in the two uppermost layers of the zone. *Diapterobates humeralis* is present in low numbers in most of the layers.

This first permafrost stage is followed by permafrost degradation, which is indicated by the sudden appearance of *Sphagnum lindbergii* and *S. riparium* at ~71 cm depth (Kuhry 2008; in Fig. 3 these are included in wet *Sphagnum*). According to the plant macrofossil record, the site was an intermediate to poor fen without permafrost for the following ~1500 calendar years (Zone C, 71–28 cm, 2250–800 cal. a BP). At this time, the oribatid community is dominated by *Limnozetes ciliatus*,

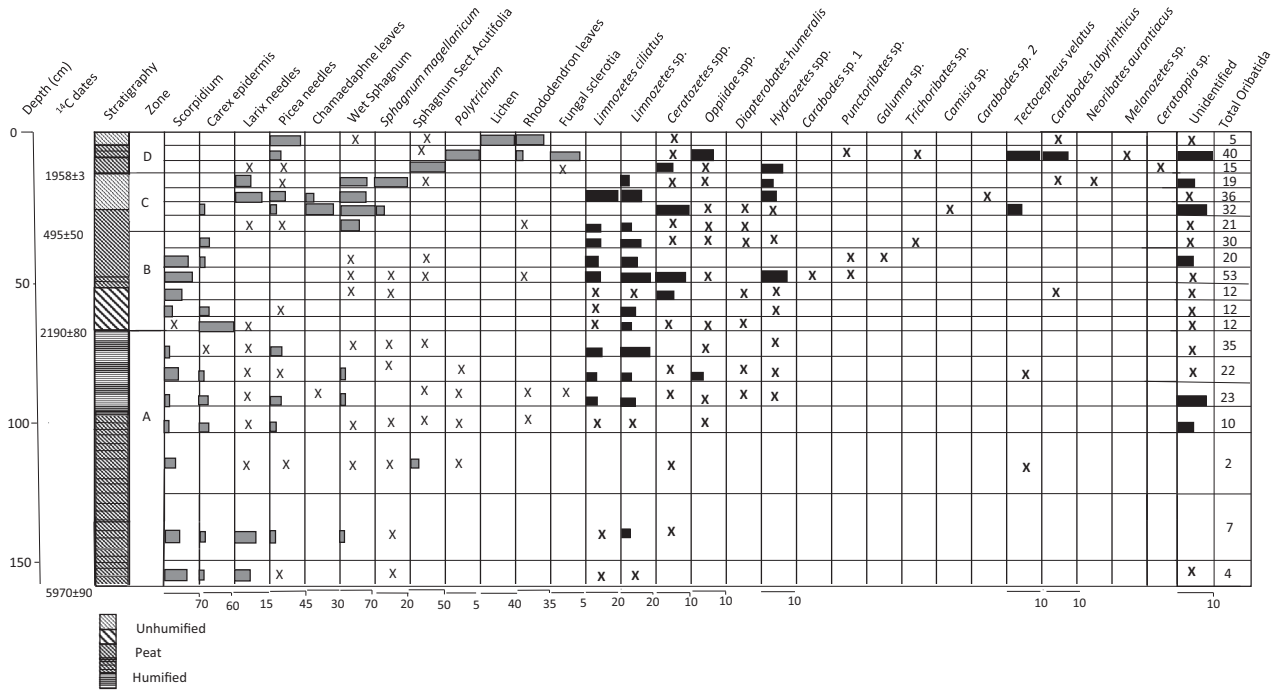


Fig. 2. Oribatid fossil mites per 25 cm³ and selected plant macrofossil taxa as volume percentages or counts per 5 cm³ in the Herchmer palsa site. 'x' denotes ≤ 3 individuals. Plant macrofossil analysis, radiocarbon dates and zonation according to Kuhry (2008). The following species are grouped into 'Wet Sphagnum': *S. jensenii*, *S. balticum*, *S. riparium*, *S. lindbergii*.

Limnozetes sp. and *Hydrozetes*. *Ceratozetes* spp. are also abundant, *Dipterobates humeralis* is occasionally present, *Carabodes labyrinthicus*, *Tectocephus velatus* and *Neoribates aurantiacus* are absent.

