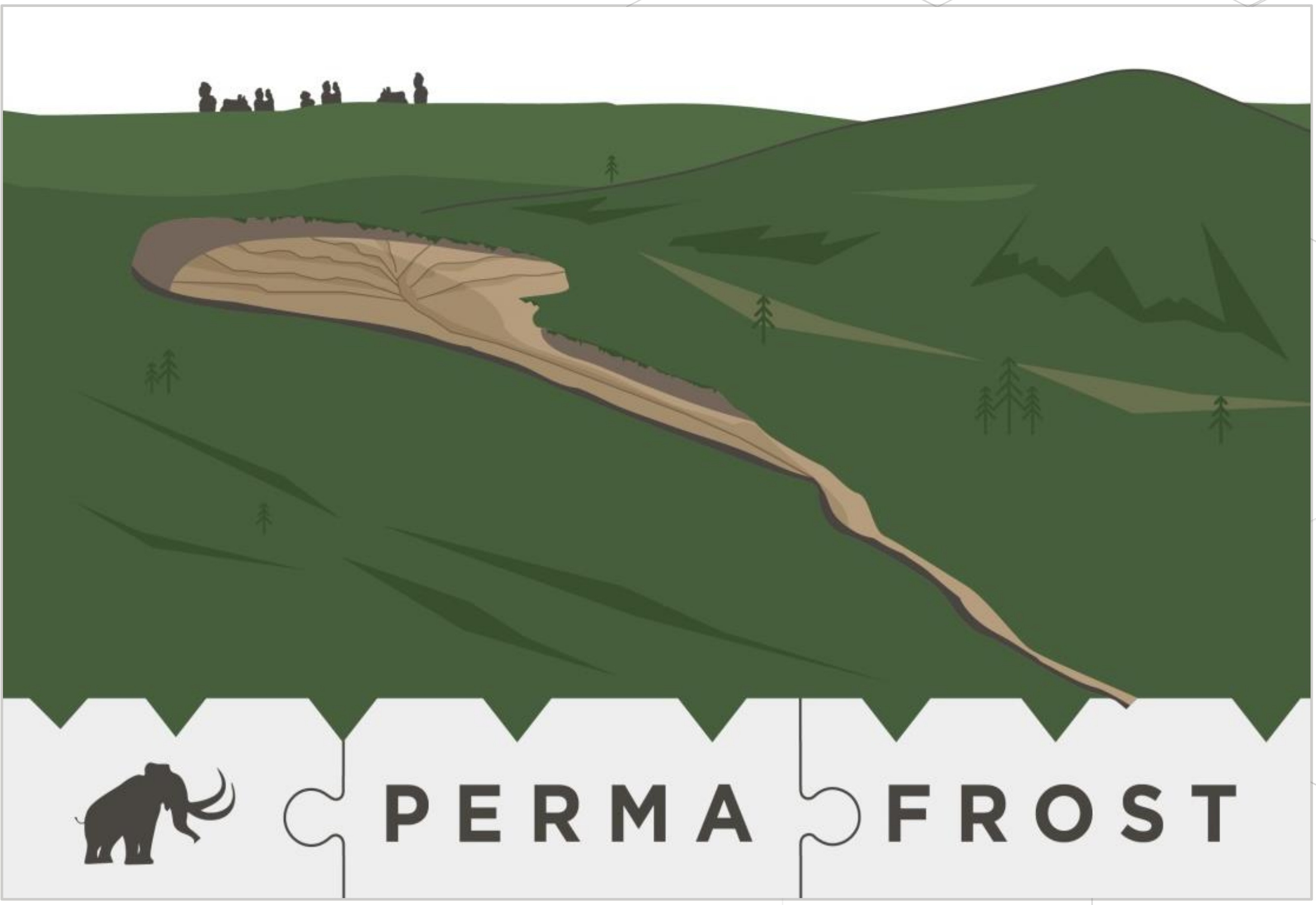
Dissertation

Palaeo-environments at the Batagay site in West Beringia during the late Quaternary

By Kseniia Ashastina



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Graphical illustration of the Batagay outcrop based on various photographs
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Abbreviations

Abbreviation	Meaning
°C	Temperature in degree Celsius
^{14}C	Radiocarbon dating method
a.s.l.	Above sea level
AMS	Accelerator mass spectrometry
bgs	Below ground surface
BP	Before present (1950)
ca.	Latin: circa; approximately
cf.	Latin: confer; compare
e.g.	Latin: exempli gratia; for example
***et al*.**	Latin: et alia; and others
LGM	Last Glacial Maximum
LIG	Last Interglacial
MIS	Marine Isotope Stage
OSL	Optical Stimulated Luminescence, dating method
pCCA	partial canonical correspondence analysis
pMC	Per cent modern carbon
Sect.	Latin: section; section – taxonomic rank
sp.	species
Subsp.	subspecies
TC	Total carbon
TIC	Total inorganic carbon
TN	Total nitrogen
TOC	Total organic carbon
δ^{18}O	Delta-o-18, Stable oxygen isotope analysis

Chapter 1. General Introduction

Global warming is postulated to affect life all over the planet (IPCC, 2014). Changes in climate are expected to trigger changes in ecosystems of all kinds and on all levels (e.g. Parmesan and Yoke, 2003). Warming modifies plant and animal diversity, bringing some species to extinction while expanding ecological niches for other species; it affects soil chemical and physical parameters, microbial activity and effects dynamics of all processes (e.g. Walther *et al*., 2002). But we should not focus solely on climate and underestimate interactions occurring between all the components of the global biosphere. It is essential to estimate the time of biotic response to climate change; the response could be both, barely perceptible during a human lifespan or, on the contrary, follow immediately (e.g. Alley *et al*., 2003; Dakos *et al*., 2008). Recent climatic changes are neither the first nor the last to appear. In order to understand today's processes, the natural variability of the climatic conditions must be taken into account (e.g. Zachos *et al*., 2001). Therefore, the primary task is to reveal the natural variability of climate and understand the complex interdependent reactions of the ecosystem components to occurring deviations. Only with this knowledge can changes be predicted and prepared for.

As we all know "the past is the key to the future" (Lyell, 1876). A large number of long-term environmental changes occurred in Earth´s history (e.g. Petit *et al*., 1999). They can be reconstructed on the basis of analysing palaeo-records, such as: lake sediments, ice cores, peat accumulations, deep sea sediments, and permafrost archives (e.g. Birks and Birks, 1980; Bradley, 1999). Permafrost is one of the best media to preserve past life in a frozen state. Due to fossil evidence from various palaeo-records, climatic changes and such dramatic issues as extinction events were discovered.

The latest fundamental change in global ecosystems started at the beginning of the Quaternary Period, 2.6 million years ago, and continues today (e.g. Bennett, 2004; Rull, 2008). The Quaternary is characterised by alternating warm and cold climatic phases (e.g. Williams *et al*., 1998; Stauffer, 1999). During cold phases, mountain glaciers and vast ice sheets formed. Ice sheets fixed huge amount of water, causing a global sea-level drop. During warm phases, ice sheets and glaciers retreated and the sea-level rose (Velichko, 1975).

Sea-level fluctuations during the Quaternary caused major environmental impacts in the shallow shelf seas in northern Eurasia (Fig. 1.1). According to Hopkins (1972), the maximum sea-level fall of the Bering and Chukchi seas was 135 m, resulting in an advance of the coastline by several hundred kilometers north of its recent position. The landmass emerging in this manner connected Eurasia and North America during cold stages and became inundated during warm stages. This area – Beringia (Hulten, 1937) – enabled migrations and exchanges of flora and fauna between the two continents, and human arrival in North America. Beringia is a key region for studying the development of the arctic flora and understanding the mechanisms underlying the Quaternary biotic impoverishment in northern latitudes. What makes this area so special?

Beringia, the area between the mouths of the Siberian Lena River and the Canadian Mackenzie River, remained free of continental ice sheets at least during the late Quaternary (Svendsen *et al*., 2004; Barr and Clark, 2012). Instead of ice sheets, perennially frozen ground developed here (Sher, 1984). This ice sheet-free area was a center of dispersal of one of the greatest northern ecosystems – mammoth-steppe or tundra-steppe (e.g. Giterman, 1968; Hopkins, 1972; Guthrie, 1986; Yurtsev, 1982; Kahlke, 2015). This biome extended from the Atlantic east coast crossing Eurasia and the Beringia land bridge to North America (Matthews, 1982). The name "tundra-steppe" suggests that the ecosystem consisted of a mixture of tundra and steppe biota. This assumption was later evaluated using palaeo-data like pollen (e.g. Kaplina, 1978; Anderson and

Lozhkin, 2002) and plant macrofossils (Kienast *et al*., 2005). Numerous findings of mammal bone remains have suggested that this ecosystem was characterised by the coexistence of species that nowadays are either extinct or fill different ecological niches (e.g. Nehring, 1890; Tugarinov, 1929). For example, woolly mammoth, woolly rhinoceros, cave lions and cave bears are now extinct, whereas reindeer and musk ox currently inhabit the northern tundra, and saiga antelope, horse and bison are restricted to southern steppes. The former composition of animals and plants is reflected in the name “mammoth-steppe” and suggests that environmental conditions at this time lack a modern analog.

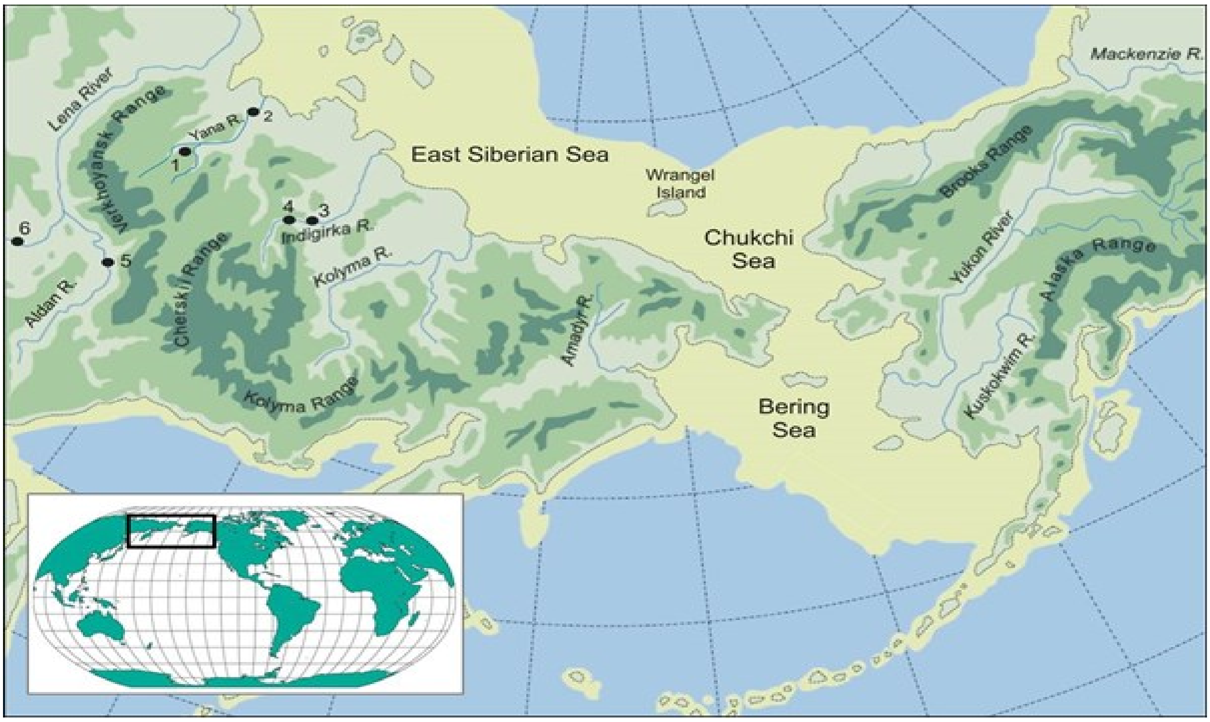

Figure 1.1. A map of northeastern Asia and part of North America (Modified after Elias and Crocker, 2008). Yellow colour illustrates shallow shelfs (-120 m) of the arctic seas. Black circles indicate locations of palaeo archives: 1 – Batagay, the Yana Highlands, 2 – YRH Site, 3 – Vorontsov Yar, Indigirka River, 4 – Sypnoy Yar, Indigirka River, 5 – Mamontova Gora, Aldan River, 6 – Diring Yuriakh, Lena River. The map of the northern hemisphere is from https://freeclipartimage.com/article/top-78-world-map-clip-art.

The data available from northeastern Asia provide information about the past Beringian ecosystem and its response to the Pleistocene climatic shifts. The composition of biocenoses fluctuated with climatic changes (Sher *et al*., 1976). Beringia was refugium for both plants and animals (e.g. Sher, 1997; Brubaker *et al*., 2005; Boeskorov, 2006; Gavin *et al*., 2014). The mammoth-steppe ecosystem endured over several glacial/interglacial cycles, but perished after 11,700 a BP, when a massive ecosystem restructuring took place and some large herbivores disappeared. The last living mammoths, discovered so far, existed 9,670±60 a BP on the mainland and 3,730 a BP on Wrangel Island (Stuart *et al*., 2002). The woolly rhinoceros became extinct around 12,155±37 a BP (Stuart and Lister, 2012), the steppe bison around 8,215±45 a BP (Murton *et al*., 2017) and the wild horse about 2,150±200 a BP (Boeskorov, 2006). Vegetation cover suffered somewhat less — tundra-steppe vegetation remnants are still to be found in northeast Asia. However, steppe and tundra-steppe occupy now only small extra-zonal patches on south-facing slopes all over north-eastern Siberia (Yurtsev, 1982; Reinecke *et al*., 2017).

Beringia was vast, and despite available data there are still many open questions. Unresolved questions include those relating to the spatial distribution of palaeo-archives: most of the available data originate from sites at today´s coastal area. For example, along the coast of the Arctic Ocean (e.g. Romanovskii, 1961; Sher *et al.*, 1977; Kaplina and Chekhovskij, 1987; Schirrmeister *et al.*, 2011a,b; Wetterich *et al.*, 2008) and at river banks (e.g. Kaplina and Sher, 1977; Kaplina *et al.*, 1980; Kaplina and Giterman, 1983; Kiselev *et al.*, 1987), where frozen material is exposed by active wave abrasion and thermodenudation. Despite numerous palaeo-ecological studies of the permafrost outcrops in the northern coastal areas, the vast inland areas are sparsely investigated and, therefore, ecosystem responses to varying climatic continentality are unclear. Only few studies (Fig. 1.1) are available from inland permafrost archives: the Mamontova Gora (e.g. Agadzhanyan and Boyarskaya, 1969; Pewe *et al.*, 1977; Astakhov and Isayeva, 1988), Diring Yuriakh (Alekseev *et al.*, 1990), Vorontsov Yar (Biske, 1960) and Sypnoy Yar (Kaplina and Sher, 1977). Therefore, the inland Yana Highlands (Fig. 1.2) are one of the least-studied areas of inland Beringia.

Figure 1.2. The Yana Highlands study area. Yellow circle indicates location of the Batagay permafrost outcrop. White triangular indicates the location of the YRH Site. Picture has been modified from satellite pictures, Google Earth 7.1.2.2041. Batagay region, Russia, 67° 34' 41.83" N, 134°45'46.91" E, 4 July 2013, viewed 10 December 2017, http://www.google.com/earth. The map of the northern hemisphere is from https://freeclipartimage.com/article/top-78-world-map-clip-art.

The arctic palaeolithic archaeological site (YRH site) dated back to 27 ka BP was discovered 340 km north of the Yana Highlands (Fig. 1.2; Pitulko *et al.*, 2004). Which surprises are still to be found there?

A recently exposed unique permafrost exposure was found 10 km southeast of the town Batagay, which is the municipal center of the Verkhoyansky district. This sediment sequence was scarcely explored so far and gives the unique opportunity to deepen scientific knowledge about the

Quaternary ecosystems of the Yana Highlands. The data for the present thesis originates from the Batagay permafrost exposure. This permafrost sequence was explored with the intention to fill the following scientific knowledge gaps:

(i) Describe the new permafrost outcrop, determine its sedimentary units and their age, establish the main formation processes, and discuss the first climatic implications.
(ii) Reconstruct the palaeo-vegetation in order to report the first palaeo-ecological results for this unique inland outcrop.
(iii) Elucidate the history of Beringian flora by exploring the origin and phylogeographical reationships of endemic plants.
(iv) Trace the changes in palaeo-vegetation cover and investigate if these could have been influenced by grazing pressure or if they are of solely climatic origin.

1.1. Permafrost as a palaeo-archive

The Batagay outcrop potentially provides an outstanding permafrost palaeo-record. Perennially frozen ground is one of the best palaeo-archives due to a number of properties. Permafrost is any type of "soil or rock which is experiencing below 0 °C temperatures for at least two consecutive years" (Harris, 1988), this means that any kind of material enclosed within permafrost will remain frozen or partially frozen. According to Zhang (1999), the permafrost zone underlies today about 24% of the landmasses of the Northern Hemisphere and about 64% of the area of the Russian Federation (Fig. 1.3; Brown *et al.*, 1997). Of course the permafrost of this huge territory is not homogenous but varies between different geographical settings. Permafrost formed in mountain areas is called *alpine*, over the plains *lowl*and, and on the Arctic Ocean shelf *subsea* (Subcommittee, 1988).

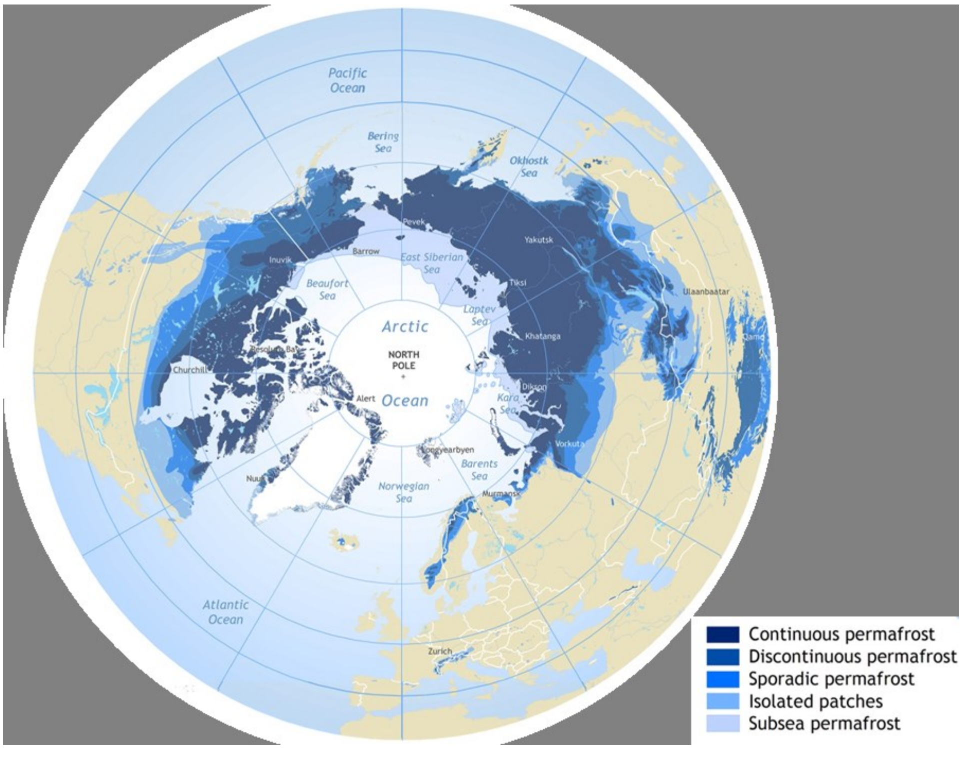

Figure 1.3. Permafrost distribution in the Northern Hemisphere. From Brown *et al.*, 1997.

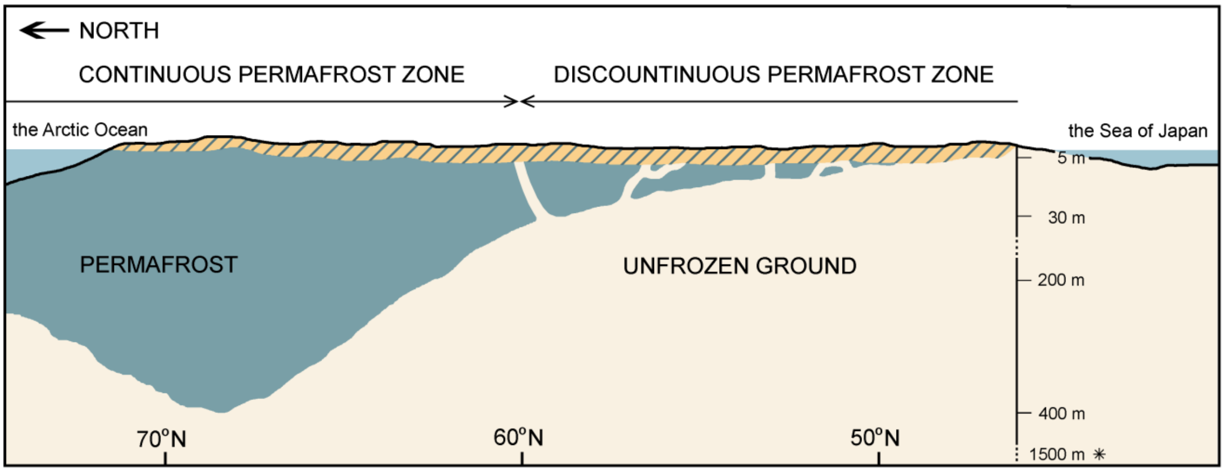

Figure 1.4. Vertical and longitudinal distribution of permafrost in Eastern Siberia. Yellow dashed lines indicate active layer thickness decreasing northward. 1500 m* stays for maximum permafrost depth measured in Central Siberia. Diagram modified after Koppe, 2003.

Permafrost can be classified further according to the percentage of the area underlain by perennially frozen ground. Zones can be described as continuous (90-100%), discontinuous (50-90%), sporadic (<50%) and isolated (few patches) permafrost (Subcommittee, 1988) (Fig. 1.4). A third classification is based on the timing of deposition and freezing of the sediment: "permafrost that formed after the deposition of the soil material in which it occurs" is called *epigenetic*, and "permafrost that formed more or less simultaneously with the deposition of the soil material in which it occurs" is called *syngenetic* (Fig. 1.5) (Subcommittee, 1988).

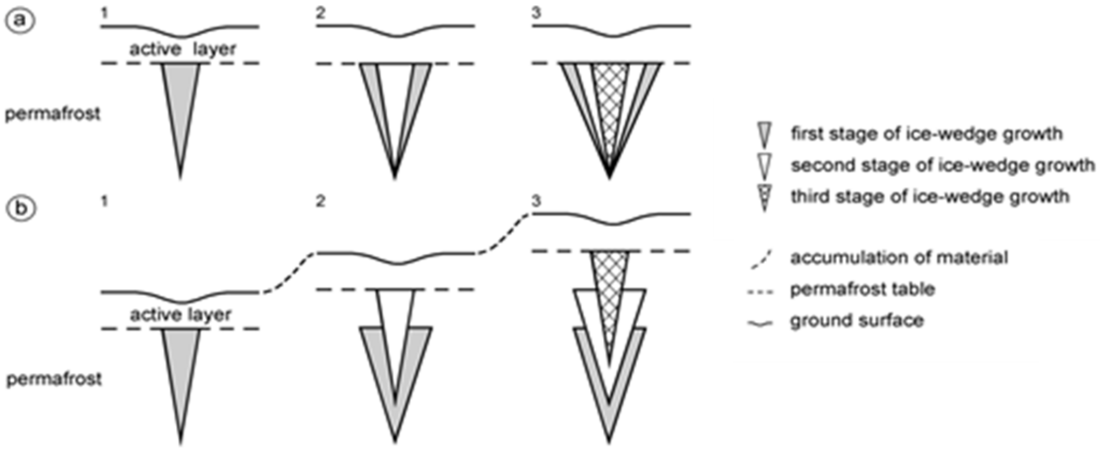

Figure 1.5. Schematic representation of the epigenetic (a) and syngenetic (b) ice-wedge growth. Numbers 1-3 indicate stages of ice-wedge formation. Epigenetic ice-wedge growth is directed sideways, while syngenetic is directed upwards along with accumulation of host sediment. Modified from Mackay (1990).

Permafrost formation in mineral soil involves frost cracking and building up of ice wedges. In winter, the frozen soil contracts due to cooling. First frost cracks appear at the ground surface (Fig. 1.6a). During spring, snow melt water may fill the crack, which later could be resealed due to expansion of the thawing soil. In case the crack stays open and forman ice vein within permafrost before the crack can close due to expansion of the warming soil. The ice vein persists in the permafrost throughout summer and autumn (Fig. 1.6b). Renewed cooling and cracking may occur during the next winter. This cycle recurs year after year: cracks appear at the center of the ice wedge, forming a foliated ice structure, with every foliated layer containing material of one year. In the other words, older ice can be found at the sides of an ice wedge, while the newer ice is accumulates in the middle (Davis, 2001). In this way, epigenetic ice wedges grow wider through time.

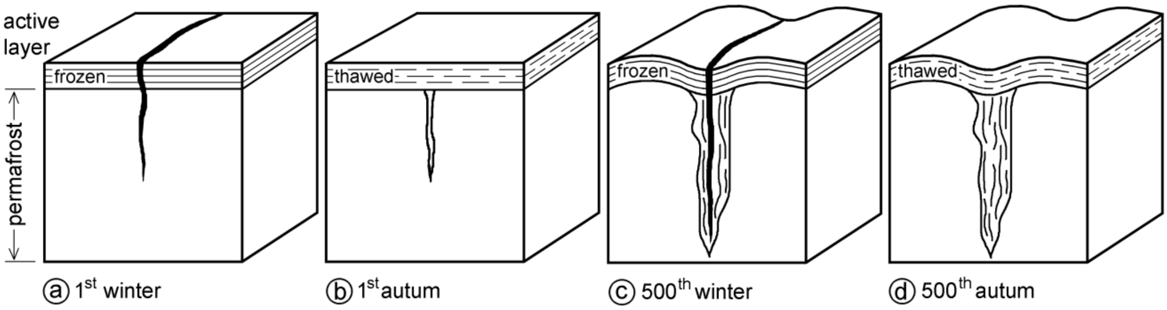

Figure 1.6. Stages of ice-wedge development through repeated freeze-thaw cycles. Based on Figure 1 of Lachenbruch (1962).

Active layer is the top-most soil layer, from several centimetres to several metres, that annually freezes and thaws above permafrost. A typical permafrost pattern develops here - ice-wedge polygons (Fig. 1.7a,b). Below the active layer, both the material within the ice wedges and in the hosting sediments remains perennially frozen. Depositional environment and accumulation processes can be deducted by exploring cryostructures and sedimentological properties. Organic material found within permafrost sediments also derives valuable information. Permafrost can reach an enormous depth (Fig. 1.4) and varies in ice and organic content. As permafrost started to form in the early Pliocene (Kaplina, 1981), the analysis of frost-preserved organic matter offers the possibility of investigating and reconstructing the regional environmental and climatic history over long time spans.

The newly exposed Batagay permafrost outcrop, located in interior northern Yakutia, in the Yana Highlands, provides the unique opportunity to enrich scientific knowledge on the Quaternary ecosystems in high latitudes. Check Box 1 summarises the present-day permafrost features observed in the Highlands.