The second permafrost stage that developed at the site is found at depths 16–28 cm, dated to ~500 cal. a BP (Kuhry 2008). This can be interpreted from the rapid succession from *Sphagnum jensenii/balticum* from the previous zone through *Sphagnum* Sect. *Acutifolia* to the appearance of *Dicranum* in the plant macrofossil record (Fig. 3; Zone D, ~800–400 cal. a BP). *Tectocephus velatus* is present in the depths between 18–24 cm. *Carabodes labyrinthicus* is present at depth 18–20 cm, in the layer with abundant *Dicranum* remains.

A partial collapse of permafrost follows, indicated by dominance of *S. jensenii/balticum* and *S. lindbergii* (wet *Sphagnum*) remains at 0–16 cm depth (Zone E, ~400–0 cal. a BP). In the oribatid assemblages, *Limnozetes* sp. and *Limnozetes ciliatus* dominate in these layers. *Ceratozetes* sp. is occasionally abundant (Fig. 3). *Carabodes labyrinthicus* and *Tectocephus velatus* are absent. Also, *Dipterobates humeralis*, which was present in previous zone, is absent.

McClintock fen site. – The first stages at the McClintock fen site were dominated by a *Picea-Sphagnum jensenii/balticum* treed wet fen community (Fig. 4). Prior to ~1950 cal. a BP (depth of 106–114 cm), wet *Sphagnum* species are partly replaced by *Sphagnum fuscum* and *Polytrichum*, indicating relatively drier *in situ* conditions

(Fig. 4). Wetter conditions prevail again afterwards, with *Sphagnum jensenii/balticum*, *S. lindbergii* and *S. riparium* abundant in the record (Kuhry 1998). At depths between 40–60 cm, *Picea*, *Rhododendron*, *Polytrichum* and *Sphagnum fuscum* are again prominent. According to the plant macrofossil record, the site remained permafrost-free throughout its history, even though there is evidence for relatively drier *in situ* conditions indicated by the prevalence of *Polytrichum*, *Rhododendron* and *Sphagnum fuscum* prior to 1980 BP and in subrecent times (depths 40–60 cm, no dates are available).

Throughout the fen profile, the oribatid mite assemblages are dominated by *Limnozetes ciliatus*, *Limnozetes* sp. and *Hydrozetes* spp. *Carabodes labyrinthicus*, *Tectocephus velatus* and *Dipterobates humeralis* appear in the peat profile between depths 90–122 cm (Fig. 4). This combination of *C. labyrinthicus* and *T. velatus* occurring together with hygrophilous/aquatic species (*Limnozetes* and *Hydrozetes* spp., Weigmann 2006), is similar to the oribatid assemblage in the upper part of zone B in McClintock peat plateau site. Both these mite species are absent from the relatively dry interval recognized based on plant macrofossils at depths 40–60 cm.

Discussion

Oribatid mites indicating palsa hummock development

In the Herchmer palsa site, the plant macrofossil record indicates a very recent permafrost aggradation (Kuhry