Box 1. Permafrost and periglacial features in the Yana Highlands

The Yana Highlands belong to the continuous permafrost zone. The permafrost here is 380-450 m thick, varying according to geologic, hydrogeologic and orographic factors (Geology of USSR, 1979). The active-layer thickness is 15-25 cm in fine-grained sediments and 70-80 cm in coarse-grained sediments. On south-facing slopes, it can reach depths of 4.5 m (Geology of USSR, 1979). Modern permafrost landforms ice-wedge polygons on river flood plains. As visible in Figure 1.7, the crack pattern slightly differs from site to site: it is hexagonal in homogeneous material and orthogonal in heterogeneous material (Davis, 2001). The observed ice-wedge polygons degrade: the top parts of ice-wedges thaw causing transformation of low-center polygons into high-center polygons. Another prominent feature of a permafrost landscape is a presence of small steps (terracettes) on the slopes of the Yana River terraces near Verkhoyansk. They form a parallel horizontal pattern, especially evident on the steep part of the slopes (Fig. 1.7c; Davis, 2001).

Figure 1.7. (a), (b) - Ice-wedge polygons in the Yana River flood plain. Pictures were taken on 13 June 2014. (c) - cryoturbation steps on an eastern slope of the Yana River terrace, 40 km downstream from Verkhoyansk. The estimated spacing between the steps is 0.3 to 0.5 m. The picture was taken on 16 June 2014.

The current development of permafrost features implies high soil moisture, which is the result of two factors - low evaporation rates and the presence of permafrost that prevents drainage deeper than permafrost table.

The Yana Highlands are located in the northern inland part of the Sakha Republic (Yakutia), Russian Federation. The area is rich in mineral resources. The Batagay outcrop is a huge amphitheather-like thermoerosional cirque (Fig. 1.8). The outcrop is exposed in the foothills of Mt. Khatyngnakh (381m a.s.l.), 2.5 km north-east from the left bank of the Batagaika River, a tributary to the Yana River. According to L. Vdovina (geologist, Yana Geological Service, personal communication, 2017), there are two possible triggers that led to the evolution of the Batagay (thermokarst) outcrop. First, during tin mining on top of Mt. Khatyngnakh, trucks transporting tin ore used the same route downslope to the Batagaika River. The resulting damage to the vegetation and organic layer, together with a changed albedo, initiated thawing of the ice-rich permafrost deposits. The second proposed trigger, which has led to the same chain of consequences, could have been forest logging in the area. Prisoners of the nearby Ese-Khayya labor camp logged trees for the camp and the locals. Dragging timber over the same route caused erosion and thermal degradation that, in the end, led to the exposure of the permafrost sequence.

Stages of the outcrop development can be tracked on aerial photographs and illustrate two stages: limited activity, from 1968 to 1990, and highly active since 1991 (fig. 1.8b-f; Kunitsky *et al.*, 2013).

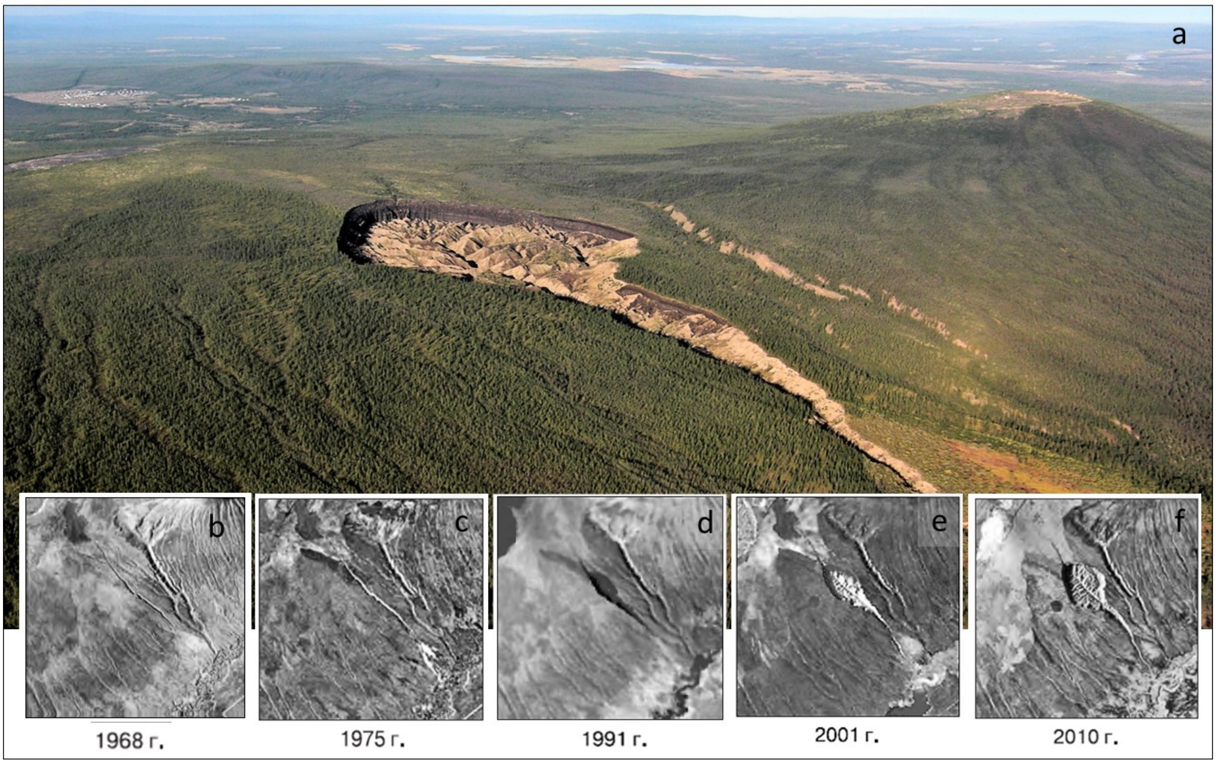

Figure 1.8. (a) View from a helicopter on the Mt. Khatyngnakh and the Batagay outcrop. Photograph taken on 17 August 2011, provided by L.Vdovina. (b)-(f) aerial photographs illustrating the stages of the outcrop development: (b), (c) – limited activity stage, (d), (e), (f) – highly active thawing. Modified after Kunitsky *et al*., 2013.

The limited activity stage included the formation of a gully and its deepening and slow widening over time. The highly active stage resulted in the expansion of the gully into the large thermocirque (Fig. 8a and 9a). This outcrop has a steep, nearly vertical, ice-rich headwall 80 m high (Günther *et al*., 2015) and steep flanks. Due to thermo-denudation rates of up to 30 m per year, the outcrop reached a width of up to 800 m in 2014 (Günther *et al*., 2015, 2016) and is the largest thaw slump (*megaslump*) in the world. The thermo-erosional cirque grows with accelerating rates and uneven thawing along the margins, possibly due to varying ice content of the deposits (Günther *et al*., 2015). The estimated denudation rate is 210-450 m^3/year per 1 m of the outcrop margin (Kunitsky *et al*., 2013). Some of the thawed material accumulates at the bottom of the erosional cirque among 30 m high residual hills and some is washed away. The meltwater flows downslope to the Batagaika River and dams the river with its sediment load (Fig. 1.9c-f).

Previous studies on the Batagay permafrost exposure focused on thermal denudation processes, the structure of the outcrop and stable-isotope composition of the ice wedges (Kunitsky *et al*., 2013; Günther *et al*., 2015; Murton *et al*., 2017; Vasil´chuk *et al*., 2017; Opel *et al*., 2018). The findings of faunal remains of the mammoth steppe, including carcass of horse (*Equus* sp.) and bison (*Bison priscus*), as well as bone remains of cave lions (*Panthera leo spelaea*), woolly rhinoceroses (*Coelodonta antiquitatis*), mammoths (*Mammuthus primigenius*) and other extinct Pleistocene animals (Novgorodov *et al*., 2013), provide evidence that a potentially rich palaeo-environmental archive is preserved in the permafrost sequence.

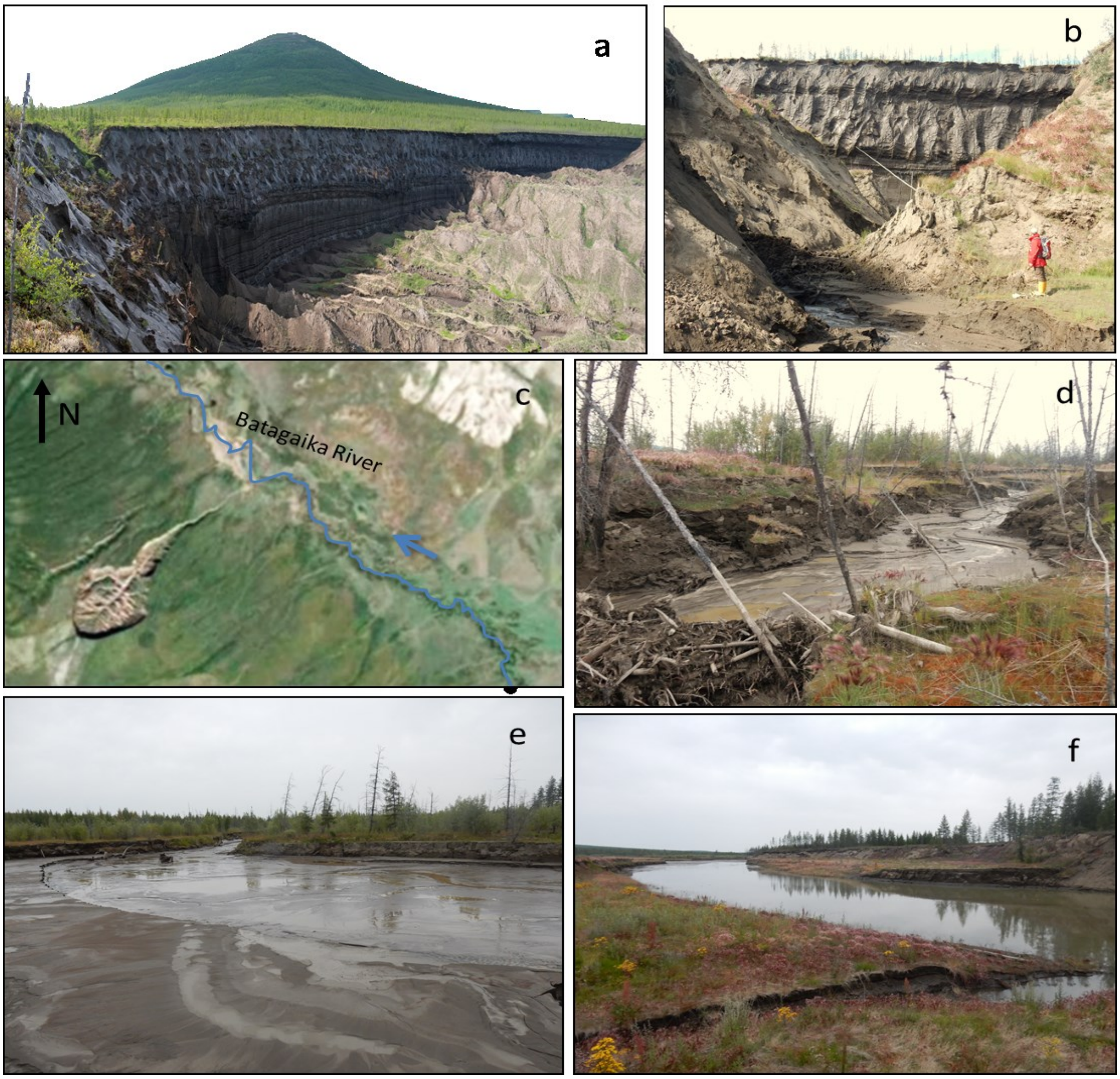

Figure 1.9. The overview of the Batagay headwall reaching 80 m height and residual hills on the bottom of the erosional cirque (a, b). (c) A map of the area with the Batagaika River. The hillslope containing the megaslump descends to the northeast. (d) The outlet streams to the Batagaika River. The Batagaika River after the inflow of the sediment-rich meltwater from the outcrop (e) and before (f). Picture (a) was taken by Frank Kienast; (b) on 27 July 2017, (d-f) on 31 July 2017.

1.2. Plant macrofossil analysis

Methods for reconstructing past permafrost environments are numerous, e.g. palynological analysis (e.g. Lozhkin, 1984; Lazarev and Tomskaya, 1987; Andreev *et al*., 2002; Anderson and Lozhkin, 2002); identification of chitin remains (e.g. Sher *et al*., 2005), charcoal (e.g. Huber, 1951; Schweingruber, 1978; Schoch *et al*., 2004) and ostracods (e.g. Wetterich *et al*., 2008, 2009); ancient DNA identification (Jørgensen *et al*., 2012; Willerslev *et al*., 2014); chemical analysis of soil (Gubin, 1999; Zanina, 2006), ice-wedge stable isotopes and gas bubbles found within permafrost (e.g. Vaikmäe, 1989; Vasil'chuk, 1991, 1992; Meyer *et al*., 2002; Opel *et al*., 2017) and paleontological analysis (Sher, 1974). Each approach gives an insight into a certain aspect of the former ecosystem. Spore-pollen analysis is useful to unravel the regional vegetation but is limited to northern plant communities, ancient DNA identification helps to find traces of living organisms, while e.g. the study of mollusks provides useful information on lake environments. Nevertheless, for the reconstruction of past ecosystems the application of only one single analysis could be ambiguous and, therefore, misleading. After taking into account all possible methodological restrictions, we chose to base our work mainly on the analysis of plant macrofossils and to use spore-pollen, entomological, charcoal and sediment analyses as complementary sources of information.The identification of vascular plant macro-remains >200 µm, e.g. fruits, seeds, leaves, twigs and inflorescences (Birks and Birks, 1980) has some advantages. First, macro remains are only locally dispersed due to their relatively big size. Therefore, they give a precise picture of the local vegetation. Second, they can be frequently identified to the species level.