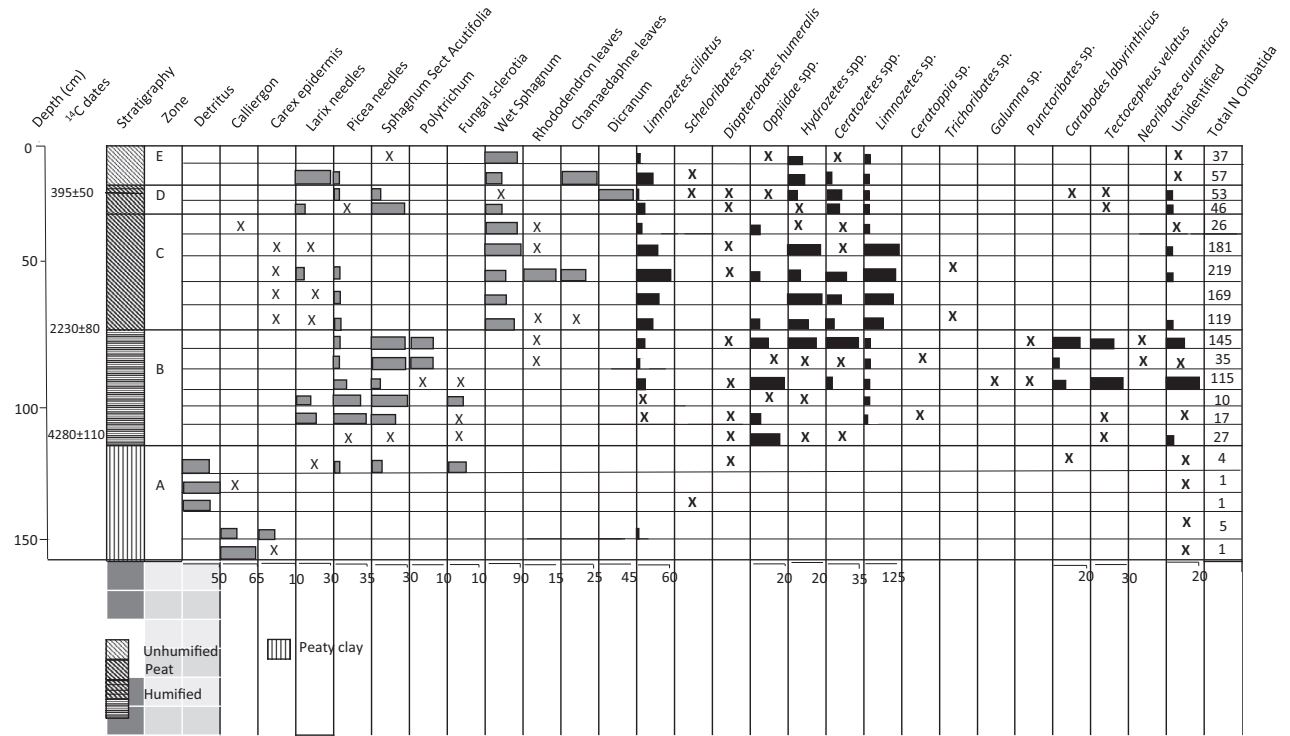


Fig 3. Oribatid fossil mites per 25 cm³ and selected plant macrofossil taxa as volume percentages or counts per 5 cm³ in the McClintock peat plateau site. ‘x’ denotes ≤3 individuals. Plant macrofossil analysis, radiocarbon dating and zonation according to Kuhry (2008). The following species are grouped into ‘Wet *Sphagnum*’: *S. jensenii*, *S. lindbergii* and *S. riparium*. *Sphagnum fuscum* and *S. warnstorffii* are included in *Sphagnum* Sect *Acutifolia*.

2008). The oribatid subfossil record is in line with this interpretation: At this time (Zone D), *Limnozetes ciliatus*, *Limnozetes* sp. and *Hydrozetes* spp. disappear from the oribatid record and *Tectocephus velatus* becomes dominant. *Carabodes labyrinthicus*, previously identified as permafrost indicator species in northern European palsas mires (Markkula *et al.* 2018), is abundant at 6 cm depth. A similar succession from a community of hygrophilous species to a dominance of *C. labyrinthicus* and *T. velatus* after palsa development has been recorded from a mire in northern Finland (Markkula *et al.* 2018).

Tectocephus velatus is thought to be a habitat generalist, but it is recorded to be the dominant species in the dry palsa hummocks in northern European palsa mires (Markkula 2014). *Carabodes labyrinthicus* occurs commonly in northern European peatlands in palsa hummocks among lichens (Markkula 2014; Markkula *et al.* 2018), upon which it feeds (Hågvar *et al.* 2014). This species is also commonly found under tree bark (Salvatulin 2019) and in tree canopies (Behan-Pelletier & Walter 2000), suggesting tolerance to very dry conditions. *C. labyrinthicus* has a wide geographical distribution and is found in boreal forests both in Central Europe (Nicolai 1986) and North America (Reeves 1988), and is recorded from e.g. Alaska and the Yukon Territories, but not from tundra underlain by permafrost in the Russian far east (Ryabinin 2015). However, due to its’ abundance in

permafrost mires (Markkula 2014; Markkula *et al.* 2018) and preference for a dry microhabitat, *C. labyrinthicus* seems to be a good indicator of permafrost in sub-Arctic peatland ecosystems.

Another possible permafrost indicator species, *Neoribates aurantiacus*, is found in the peat layer directly underlying the palsa peat (depth 16 cm) at the Herchmer site, together with *Carabodes labyrinthicus*. *N. aurantiacus* is known to occur in low numbers in palsa mires in Northern Europe, and its’ distribution is strongly connected to the presence of lichens (Markkula *et al.* 2018). It is not certain, however, whether these findings of subfossil remains of *C. labyrinthicus* and *N. aurantiacus* indicates a rapid transition towards permafrost conditions, or if it is a result from taphonomy. It is possible that oribatid mites move downwards in the peat for overwintering, in particular in palsa hummocks, which are barren, dry and cold habitats during winter, when wind blows the snow away and there is no insulation provided by snow cover (Markkula, personal observation). Studies based on isotope signals have shown that even though horizontal mobility is low among oribatid mites, they can move vertically between living and feeding places in forest soil and inside *Sphagnum* hummocks in peatlands (Scheu & Falca 2000; Lehmitz & Maraun 2016).