The macrofossil method contains 6 stages: sampling, sieving, drying, picking, identifying and, finally, compiling a vegetation reconstruction. In this thesis, stage one – the sampling – meant taking an appropriate amount (ca. 5l) of frozen material from the permafrost outcrop. In stage two – the sieving – sediment particles should be removed from the fossil remains by wet sieving with mesh sizes 0.5 and 0.25 mm. Stage three is the air drying of the fossils. These first three stages can be conducted directly in the field, whilst the next stages must be carried out in a lab. Stage four is the picking. Well-preserved macrofossils should be picked from the dried bulk material using tweezers and a stereomicroscope. During stage 5 plant remains are identified. The basis for the species recognition is the taxonomy and the morphological characteristics of the macrofossils, in particular size, colour, and texture (Birks and Birks, 1980). One difficulty in this context is that the macro-remains found within permafrost can be incomplete as some hard parts might have been destroyed and/or soft parts might have decayed. Due to these problems with the recognition of macrofossils to the species level, the following system indicating various levels of identification certainty was used in this work. The system is illustrated by the example of a poppy plant: Papaveraceae -family is certain;

Papaver - genus is certain;

Papaver polare - species is certain;

Papaver sect. *Scapiflora* – section Scapiflora is certain, species is less certain due to unclear taxonomy within that section.

The final step is to reconstruct the vegetation and the environment. Using the taxa list together with the knowledge about the host sediment and the sedimentary environment, characteristic features of the past environment and ecosystem can be reconstructed (Birks and Birks, 1980). First, a reconstruction of the plant communities is needed. A plant community is an assemblage of taxa that exists in a shared habitat, where each member of the plant community fills the certain ecological niche. According to Hutchinson (1978), a niche is the range of environmental tolerances of a species to which the species is adapted. The ecological niche of a plant community can provide more valuable information on past environments than those of single plant taxa, due to the fact that the niche of the community is more restricted than niches of its individual components (Birks and Birks, 1980). Nevertheless, fossil assemblages are incomplete due to decay of plant remains. The reconstruction of past plant communities should be based on analogies with modern taxonomic communities. For the vegetation reconstruction, we considered the presence/absence of plant taxa only. The quantity of identified remains might be misleading, as the number of fossils found does not necessarily reflect the actual abundance of the taxa in the palaeo-vegetation. The fossil number can be affected by taphonomy, preservation and reproductive strategy of the plant species. For this reason, not all plant taxa that formed the palaeo-vegetation are sufficiently preserved in the fossil record. Despite such restrictions, past vegetation units can be effectively reconstructed on the basis of few identified species that serve as indicator species for certain plant communities. Following the methodology of Kienast *et al*. (2005, 2008, 2011) for the reconstruction of palaeo-vegetation, the identified vascular plant taxa were grouped into plant communities (syntaxa) in line with their ecological preferences and present-day occurrences (Dierßen, 1996; Hilbig, 1995; Reinecke *et al*., 2017). The identified plant communities and the phytosociological nomenclature of taxa follow the Braun-Blanquet classification (Weber *et al*., 2000).

1.3. Study area

1.3.1. Geology

The Yana Highlands are located within the Verkhoyansk geosyncline – a complex of 12-14 km thick deposits that formed from the Carboniferous to the Jurassic. The Yana Highlands belong to the western part of the Verkhoyansk-Kolyma Orogen and are surrounded by the Verkhoyansk Mountains (highest peak: 2389 m a.s.l.) and are connected to the Yana Lowland in the north. The Verkhoyansk Mountains were formed at the beginning of the late Cretaceous Period (Geology of USSR, 1979). Subsequently, the ranges were eroded, such that during the Palaeogene the Verkhoyansk Mountains were hilly highlands. Renewed tectonic uplift started in the late Oligocene and Miocene epochs and continued also during the Quaternary Period. Granitoid intrusions and acidic dike formations are typical for this territory.

Spirazhskij (1940) explored the northern slope of the Verkhoyansk Mountains and found morphological evidence of glaciations and end moraines consisting of siltstone accumulations up to 50 m high. According to Atlasov (1938) and Kolosov (1947), valley glaciers also developed in the mountains surrounding the Yana Highlands. Strelkov *et al*. (1965) and Siegert *et al*. (2007) suggested that glaciers of the western Verkhoyansk Mountains almost reached the Lena River during the LGM but the highlands remained unglaciated. Stauch and Lehmkuhl (2010) and Popp *et al*. (2007) dated moraines on the eastern and western flanks of the Verkhoyansk Mountains and confirmed the results of Katasonov (1954): within the Yana Highlands themselves there are no moraines and other morphological features indicating the existence of glaciers, and so it is likely that moraines never reached altitudes below 800-1000 m a.s.l.

1.3.2. Climate

The absence of valley glaciers could be explained by the local climate. The Yana Highlands lie within the continental subarctic climate zone (Köppen, 1884). Despite its relatively small distance from the ocean of 410 km (Robertson Group and Geological Institute, 1991), the town of Verkhoyansk is described as the coldest permanently inhabited location in the Northern Hemisphere (Lydolph, 1985; Ivanova, 2006). This means that the continental climate has a great seasonal temperature range coupled with a low annual precipitation rate. Air masses that form above Siberia throughout the year have a great impact on the seasonal variability of climate. Wintertime is influenced by a high-pressure air cell - the Siberian anticyclone. The Siberian anticyclone has its main centre above Mongolia, stretches beyond the Verkhoyansk Mountains and forms another pressure peak above the Yana Highlands. This cold high-pressure area blocks the penetration of warmer, moister air masses and, at the same time, results in an extreme cooling of the air near the surface because outgoing longwave radiation from the ground can escape through a cloudless sky into space (e.g. Guthrie, 2001). In summer, the situation changes – a southwest Asian low pressure system dominates the region. It brings high summer wind velocities and precipitation (Oliver, 2008).

Meteorological observations at the Verkhoyansk weather station since 1888 (RIHMI-WDC, 2016) reflect the extreme continental climate (Table 1): the mean annual air temperature is -14.9 °C (observation period 1936-2015) and annual precipitation amounts to only 181 mm. The seasonal differences in temperature and precipitation are very prominent: in January, when the Siberian anticyclone is dominant, the average air temperature is -44.7 °C. In the winter months only 27% of the annual precipitation is recorded. Wind velocities are also low. Summer weather is completely different owing to the Southwest Asian cyclone: the average June temperature is +15.5 °C. Maximum precipitation is recorded in June-August, resulting in 51% of the total annual amount (RIHMI-WDC, 2016). In summer, wind velocities increase compared to those in winter; wind speeds up to 15 m/s are observed in narrow valleys along rivers and mountain regions (Geology of USSR, 1979). Loose sediments covering exposed river floodplains, barren steep river terraces and roads, supply material for summer dust storms (Fig. 1.10).

Table 1. Climatic parameters recorded at the Verkhoyansk weather station. Winter average air temperature corresponds to January; average summer temperature is shown for July. Annual precipitation is indicated for February and July.

Parameter Season	Air temperature, °C		Precipitation, mm	Wind velocity, m/s
	average	min/max		
winter	-44.7	-67.8	22	0.7
summer	+15.5	+37.3	93	3.5

Figure 1.10. Photograph of dust storm over the town of Verkhoyansk observed from the eastern slope of the Yana River terrace. Photograph taken on 14 June 2014.

1.3.3. Hydrology

The Yana is the main river in the area; it is 872 km long and has 93 tributaries. One of the largest confluents is the Adycha River (701 km), joining the Yana downstream of Batagay (Fig. 1.2; State Water Register, 2018). The study area is located in the Upper Yana section, which ranges from the source to the Adycha River inflow. The Yana River floodplain is 7-10.5 km wide and contains numerous ox-bow lakes. The channel bed is tortuous with 10 km long meanders and shallow with an average depth of 2 m.

All the rivers of the region have a similar hydrological regime. Most of the water is supplied by rain and snowmelt. Spring high floods are caused by snowmelt in the mountains, while during the summer and autumn occur freshets triggered by rains and melting of naleds (perennial river ice). Rivers start to freeze in the beginning of October and break up at the end of May/beginning of June. The mean annual water discharge of the Yana near Verkhoyansk is 150 m^3/s; the highest amounts are recorded during the ice-free months (June - September). Winter discharge corresponds to only 5% of the annual value (State Water Register, 2018).

During summer freshets, river terraces are actively eroded; the mean annual concentration of suspended fine material is 130 g/m^3, measured in Verkhoyansk, while the total suspended sediment load of the Yana River is 4.35 million tons, measured in the lower Yana.

1.3.4. Soil and *vegetation*

In northern Asia, soil development takes place under harsh climatic conditions. The shallow depth of the permafrost table influences plants, especially the depth of root penetration, and the activity of soil microorganisms. Most soils in the Verkhoyansk region have a thin organic horizon and a high acidity (Elovskaya, 1987). The Yana Highlands are located in the taiga zone. Due to the elevation gradient, soil and vegetation cover change in line with altitudinal zonation of a continental type (Tolmachev, 1949). The following soil-vegetation complexes occur with increasing altitude: taiga zone, subalpine zone, dry alpine tundra and zone of the cold goltsy deserts. Goltsy (bald tops) are mountain tops that are covered by rocks and are sparsely vegetated, typical for Siberian mountains and the Ural Mountains (Walter, 1974).

The floodplain of the Yana River hosts forb- and grass- meadows together with forests of larch (*Larix dahurica* subsp. *caj*ander*i*), birch (*Betula divaricata*, *B*. *fruticosa*), alder (*Alnus*), willow (*Salix*). Moist meadows of floodplains with *Calamagrostis neglecta*, *C. langsdorfii, Poa* sp., *Polygonum tripterocarpum*, *Polemonium acutiflorum*, *Lloydia serotina*, *Pedicularis verticil lata*, *Ranunculus affinis*, *Anemone ochotensis*, *Pulsatilla flavescens*, *Dracocephalum palmatum*, *Oxytropis adamsina*, *O. deflexa*, *Cerastium maximum, Carex sp.* serve as pastures for horses and cattle (Zakharova *et al*., 2005; Nokhsorov, 2017). In wintertime parts of *Arctophila fulva, Equisetum variegatum, scirpoides Carex aquatilis* var. *minor, Eriophorum angustifolium, Comarum palustre* are the food source for cattle (Nohsorov, 2017). The key soil types (all soil types within the text are given according to Unified State…, 2014) in the floodplains are taiga Histic Gyosols Dystric and Entic Podzols.

Characteristic features of the soil distribution in the Yana floodplain are the presence of Haplic Cambisols Eutric and the presence of extra zonal mountain cold-steppe soils (Mollic Leptosols Eutric) on the south-facing slopes of mountains and river terraces. These steep slopes are a suitable habitat for a xerophytic forb- and grass-dominated vegetation. Within the generally dry Yakutia, the upper reaches of the Yana drainage system experience the lowest precipitation, resulting in a high percentage of steppe vegetation in the study area (Yurtsev, 1982). According to Reinecke (2017), the steppes belong to petrophytic *Carici duriusculae-Festucetum lenensis* and typical *Pulsatilletum flavescentis* associations. Among the common plant taxa are *Festuca lenensis, Poa botryoides, Koeleria gracilis, Agropyrum cristatum, Carex pediformis, C. duriuscula, Stellaria jacutica, Phlox sibirica, Calmagrostis purpurascens, Artemisia commutata, A. frigida*, *Astragalus fruticosus, A. inopinatus, Thymus serpyllum*, *Dracocephalum palmatum*, *Pulsatilla flavescens, Potentilla nivea*, *Alyssum obovatum, Eritrichium villosum*, *Anemone flavescens*, *Silene samojedorum* (personal observation, 2014, 2017; Yurtsev, 1961; Reinecke *et al*., 2017) and endemics of the Yana-Kolyma Highlands: *Potentilla tollii*, *Oxytropis scheludjakovae, Stellaria jacutica.* In the height interval from 500 to 900 m a.s.l. (Nikolin, 2012), the taiga zone is replaced by a subalpine zone. Here, shrubs of stone pine (*Pinus pumila*), *Duschekia fruticosa* and *Betula middendorfii* are common. The understory is poor in species and consists of *Diapensia lapponica*, *Arctostaphylos alpine, Vaccinium uliginosum* and *Rhododendron* sp. The ground is covered by a thick layer of lichens and mosses that allow only a few species to establish: *Pedicularis dasyantha*, *P. oederi, Bistorta major* subsp. *elliptica*, and *Luzula capitate*. The soil type is a Histic Podzol.

The dry alpine tundra zone extends from 900 to 1600 m a.s.l. and is covered with *Salix cuntea*, *S. reticulate, Ledum decumbens* and *Cassiope tetragona* is developed on Spodic Cryosols (Nikolin, 2012). In the wet areas of the micro-relief mosses dominate and at the dry sites lichens: *Stereocaulon paschale, Cetraria cucculata, C. nivalis, C. isl*and*ica, C. Crispa, Cladonia rangiferina, Cl. mitis, Cl. uncialis, Cl. amaurocrea, Cl. Pyxidata, Sphaerophorus globosus* and *Ochrolechia tartarea.*

The goltsy zone has only poorly developed Lithic Leptosols Brunic soil.

1.4. Publication outline

The thesis consists of three independent research papers that correspond to the three following chapters. Each chapter aims to answer one of the rised questions:

(i) Describe the new permafrost outcrop, determine its sedimentary units and their age, establish the main formation processes, and discuss the first climatic implications.

(ii) Reconstruct the palaeo-vegetation in order to report the first palaeo-ecological results for this unique inland outcrop.

(iii) Elucidate the history of Beringian flora by exploring the origin and phylogeographical reationships of endemic plants.

The stratigraphy of the Batagay outcrop has not yet been studied in a detail, but is the basis for palaeontological investigations. Therefore, the first publication describes the Batagay permafrost outcrop and reports the results on the sedimentary processes that formed the permafrost sequence and on the chronology. The second paper presents results of a multidisciplinary approach for reconstructing the palaeo-vegetation and Pleistocene environments of the Yana Highlands. The third paper focuses on the endemic plant *Stellaria jacutica*, found within a sample attributed to the Last Interglacial and having implications to the phylogeography in Beringia.

Chapter 2: Palaeoclimate characteristics in interior Siberia of MIS 6–2: first insights from the Batagay permafrost mega-thaw slump in the Yana Highlands

Kseniia Ashastina, Lutz Schirrmeister, Margret Fuchs, and Frank Kienast,

published in *Climate of the Past*

The first paper describes the stratigraphical, cryolithological and geochronological characteristics of the permafrost sequence at the Batagay outcrop, Russia. This description forms the stratigraphical framework for any further palaeontological studies and reports.

The aims of the paper were:

1. To provide a stratigraphic description of the outcrop, to obtain the first geochronological dates for age estimation of each stratigraphic unit.

2. To correlate the units with climatic phases that occurred at the site during the sequence of formation and to identify the governing sedimentation processes.
3. To compare the Batagay sequence to coastal permafrost exposures in order to account for climatic differences.

We inferred that the permafrost sequence consists of five stratigraphic units that can be observed in the headwall of the outcrop. Using different dating methods (optically stimulated luminescence, OSL, and ^{14}C -dating), we constrained the temporal framework of the formation of each unit. According to our oldest dated sample, the accumulation of the sequence started at least in the late Middle Pleistocene (MIS 6). The lithological units indicate a succession of several distinct climate phases - the cold and warm phases of the Late Pleistocene. The main difference between the Batagay sequence and the coastal sequences is the absence of evidence for subaquatic deposition and a higher proportion of aeolian deposition.

Author contribution

F.K. designed the study concept and arranged the expedition. K.A. and F.K. carried out the field work and sampling. K.A. designed the concept of the manuscript. L.S. accomplished the sedimentological analysis and plotted the graphs. M.F. designed and performed the OSL dating procedure and interpretation. K.A. prepared the manuscript with contributions from all co-authors. F.K., L.S. and K.A. revised the draft.

Chapter 3: Warm stage woodlands and cold stage steppes: Pleistocene palaeovegetation in North Yakutia's most continental part recorded in the Batagay permafrost sequence

Kseniia Ashastina, Frank Kienast, Svetlana Kuzmina, Natalia Rudaya, Elena Troeva, Werner H. Schoch, Christine Römermann, Jennifer Reinecke, Volker Otte, Grygory Savvinov, Karsten Wesche.

Quaternary Science Reviews, under review

In the largest chapter of the thesis, Chapter 3, we conducted multidisciplinary analyses of the samples from the Batagay outcrop. Each of the performed methods – macro- and microfossil, charcoal and invertebrate identification – has certain constraints, but merging the results gives a better and more complete impression of the vegetation history.

The main research issues we addressed in this paper were:

1. To present first results of the palaeoecological analysis of the Batagay outcrop and provide a reconstruction of palaeo-vegetation from MIS 6 to 2 with a focus on the Last Interglacial and the Last Glacial Maximum.
2. To compare the results with modern vegetation in order to decipher the impact of climatic shifts on the vegetation.

3. To compare the reconstructed vegetation of the inland site Batagay with palaeo-records available from sites in today's coastal zone.
4. To reveal potential non-climatic impacts on the palaeo-vegetation such as disturbances and eutrophication related to the presence of megaherbivores.

Forty-five analysed samples provided an uneven amount of fossil material. Therefore, we gave a detailed vegetation reconstruction of two fossil-rich samples representing the Last Glacial Maximum and Last Interglacial. These two climatic and, hence, environmental extremes, displayed in palaeo vegetation, served as reference vegetation that was compared to the data from all other samples poor in fossils. We found that meadow steppes formed the primary vegetation during the Pleistocene cold stages. During the Last Interglacial (warm stage), meadow steppes were present as well but as a constituent of open coniferous woodland. Additionally, we revealed that the region was a northern refuge throughout the late Quaternary for trees and possibly an interglacial refuge for large herbivores of the mammoth faunal complex. The latter was derived from the presence of ruderal plants that indicate zoogenic disturbances of the plant cover.

Author contribution

F.K. designed the study concept. K.A. and F.K. arranged the expedition. G.S. granted us permission to work at the site. K.A. and F.K. carried out field work and sampling. K.A. carried out the macrofossil analysis, produced pictures and tables under supervision of F.K. The modern vegetation was analysed by K.W., C.R. and J.R. The DCA graph was plotted by J.R., she also provided an interpretation. S.K. conducted the entomological analysis, produced pictures and compiled the corresponding figure and a table. V.O. worked on the identification of mosses and the interpretation of these results. N.R. carried out the spore-pollen analysis and produced the spore-pollen diagram. W.H.S. identified charcoal remains. K.A. analysed and combined the results from all co-authors and wrote the first draft of the manuscript with help of F.K. F.K., J.R., S.K. and K.W. participated in editing the article. K.A. prepared the manuscript for submission. F.K., K.A., K.W., J.R., S.K., N. R., W.H.S., C.R., V.O. and E.T. revised the draft.

Chapter 4: Pleistocene refugia in Western Beringia: fossil evidence of a Yakutian endemic plant for the last interglaciation

Kseniia Ashastina, Frank Kienast, Elena Troeva

Review of Palaeobotany and Palynology, draft

A seed of a recent steppe endemic of northeast Siberia was found within the sample of Last Interglacial age. This is the oldest discovered seed of *Stellaria jacutica*, which could add valuable data to revealing the history of steppes in northeastern Asia. The purpose of the paper was to summarize all available data on *S. jacutica* species and to propose the timing and possible migration route of the plant. The studied seed, along with the fossil record, examined in Chapter 3, proves that modern steppe occurrences in the Yana Highlands did not establish recently but that they are relicts of a formerly closed steppe belt extending from central Siberia to northeast Yakutia during the Pleistocene.

Author contribution

K.A. and F.K. took the samples and identified plant fossils. K.A. and F.K. designed the study concept. K.A. contacted botanical gardens to confirm the identification, drafted the manuscript, made maps and photos. F.K., K.A. and E.T. revised the manuscript.

Chapter 2.

Palaeoclimate characteristics in interior Siberia of MIS 6–2: first insights from the Batagay permafrost mega-thaw slump in the Yana Highlands

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Palaeoclimate characteristics in interior Siberia of MIS 6–2: first insights from the Batagay permafrost mega-thaw slump in the Yana Highlands

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Abstract. Syngenetic permafrost deposits formed extensively on and around the arising Beringian subcontinent during the Late Pleistocene sea level lowstands. Syngenetic deposition implies that all material, both mineral and organic, freezes parallel to sedimentation and remains frozen until degradation of the permafrost. Permafrost is therefore a unique archive of Late Pleistocene palaeoclimate. Most studied permafrost outcrops are situated in the coastal lowlands of northeastern Siberia; inland sections are, however, scarcely available. Here, we describe the stratigraphical, cryolithological, and geochronological characteristics of a permafrost sequence near Batagay in the Siberian Yana Highlands, the interior of the Sakha Republic (Yakutia), Russia, with focus on the Late Pleistocene Yedoma ice complex (YIC). The recently formed Batagay mega-thaw slump exposes permafrost deposits to a depth of up to 80 m and gives insight into a climate record close to Verkhoyansk, which has the most severe continental climate in the Northern Hemisphere. Geochronological dating (optically stimulated luminescence, OSL, and ^{14}C ages) and stratigraphic implications delivered a temporal frame from the Middle Pleistocene to the Holocene for our sedimentological interpretations and also revealed interruptions in the deposition. The sequence of lithological units indicates a succession of several distinct climate phases: a Middle Pleistocene ice complex indicates cold stage climate. Then, ice wedge growth stopped due to highly increased sedimentation rates and eventually a rise in temperature. Full interglacial climate conditions existed during accumulation of an organic-rich layer – plant macrofossils reflected open forest vegetation existing under dry conditions during Marine Isotope Stage (MIS) 5e. The Late Pleistocene YIC (MIS 4–MIS 2) suggests severe cold-stage climate conditions. No *alas* deposits, potentially indicating thermokarst processes, were detected at the site. A detailed comparison of the permafrost deposits exposed in the Batagay thaw slump with well-studied permafrost sequences, both coastal and inland, is made to highlight common features and differences in their formation processes and palaeoclimatic histories. Fluvial and lacustrine influence is temporarily common in the majority of permafrost exposures, but has to be excluded for the Batagay sequence. We interpret the characteristics of permafrost deposits at this location as a result of various climatically induced processes that are partly seasonally controlled. Nival deposition might have been dominant during winter time, whereas proluvial and aeolian deposition could have prevailed during the snowmelt period and the dry summer season.

1 Introduction

During Late Pleistocene marine regression stages, ice-rich deposits several dozen metres in thickness – the Yedoma Ice Complex (YIC), formed on the now-inundated Laptev and East Siberian Sea shelves and on the coastal lowlands of

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northern Yakutia (Romanovskii et al., 2000a; Schirrmeister et al., 2013). Because they contain syngenetically frozen sediments and well-preserved fossil remains, YIC deposits provide a unique Late Pleistocene palaeoenvironmental archive. Due to their importance as sinks of organic carbon and as palaeoenvironmental archives, ice complex deposits have been of great scientific interest for decades (e.g. Kaplina, 1981; Giterman et al., 1982; Kienast et al., 2005; Sher et al., 2005; Walter et al., 2006; Strauss et al., 2013). Nevertheless, the main depositional processes that resulted in ice complex formation are still not yet fully understood and remain a subject of controversy (Schirrmeister et al., 2013; Murton et al., 2015). The concept of a purely aeolian origin of the mostly silty and fine-sandy, ice-rich deposits has become a widely accepted view in recent time (Zimov et al., 2012; Astakhov, 2014; Murton et al., 2015), but the assumption that loess covered the whole area during the Late Pleistocene contradicts cryolithological studies (Schirrmeister et al., 2011b). For this reason, the hypotheses of nival formation (Kunitsky, 1989), proluvial and slope genesis (Slagoda, 2004), and alluvial (Rozenbaum, 1981), or polygenetic genesis (Konishchev, 1981; Sher, 1997) are noteworthy.

YIC deposits in Yakutia are mainly accessible at natural outcrops along the sea coast or at river banks, primarily in the coastal lowlands; these areas are now under a certain influence of maritime climate, or a polar climate (ETf) according to Köppen (1884). However, this maritime climate influence was restricted to the time of sea level high stands during Quaternary warm stages. During cold stages, when the sea level was low, today's coastal sites were farther inland and under more continental climate influence. All discussed processes of YIC formation are either related to climate-dependent deposition (aeolian and nival processes) or to geomorphology (slope and alluvial deposition). To distinguish between aeolian and other processes in the resulting formation, the examination of YIC deposits in locations with climate and morphology differing from that in the northern coastal lowlands, i.e. more inland and in mountainous areas, is thought to contribute to a better understanding of the YIC genesis by comparing the lithological characteristics in different localities.

The Yana Highlands represent such a location because they form the benchmark for an inland climate north of the Arctic Circle. Verkhoyansk, located in the Yana Highlands, is recorded as the pole of cold; the Yana Highlands represent the region with the most severe climatic continentality in the Northern Hemisphere (Voeikov Main Geophysical Observatory, 1981; Harris et al., 2014). Kunitsky et al. (2013) reported on a rapidly proceeding permafrost thaw slump near Batagay, Verkhoyansky district, Sakha Republic (Yakutia), which has grown tremendously in the past 30–40 years. Due to thermo-denudation rates of up to 15 m per year, the mega-thaw slump reached a width of up to 800 m in 2014 (Günther et al., 2015). Situated in the Yana Highlands (Fig. 1), the Batagay exposure formed unaffected by fluvial or coastal abrasion processes. It is one of the few active permafrost out-

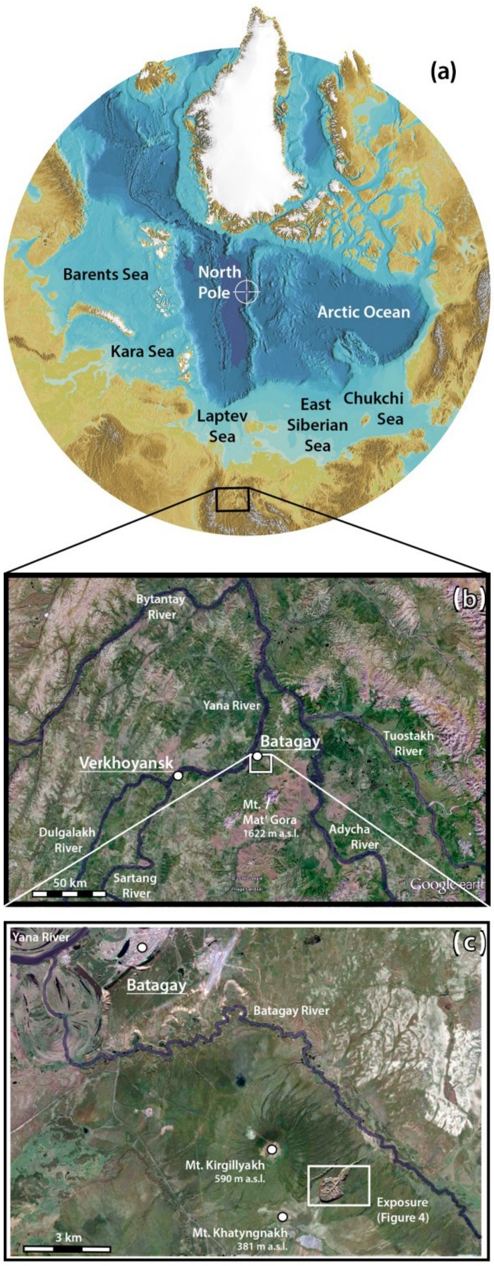


Figure 1. **(a)** Location of the Yana Highlands in northeastern Siberia. Map modified from the International Bathymetric Chart of the Arctic Ocean (Jakobsson, 2012). **(b)** Location of the study area on the right southeastern bank of the Yana River valley. **(c)** Location of the Batagay mega-slump (framed) at the northeastern slope of Mt. Khatyngnakh, left bank of the Batagay River. Panels **(b)** and **(c)** have been modified from satellite pictures, Google Earth 7.1.2.2041. Batagay region, Russia, 67°34′41.83″ N, 134°45′46.91″ E, 4 July 2013, viewed 25 April 2016, http://www.google.com/earth.