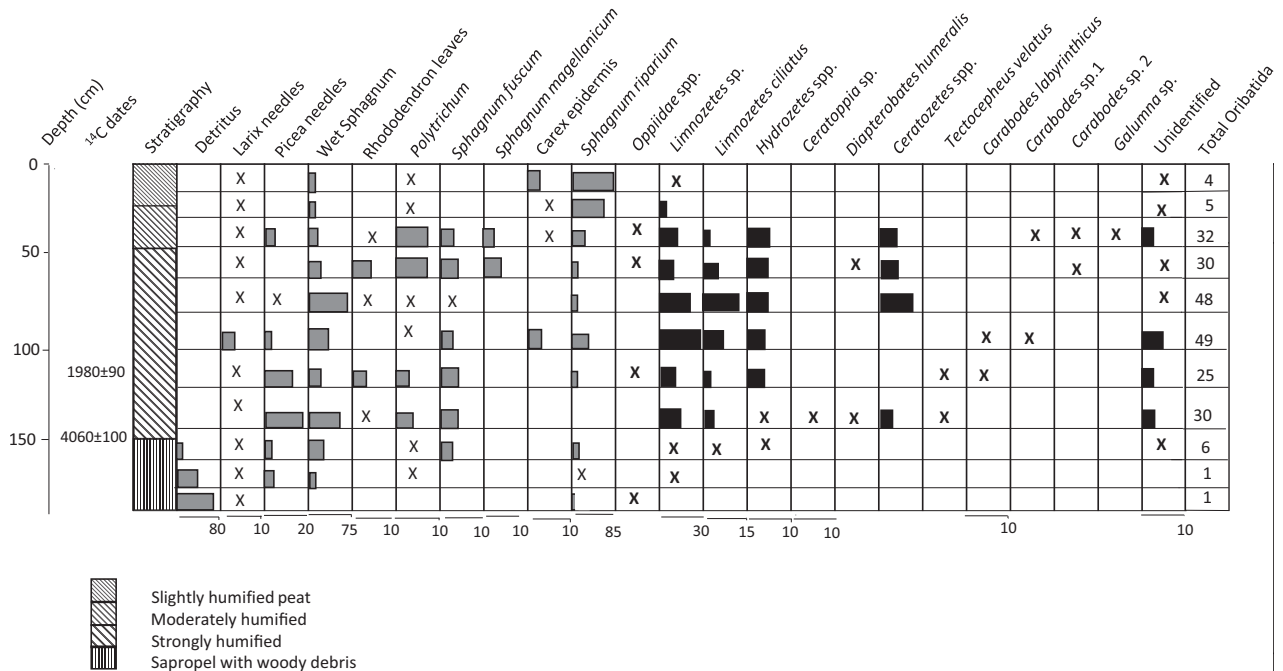


Fig. 4. Oribatid fossil mites per 25 cm³ and selected plant macrofossil taxa as volume percentages or counts per cm³ in the McClintock fen site. 'x' denotes ≤ 2 individuals. Plant macrofossil analysis and radiocarbon dates according to Kuhry (1998). The following species are grouped into 'Wet Sphagnum': *S. jensenii*, *S. balticum*, *S. cuspidatum*, *S. lindbergii*.

Permafrost dynamics in peat plateau and fen sites

Plant macrofossil records from the McClintock peat plateau site indicated two previous periods of permafrost aggradation and degradation, dated to >2250 (zone B) and ~500 (zone D) cal. a BP. The latest permafrost aggradation event into the present-day peat plateau conditions is of very recent age or occurred under wet surface conditions (see Kuhry 2008). These permafrost dynamics are well reflected in the oribatid mite assemblages. *Carabodes labyrinthicus* and *Tectocephus velatus* are abundant in the upper part of zone B, and present in zone D. Also, *Neoribates aurantiacus* is present in the upper parts of zone B. *Diapterobates humeralis*, an arboreal species in boreal forest, also frequently found in tussock tundra in areas of permafrost (Behan-Pelletier and Lindo 2019), occurred together with *T. velatus* in zone B. However, it was also present in zone C and absent from the top peat layers in the Herchmer site.