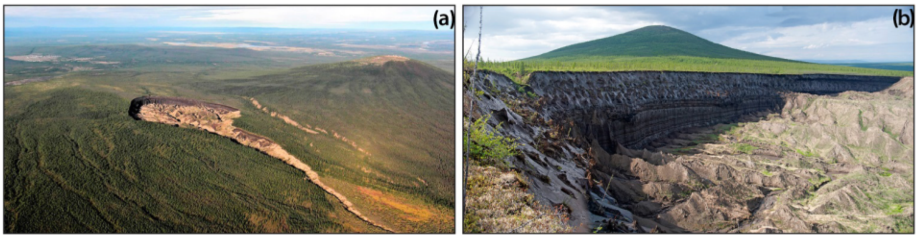


Figure 2. General views of the Batagay mega-slump. **(a)** From aircraft (L. Vdovina, Yana Geological Service, 17 August 2011). **(b)** The exposure at its deepest incision was photographed from the southern edge of the cirque (19 June 2014). For orientation, note Mt. Kirgillyakh in the upper right **(a)** or in the background **(b)**.

crops in interior Yakutia that exposes a long climate record of the Late Pleistocene or even older ages (Fig. 2).

Previous studies on the Batagay permafrost exposure reported on the structure and composition of the upper 12.5 m of the outcrop, discussed thermal denudation processes (Kunitsky et al., 2013), estimated expansion rates using remote sensing data (Günther et al., 2015), or described findings of mammoth faunal remains, including carcasses of horses (*Equus* sp.) and bison (*Bison priscus*), as well as bone remains of cave lions (*Panthera leo spelaea*), woolly rhinoceroses (*Coelodonta antiquitatis*), mammoths (*Mammuthus primigenius*), and other extinct Pleistocene animals (Novgorodov et al., 2013).

In this study, we describe the structural and sedimentological characteristics of the Batagay permafrost sequence. The main aims of our study are (i) to deduce a cryostratigraphical classification of this exceptional YIC sequence and its underlying units in comparison to other YIC records in northeastern Siberia, (ii) to differentiate the depositional processes and underlying climate conditions, and (iii) to highlight common features of and differences between coastal and inland YIC sequences in Yakutia to shed light on their formation processes and palaeoclimate history (Fig. 3).

2 Study site

The Batagay outcrop (67°34′41.83″ N, 134°45′46.91″ E) is located 10 km southeast of Batagay, the municipal centre of the Verkhoyansk district, Sakha Republic (Yakutia). The study site is located on the left bank of the Batagay River, a tributary to the Yana River, and descends down between 300 and 240 m a.s.l. into the foothills of Mt. Khatyngnakh, 381 m high (Fig. 1c). According to Günther et al. (2015), the height difference between the headwall and the outflow of the slump into the Batagay River is 145 m along a distance of 2300 m, while the maximum slump width is 800 m.

The study area belongs to the western side of the Verkhoyansk-Kolyma Orogen, which is characterized by the occurrence of Tertiary dark grey terrigenous siltstone (alevrolits) and argillite, mudstone that has undergone low-grade metamorphism (Vdovina, 2002; Fig. 3 geological map). Both siltstone and mudstone deposits contain layers of sands forming crumpled and broken sediment packs with intrusive rocks. In places, a weathered clayey crust covers the Neogene rocks. The Neogene is represented by clay deposits interspersed with pebbles and gravel, loam, sandy loam, and sands. Quaternary deposits are present as discontinuous layers covering older beds of hard rock and dispersed rocks (Kunitsky et al., 2013).

According to the climate classification of Köppen (1884), Batagay is characterized by a continental subarctic climate (Dfd). Continental climate is described by relatively low precipitation and a great seasonal (or in lower latitudes diurnal) temperature gradient forming under the influence of a large landmass and a great distance to the sea.

Meteorological observations recorded at the Verkhoyansk weather station continuously since 1888 revealed the greatest temperature range on earth. The mean July air temperature is accordingly +15.5 °C and the mean January air temperature is −44.7 °C. From an absolute winter minimum of −67.8 °C to the summer maximum of +37.3 °C, the temperature range equals 105.1 °C. The absolute winter minimum of −67.8 °C is accepted as the lowest temperature measured in the Northern Hemisphere (Lydolph, 1985; Ivanova, 2006). Verkhoyansk is therefore considered the northern pole of cold. The mean annual precipitation is only 181 mm, with the lowest rate during the winter (13 %) and the highest rate during the summer months (51 %) (USSR Climate Digest, 1989). In contrast, Ust-Yansk (70°55′ N, 136°26′ E) as an example of tundra climate (ET) in today's coastal zone, is characterized by a mean July temperature of +9.9 °C and a mean January temperature of −38.7 °C (https://de.climate-data.org/location/761428/). The seasonal temperature gradient is thus lower than inland. Annual precipitation equals 231 mm in the lowlands.

The location of the study area in the coldest part of the Northern Hemisphere is reflected by a mean annual ground temperature (MAGT) of −7.7 °C (Romanovsky et al., 2010) and a permafrost thickness of 300–500 m (Yershov and Williams, 2004). The permafrost formation, which started during the late Pliocene, was most likely influenced by local glaciers from the Chersky and Verkhoyansk moun-

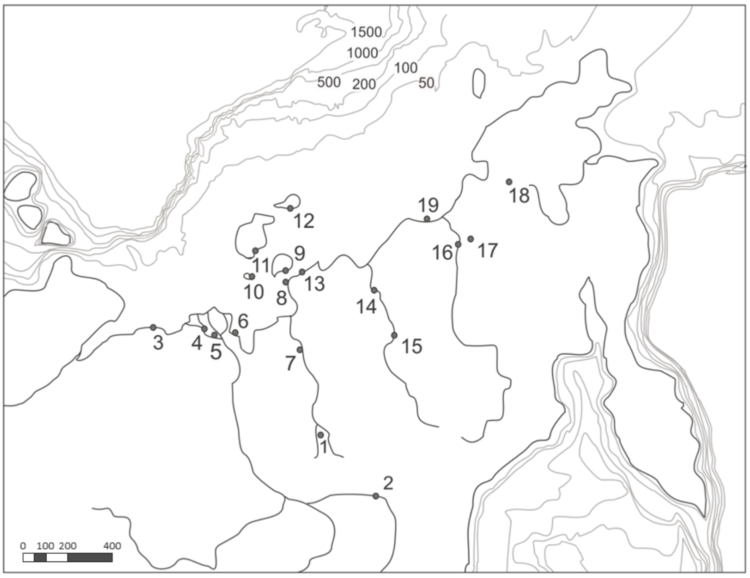


Figure 3. Overview map of the study region. Dots indicate sites mentioned in the text: 1 – Batagay outcrop, Yana Highlands; 2 – Mamontova Gora, Aldan River; 3 – Cape Mamotov Klyk, Laptev Sea; 4 – Diring Yuriakh Island, Lena Delta; 5 – Kurungnakh Island, Lena Delta; 6 – Bykovsky Peninsula, Laptev Sea; 7 – Mus-Khaya, Yana River; 8 – Cape Svyatoy Nos, Laptev Sea; 9 – Bol'shoy Lyakhovsky Island, New Siberian Archipelago; 10 – Stolbovoy Island, New Siberian Archipelago; 11 – Kotel'ny Island, New Siberian Archipelago; 12 – Island New Siberia, New Siberian Islands; 13 – Oyogos Yar, Dmitry Laptev Strait; 14 – Allaikha outcrop, Indigirka River; 15 – Sypnoy Yar, Indigirka River; 16 – Duvanny Yar, Kolyma River; 17 – Molotkovsky Kamen, Malyj Anjuy River; 18 – Lake El'gygytgyn; 19 – Chukochiy Yar, Chukochiy Cape. Combined and modified from Map of USSR, Main Bureau of Cartography and Geodesy, Moscow, 1958, pp. 3, 4, 8; the National Atlas of Russia, Volume 2, Main Bureau of Cartography and Geodesy, Moscow, 2004.

tains (Grinenko et al., 1998). Ice wedge casts in the Kutuyakh beds along the Krestovka River, northeastern Yakutia, indicate that permafrost already existed in northern Yakutia in the late Pliocene (Kaplina, 1981).

Similar to sites in the Yakutian coastal lowlands (Kaplina et al., 1980; Nikolskiy et al., 2010), thick YIC deposits also exist along the Aldan River in Central Yakutia (Markov, 1973; Péwé et al., 1977; Baranova, 1979; Péwé and Journaux, 1983) as well as in the valleys of the Yana Highlands (Katasonov, 2009; Kunitsky et al., 2013). As the result of intense thermal degradation, the Batagay mega-slump formed in just 40 years and cut about 60–80 m into ice-rich permafrost deposits (Kunitsky et al., 2013), dissecting them down to the bedrock at a depth of 110 m below ground surface (m b.g.s.) or 240 m above sea level (a.s.l.) (L. Vdovina, personal communication, 2014). A characteristic feature for the contact zone to the bedrock is the presence of cryogenic eluvium, frost weathering products of the siltstone that overlay leucogranite (alaskite).

The modern vegetation around the outcrop is light coniferous forest composed of larch (*Larix gmelinii*) and Siberian dwarf pine (*Pinus pumila*) as well as, in the shrub layer, *Salix spp.*, *Alnus fruticosa*, *Betula divaricata*, and *B. exilis*. Among dwarf shrubs, *Ledum palustre* and *Vaccinium vitis-idaea* are common. The ground is mostly wet and is densely covered with a thick layer of lichens and mosses, allowing only a few grasses and herbs to establish.

3 Methods

We described the Batagay permafrost sequence during the June 2014 field campaign. We used a Nikon D300 SLR camera to take photographs to be used for cryolithostratigraphical classifications. A Hama polarizing filter was used to highlight ground ice bodies for differentiating the cryolithological units. The 60 m high outcrop was sampled from top to bottom along its height, ideally in 1 m steps, but depending on its accessibility. The profile was sampled along three different transects: section A (0 to 10 m b.g.s.), section B (40 to 50 m b.g.s.), and section C (1 to 44 m b.g.s.) (Figs. 4, 5). Since the steep outcrop wall was not approachable due to the danger of falling objects along most of its length, samples were taken mainly from thermokarst mounds (*baidzherakhs*) in section C (Fig. 4b). The sampling procedure was carried out as follows: (1) the cryolithological characteristics at each sampling point were described and photographed, (2) the sampling zone was cleaned, and (3) frozen deposits were taken using a hammer and a chisel and placed into plastic bags. The wet sediments were air-dried in the field and split into subsamples for sedimentological and biogeochemical analysis in the laboratories of the Alfred Wegener Institute in Potsdam.

Grain size analyses of the < 2 mm fraction were carried out using an LS 200 laser particle analyser (Beckman Coulter GmbH). Total carbon (TC) and total nitrogen (TN) were measured with a vario EL III element analyser and the total organic carbon (TOC) content was measured with a vario MAX analyser. Using the TOC and TN values, the TOC / TN (C / N) ratio was calculated to deduce the degree of organic matter decomposition. The lower the C / N ratio is, the higher the decomposition degree and vice versa (White, 2006; Carter and Gregorich, 2007). For TOC and stable carbon isotope ($\delta^{13}C$) analyses, samples were decalcified for 3 h at 95 °C by adding a surplus of 1.3 N HCl. Total inorganic carbon (TIC) content was calculated by subtracting TOC from TC. Using TIC values, the carbonate content as $CaCO_3$ was estimated via the ratios of molecular weight. The $\delta^{13}C$ of TOC values was measured with a Finnigan Delta S mass spectrometer and expressed in delta per mil notation (δ, ‰) relative to the Vienna Pee Dee Belemnite (VPDB) standard with an uncertainty of 0.15‰. Variations in $\delta^{13}C$ values indicate changes in the local plant association and in the degree of organic matter decomposition (Hoefs and Hoefs, 1997). Lower $\delta^{13}C$ values correspond to less-decomposed organic matter, while higher $\delta^{13}C$ values reflect stronger decomposition (Gundelwein et al., 2007). Mass-specific magnetic susceptibility (MS) indicative of magnetic and magnetizable minerals was measured using Bartington MS2 instruments equipped with the MS2B sensor type. The data are expressed in 10–8 $m^3\,kg^{-1}$ (SI).

For accelerator mass spectrometry (AMS) radiocarbon dating in Poznan Radiocarbon Laboratory, Poland, we used terrestrial plant remains that had been identified (Table 2). No aquatic plant species were detected in the sampled material. Possible reservoir effects as a result of the accidental use of freshwater aquatics are thus eliminated. The AMS laboratory is equipped with the 1.5 SDH-Pelletron model "Compact Carbon AMS" serial no. 003 (Goslar et al., 2004). The results are presented in uncalibrated and calibrated ^{14}C years. The calibration was made with OxCal software (Bronk Ramsey, 2009) using IntCal 2013.

The lower part of the permafrost exposure was sampled for optically stimulated luminescence (OSL) dating. Two samples were taken in the form of cores from unfrozen but observably undisturbed deposits at the outer margin of thermokarst mounds. The tubes were sealed with opaque tape and transported to the OSL laboratory of TU Bergakademie Freiberg, Germany. One separate sediment sample was taken for high-purity germanium (HPGe) low-level gamma spectrometry in order to determine the radionuclide concentration required for dose rate calculations. OSL samples were treated under subdued red light. The outer 2 cm material layer was removed to retrieve only the inner core part that was not exposed to any light during sampling. The outer material was used for in situ water content measurements. The inner core part was processed for quartz and feldspar separation. Quartz procedures yielded sufficient material in the 90–160 µm as well as in the 63–100 µm fractions, while K-rich feldspar yielded only sufficient quantities for one sample in the 63–100 µm fraction. The chemical mineral separation and cleaning included the removal of carbonates (HCl 10 %) and organics (H_2O_2 30 %). The feldspar was separated from quartz using feldspar flotation (HF 0.2 %, pH 2.4–2.7, and dodecylamine). Subsequently, the density separation was performed to enrich K feldspars (2.53–2.58 $g\,cm^{-3}$) and quartz (2.62–2.67 $g\,cm^{-3}$). Quartz extracts were etched (HF 40 %) to remove the outer 10 µm of individual grains. After a final sieving, homogeneous sub-samples (aliquots) of quartz and K-feldspar extracts were prepared as a monograin layer on aluminium discs within a 2 mm diameter. OSL and infrared stimulated luminescence (IRSL) measurements were performed using a Risø TL/OSL Reader DA-20 (Bøtter-

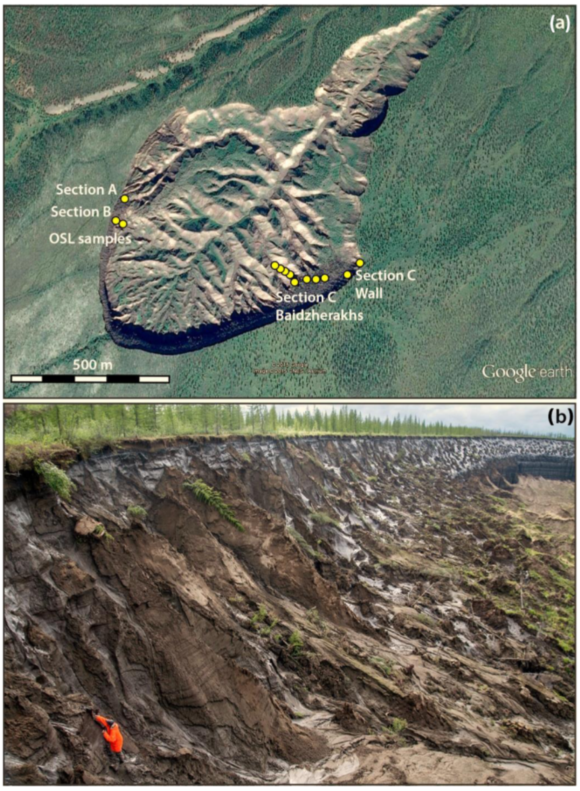


Figure 4. **(a)** Location of the studied sections in the Batagay mega-slump. Modified from Google Earth 7.1.2.2041. Batagay region, Russia, 67°34′41.83″ N, 134°45′46.91″ E, 4 July 2013, viewed 25 April 2016, http://www.google.com/earth. **(b)** Southeastern slope of the thaw slump, section C during sampling. Note person for scale.

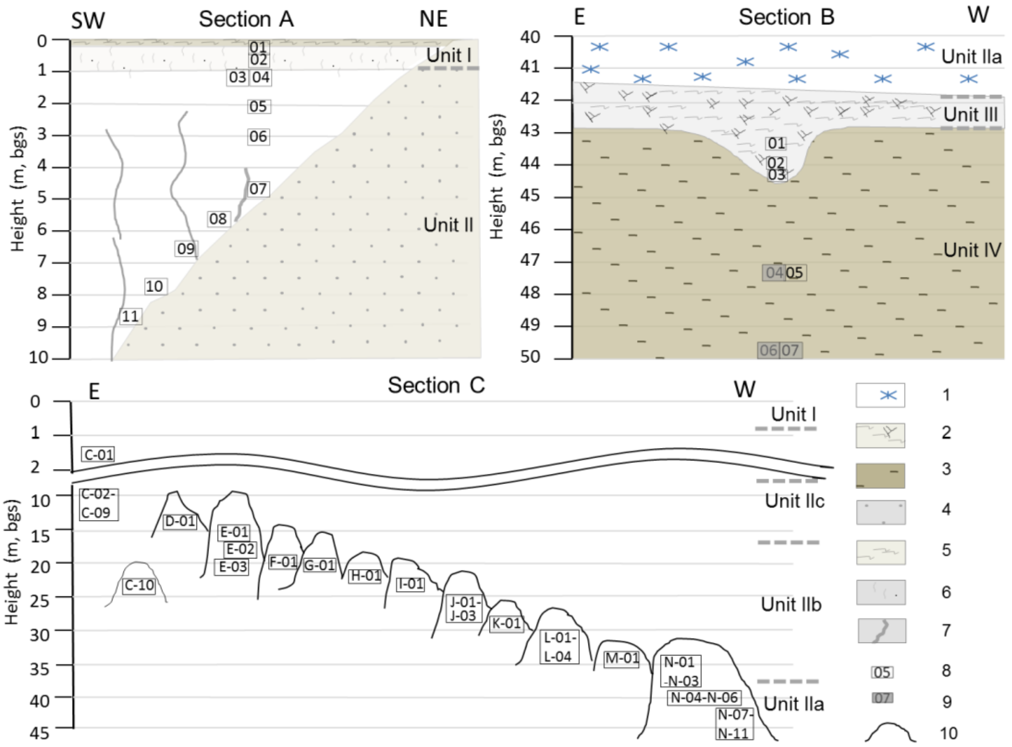


Figure 5. Sections of the Batagay permafrost exposure include the following: 1 – ice-rich sediments, 2 – organic layer with plant remains, 3 – layered cryostructure, 4 – sand, 5 – plant detritus, 6 – active layer with roots and coal, 7 – ice wedge, 8 – sediment and macrofossil sample site, 9 – OSL and sediment sample site, and 10 – *baidzherakh*.

Jensen et al., 2003) equipped with a 90 Sr beta irradiation source (4.95 Gy min^{-1}). Feldspar signal stimulation was performed at 870 nm with infrared diodes (125 °C for 100 s) and the emission was collected through a 410 nm optical interference filter to cut off scattered light from stimulation and was detected with a photomultiplier tube (Krbetschek et al., 1997). For quartz, blue LEDs of 470 nm were used for signal stimulation (125 °C for 100 s) and detection using a U 340 Hoya optical filter. Preheat and cut-heat temperatures were set to 240 and 200 °C, respectively. The measurement sequence followed the single-aliquot regenerative-dose (SAR) protocol according to Murray and Wintle (2000), including tests of dose recycling, recuperation, and correction for sensitivity changes. Appropriate measurement conditions were evaluated and adjusted based on preheat and dose-recovery tests (Murray and Wintle, 2003). Processing of measured data and statistical analyses were performed using the software Analyst v4.31.7 (Duller, 2015) and the R package "Luminescence" for statistical computing (Kreutzer et al., 2012). Sets of 10–40 equivalent doses for individual samples and grain size fractions were analysed for skewness and data scatter. To address sediment mixing that potentially affects permafrost sediments, age modelling was based on the central age model (CAM; Galbraith et al., 1999).

4 Results

4.1 Field observations and sampling

Differences in the thawing rates along the outcrop provide a variety of conditions on the bottom and along the margins of the thaw slump. The western, northwestern, and southwestern parts of the outcrop consist of nearly vertical walls that are eroding most actively (Fig. 6), while the southeastern side is a gentler slope with a gradient of up to 45° (Fig. 4b). Along the western and southern parts of the outcrop, meltwater and mud constantly flow off the steep slopes and form vertical drainage channels. The mud streams flowing downwards from the outcrop walls dissect a number of ridges up to 30 m high of frozen sediments on the bottom of the thermo-erosional gully, forming a fan that is visible in the satellite photo (Fig. 4a). Due to a slight northeastern inclination, the sediment-loaded meltwaters stream down to the Batagay River.

Table 1. Cryolithological description of the Batagay permafrost sequence.

Unit	Section	Observed depth (m b.g.s.)	Field description
I	A	0–0.09	Sod, no ice, composed mainly of modern plant litter including living plant parts.
		0.09–0.2	Light brown sediment with dusty structure. No ice. Horizon is penetrated by modern roots.
		0.20–0.43	Homogeneous light brown layer. No ice. Inclusions of oxidized iron and charcoal. Black spots 30-45 cm deep indicate relocation of solutes and incipient new mineral formation. The border to the underlying sediments is straight and horizontal.
		0.43–0.85	Brown horizon. No ice. Enriched with charcoal and modern plant roots.
	C	0.0–1.4	Silty sediments of dark grey colour, inclusions of charcoal.
		1.40	Top of an ice wedge. The border is clear with thaw unconformity.
II	A	0.85–4.0	Sandy silt in layered ice, layers of gravel, a few plant remains, and in situ rootlets.
		4.60–4.72	Reddish-coloured horizon with 8 cm wide ice veins crossing vertically. Rich in plant remains and contains an arctic ground squirrel burrow 0.2 × 0.12 m.
		5.0–5.8	Unstructured greyish sandy silt with abundant plant remains.
		5.8–6.5	Dark grey ice-rich sandy silt.
		6.5–9.5	Horizontal layers of greyish-brown sand (up to 7 cm thick) and ice bands (up to 5 cm thick); borders are well pronounced and sharp. No visible plant material.
	C	10.0	Sandy silt, horizontal layered ice bands. No visible plant material.
		16.5	Brownish-grey sandy silt, less ice-rich than above. Layered cryostructure. Inclusions of plant roots.
		19.5	Light brown horizon dissected by horizontal to sub-horizontal ice layers. Alternation of clayey and sandy layers with distinct wavy borders.
		22.0	Fulvous brown horizon with 1 mm thick ice veins.
		24.5	Homogeneous strata of greyish sediment structure and less ice. Distinct colour border with the underlying horizon. Layered cryostructure.
		32.0–32.5	Brownish-yellow horizon with abundant plant remains.
		32.5–37.0	Homogeneous strata of greyish sediment and horizontally layered ice bands.
		37.0–37.5	Alternation of grey and black layers, the latter with fulvous inclusions.
		37.5–43.5	Layered brown sediments in massive cryostructure. Clear border to the underlying unit.
III	B	40–42	Alternation of sandy silt layers with plant remains. Frozen organic sediments are extremely rich in large macroscopic plant remains, including numerous branches and twigs of woody plants. The layer with sharp boarders is visible along the wall of the outcrop. Thickness changes from 1 to 5 m filling former depressions that resemble ice wedge casts or small thermo-erosional drain channels. Pronounced erosional surface.
IV	B	42.0–50.0	Layered brown sands and narrow syngenetic ice wedges. Layered cryostructure.
V	Bottom in the central part of the thaw slump		Thick vertical ice wedges with truncated heads and dark layered sediment columns.

The outcropping sequence is composed of five visually distinct units with thicknesses changing along the outcrop (Fig. 6a). When the thickness of units is discussed, we refer to sections A and B unless otherwise stated (Fig. 6a–e, Table 1). Owing to the hillside location of the outcrop, the position of the ground surface differs between sections A and C and thus the depth below ground surface is only conditionally comparable between both sections.

A total of 11 radiocarbon dates are available for nine samples covering ages from modern to non-finite (Table 2). The OSL dating was applied to the lower sample available from Unit IV. Analytical sedimentological results are mainly available for Unit II and are summarized for sections A and B in Figs. 9 and 10 and for section C in Figs. 11 and 12.

4.2 Unit I

Unit I represents the active layer with a thickness varying from the southeast to the northwest wall of the exposure between 1.4 m b.g.s. and 0.85 m b.g.s., as measured at the end of June 2014. The well-bedded sandy sediments of Unit I were deposited in sub-layers 1–2 mm thick. The ≈ 9 cm thick modern vegetation sod is underlain by a homogeneous, brown to grey horizon containing numerous in-

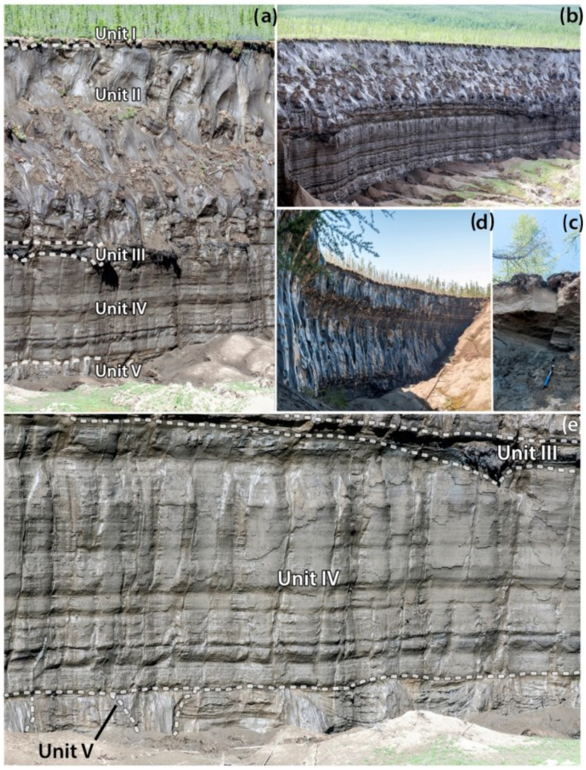


Figure 6. The cryolithological structure of the Batagay exposure in its western and southwestern part. **(a)** General position of the detected cryolithological units (I to V). **(b)** Overall view of the outcrop. **(c)** Unit I (140 cm thick active layer) and boundary to Unit II (YIC) in section A. **(d)** Unit II, steep wall of the YIC illustrating the three observed subunits differing in ice content and contour. The trees as scale on top of the wall are about 6–8 m tall. Section A is situated at the upper part of the slope, on the right side of the photo. **(e)** Detail of the three lower cryolithological Units III, IV, and V. The old ice complex Unit V with preserved syngenetic ice wedges is only partly exposed.

clusions of charcoal and iron oxide impregnations (Fig. 7b). The upper part of the layer is penetrated by modern roots. The unit is homogenously light brown to brown in colour. The lower boundary of Unit I is separated sharply from the underlying Unit II (Fig. 7a).