While in the Herchmer record there was a clear shift in taxon compositions in oribatid subfossil communities, in the McClintock record the species connected to dry conditions and permafrost co-exist with aquatic/hygrophilous *Limnozetes ciliatus*, *Limnozetes* sp. and *Hydrozetes* spp. This probably indicates the differences between palsa and peat plateau habitats, as peat plateau surfaces remain moister and can include wet spots, in contrast to those of palsas. For instance, in the vegetation survey of the

McClintock peat plateau, Kuhry (2008) reports the presence of *Sphagnum jensenii* in a permafrost-underlain fen on the peat plateau surface.

Interestingly, a similar taxon composition to that in zone B of the McClintock peat plateau site is found in the McClintock fen site, between the depths 90–122 cm, dated to roughly 1950 cal. a BP. Findings of *Polytrichum* and *Sphagnum fuscum* from the same depths provided evidence of temporary development of drier *in situ* conditions, possibly synchronous with the first permafrost stage at the McClintock peat plateau site (Kuhry 2008). However, presence of permafrost in the fen site could not be confirmed based on plant macrofossil analyses alone (Kuhry 1998). Findings of *Carabodes labyrinthicus* and *Tectocephus velatus* remains from these depths provide a new insight that permafrost occurred not only in the McClintock peat plateau site but also in the adjacent fen site prior to approximately 2000 years ago. Another relatively dry period at the fen site (40–60 cm; no dating available) can be tentatively correlated with the second permafrost stage at the peat plateau site, dated to ~500 cal. a BP. In this case, however, the oribatid record does not include any specific permafrost indicator taxa. As previously emphasized in the Material and Methods section, both the temporal resolution as well as the chronological control in the McClintock fen site is relatively poor, which precludes a precise correlation with the McClintock peat plateau record.

Indicator potential of oribatid mites in sub-Arctic peatlands

Difficulties in taxonomy are one of the limitations in oribatid mite subfossil studies (see Luoto 2009), in particular, because diagnostic body parts that are used for identification of fresh specimens are often lacking in fossils. This was also a challenge in our study, and most of the specimens analyzed could not be identified to species level.

Our results indicate that, in order to obtain high enough oribatid subfossil counts, much larger volumes of material are needed than for plant macrofossil analysis (Markkula *et al.* 2018). In this study, we used samples of 25 cm³ size. However, in certain cases it may be necessary to analyze even larger volumes of peat material.

Despite these challenges, results of this study support earlier findings suggesting that oribatid mites are potentially valuable indicators in determining past permafrost conditions in sub-Arctic peatlands (Markkula *et al.* 2018). Two oribatids, *Carabodes labyrinthicus* and *Neoribates aurantiacus*, previously identified as indicator species in northern European mires (Markkula *et al.* 2018), were connected to permafrost occurrence also in the Herchmer palsa and McClintock peat plateau mire sites. In addition, *Tectocephus velatus* can give insights of drier *in situ* and permafrost conditions, in particular when it occurs together with the above-mentioned indicator species.

Our subfossil records also included a few anomalous findings of *Carabodes labyrinthicus*. One individual was found at 52 cm depth in the Herchmer site (representing a open wet fen stage with brown mosses) and one at 113 cm depth in the McClintock site (treed *Picea-Sphagnum warnstorffii* stage). This can be a result of either taphonomy or, more likely, that specimens were brought to the site at the time by wind. Wind dispersal is common among arboreal oribatid mites (Lehmitz *et al.* 2011), and *C. labyrinthicus* is commonly found in trees. Thus, the sole presence of *C. labyrinthicus* in a peatland subfossil record should not be seen as a conclusive sign of permafrost. However, when occurring in numbers and/or together with other oribatid mite permafrost indicator species and/or suitable plant macrofossil assemblages, *C. labyrinthicus* is a good indicator.

Conclusions

Sub-Arctic peatlands are currently undergoing rapid changes in hydrology, vegetation and C-dynamics, resulting from climatic warming and permafrost thaw. More studies based on multi-proxy approaches that aim to reconstruct past environmental conditions in permafrost mires are needed to understand how these ecosystems will react to future temperature increases and resulting ecological shifts. Oribatid mites are worth to include in these analyses, as this soil faunal group

includes indicator species, which can help to detect past permafrost dynamics in peatlands. Moreover, oribatid mite subfossil indicators can reveal peatland areas that had permanently frozen peat layers in the past.

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