One ^{14}C AMS date of 295 years BP is available from a sample taken directly above the permafrost table. No features of cryoturbation were observed but the horizon included roots of modern plants. The penetration of modern roots could be a reason for the modern date.

The unit is composed of 44–59 % fine sand with a mean grain size varying between 80 and 90 µm. The MS values are between 19 and 32 SI. The carbonate content is between 2.1 and 2.7 wt %. The TOC of the active layer was below the detection limit of 0.1 wt % in section A but about 1 wt % in

Table 2. Radiocarbon dating results of the samples from the Batagay permafrost exposure. "Plant remains" stands for not identified remains of bark, twigs, and rootlets.

Lab. no.	Sample name	Depth [m b.g.s.]	Section/ unit	C [mg]	δ^{13}C (AMS)	Background pMC	Radiocarbon ages [ka BP]	Calibrated ages 2σ 95.4 % [cal ka BP]	Description
Poz-78149	19.6/A/4/1.15	1.15	A/I	1.5909	−27.3	0.29 ± 0.10	0.295 ± 0.03	0.459–0.347	Plant remains (twigs)
Poz-79751	19.6/A/5/2.05	2.05	A/IIc	2.4545	−25.1	0.25 ± 0.08	33.400 ± 0.5	37.305–38.259	Plant remains (twigs)
Poz-80390	19.6/A/5/2.05	2.05	A/IIc	1.7364	−24.6	0.29 ± 0.10	33.577 ± 472		Plant remains (twigs)
Poz-77152	20.6/A/1/460-472	4.6	A/IIc	0.7909	−24.8	0.30 ± 0.10	26.180 ± 0.22	28.965–27.878	*Plantago* sp., *Artemisia* sp., ground squirrel droppings
Poz-79756	22.6/C/2/8.5	8.5	C/IIc	2.2727	−24.3	–	12.660 ± 0.05	14.919–15.209	Plant remains (twigs)
Poz-79753	22.6/C/6/12.5	12.5	C/IIc	1.6818	−23.2	–	> 48.00		Plant remains (twigs)
Poz-79754	22.6/C/9/14.5	14.5	C/IIc	1.3049	−23.4	–	> 51.00		Plant remains (twigs)
Poz-79755	29.6/E/2/18.5	18.5	C/IIb	0.8864	−25.6	–	49.00 ± 2	51.034–52	*Papaver* sp.
Poz-78150	29.6/C/1/24.5	24.5	C/IIb	2.55	−23.2	–	110.31 ± 0.37pMC	1991 AD-2005 AD	*Alnus* sp., *Vaccinium vitis-idaea*
Poz-78878	29.6/C/1/24.5	24.5	C/IIb	1.5409	−29.6	0.35 ± 0.10	111.4 ± 0.37pMC		*Alnus* sp., *Vaccinium vitis-idaea*
Poz-66024	21.6/B/3/2	44	C/III	2.3092	−26.6	0.30 ± 0.10	> 49.00		Charcoal

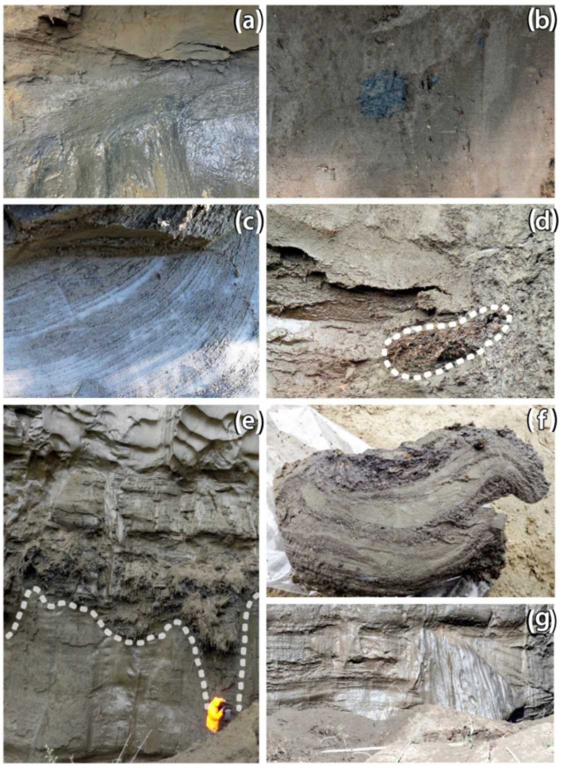


Figure 7. Typical sediment and cryostructures at the Batagay exposure. **(a)** Contact zone between the active layer, Unit I, and YIC, Unit II (section C). **(b)** Charcoal inclusions and iron oxide impregnations in Unit I (section A) at 0.20–0.43 m b.g.s. **(c)** Horizontally layered cryostructure of Unit II (section C). **(d)** Fossilized ground squirrel nest (dated ca 26 ka BP) at 4.7 m b.g.s. in Unit II (section A). **(e)** Organic-rich deposits filling a palaeo-depression ca. 42 m b.g.s. in section B; the person illustrates the position where sample no. 21.6/B/1/43 was taken. **(f)** Sample no. 21.6/B/1/43 in frozen state showing alternate bedding of sand and plant detritus layers. Thickness of the upper plant detritus layer is about 5 cm. **(g)** Ice-rich deposits in layered cryostructure enclosed by syngenetic ice wedges several metres thick in Unit V.

section C. The TN values are about 0.12 wt %. Because the TOC content was insufficient at < 0.1 wt %, $\delta^{13}C_{TOC}$ was not measurable and the C / N ratio could not be calculated.

4.3 Unit II

Unit II consists of the YIC, 30–40 m thick, composed of silty and sandy sediments in a layered cryostructure enclosed by syngenetic ice wedges, very narrow (0.08–0.2 m wide) in the northwestern part and ≤ 6 m wide in the western and southeastern parts of the exposure (Fig. 6b, d). Unit II can be described, according to unaided eye observations, as follows. The northwestern part of the YIC can be divided into three subunits that mainly differ in their ice contents; this difference results in unequal resistance to thermal erosion. Ice wedges gradually become more pronounced towards the top. The uppermost YIC subunit is stabilized by a massive ice wedge system resulting in a cliff overhang. Owing to less pronounced ice wedges and, as a result, increased thermal erosion, the middle subunit of Unit II is notched and forms a concave contour in the profile at the steepest point of the outcrop (Fig. 6d). The middle and upper subunits of Unit II are each about 8 m thick. This lower subunit of the YIC is the thickest of Unit II, reaching 20–25 m here. The southern part of unit II can also be visually divided into three subunits. Differences in ice content are not obviously prominent, but the contour of profile reveals an upper stratum and a lower stratum, each 8 m thick, and a middle, 20 m thick subunit. The deposits are characterized by grey to brown mineral-rich horizons, which alternate with thin ice-rich layers, 0.2 to 7 cm thick in layered cryostructure (Fig. 7c). The YIC deposits contain more or less evenly distributed organic material, mainly in the form of plant detritus and vertical roots of herbaceous plants. Occasionally, layers and patches with higher organic content can be found, e.g. a 0.2 m wide and 0.12 m thick brown fossilized ground squirrel nest with a high number of plant remains (Fig. 7d). The lower part of the Unit is composed of the layered brown sediments in massive cryostructure. The border to Unit III is distinct along the outcrop.

From Unit II, seven samples were radiocarbon dated. Three were double-checked and revealed similar ages. The dated plant taxa are available in Table 2. Material from 2.05 m b.g.s. in section A resulted in a date of 33 ± 0.5 ka BP, while plant material collected from a ground squirrel nest at 4.6 m b.g.s. in section A (Fig. 7c) revealed a ^{14}C AMS date of 26 ± 0.22 ka BP. In section C, dating results from 12.5 m and 14.5 m b.g.s. present non-finite ages of > 48 and > 51 ka BP, whereas plant material from 18.5 m b.g.s. was dated to 49 ± 2 ka BP.

In section C, we collected organic material with very well-preserved plant remains embedded in frozen ice-rich permafrost sediments. We assumed in situ preservation of old material in excellent condition. Dating of this sample, taken at a depth of 24.5 m b.g.s., revealed, however, that this material is of modern (1991–2005 AD) origin and was most likely eroded from the top and later refrozen in the wall.

The mean grain size of Unit II varies between 65 and 126 µm and is thus dominated by fine-grained sand. At about 30 m b.g.s., a distinct layer of medium-grained sand (mean diameter 253 µm) was detected. The MS values vary between 16 and 23 SI except for some higher values of 40, 31, and 43 SI at 43.5, 32.5, and 32 m b.g.s., respectively. The TOC ranges from < 0.1 to 4.8 wt %; higher values of ≥ 1 wt % were measured between 27.5 and 17.5 m b.g.s. in section C and 7.4 and 4.6 m b.g.s. in section A. The TN values range between < 0.1 and 0.49 wt %, while low TN values < 0.1 wt % are mostly accompanied by low TOC values. The C / N ratios are mostly low and range from 2.4 to 9.8. Only one sample at a depth of 32.5 m b.g.s. shows a higher ratio of 13.1. The $\delta^{13}C$ values are rather uniformly distributed, ranging from −26.6 to −23.9 ‰ without any clear trend. The carbonate content is not stable within the profile and varies from 1.2 to 5.9 wt %, aside from one sample at 20.5 m b.g.s. with a lower carbonate content of 0.03 wt %. Comparing the fine-grained sand fraction data and TOC contents, Unit II in section C could be subdivided into three subunits (Figs. 8, 9). The lower part of Unit II between 43.5 and 34.5 m b.g.s. (Unit IIa) is dominated by fine-grained sand (> 50 %) with low TOC (< 0.1–0.7 wt %), whereas the middle part between 32.5 and 16.5 m b.g.s. (Unit IIb) contains less fine-grained sand (20–50 %) and a higher TOC content (0.7–4.8 wt %). The upper subunit at a depth from 16.5 to 8.5 m b.g.s. (Unit IIc) is again mainly composed of fine-grained sand with low TOC.

4.4 Unit III

Unit III consists of frozen sediments that are rich in large macroscopic plant remains, including numerous branches and twigs of woody plants. Situated directly below the YIC, this horizon is detectable over the whole distance of the outcrop, mostly as a relatively thin layer of estimated ≈ 1.5 m thickness sharply delineated from the YIC and Unit IV (Fig 6a, e). In several places, however, there exist accumulations of Unit III organic matter ≈ 5 m thick filling former depressions that resemble ice wedge casts or small thermo-erosional drain channels (Figs. 7e, 8b). Unit III was sampled in the lower part of such a pocket-like accumulation below the coarse woody layer at a depth of about 40 to 44 m b.g.s. The samples taken in section B consist of organic material, including numerous seeds, fruits, and plant debris in a distorted fine bedding alternating with silty fine sand beds (Fig. 7f). Plant macrofossil analyses detected numerous taxa characteristic of northern taiga forests as they occur today at the study site. The main components of the reconstructed vegetation were larch (*Larix gmelinii*) as well as birch (*Betula* spp.) and shrub alder (*Alnus fruticosa*). No aquatic plant taxa were detected.

The erosional surface is pronounced. One sample from Unit III was taken for ^{14}C AMS dating from the lower part of a sediment-filled depression about 6 m below Unit II in section B at a depth of 44 m b.g.s. The dating resulted in an infinite age of > 44 ka BP.

The sedimentological characteristics of the lowermost part of Unit III were studied in section B with two samples from depths of 43 and 44 m b.g.s. (Figs. 7f, 11, 12). The major fraction in the grain size distribution (GSD) of Unit III is fine-grained sand, accounting for 41–45 %. MS equals 30 SI. The TOC values are ≈ 3.3 wt %, the C / N ratio is ≈ 13, the $\delta^{13}C$ values range from −26.5 to −26.1 ‰, and the carbonate content is 2.5–2.8 wt %.

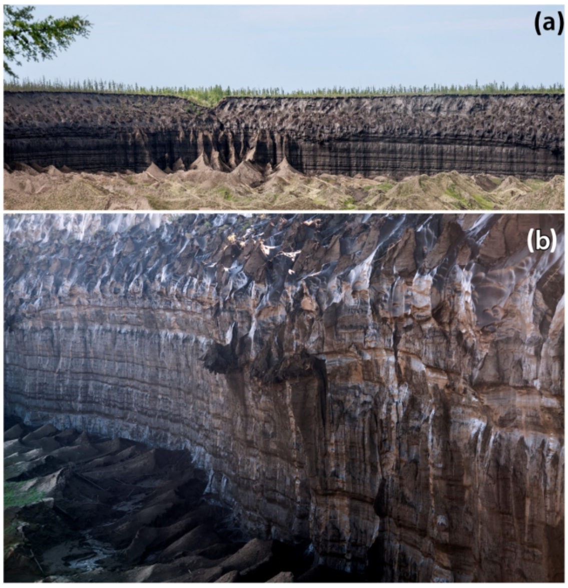


Figure 8. **(a)** Total view of the southwestern part of the outcrop showing that the sequence continues homogeneously over large distances. In the left central part of the photo, note the section of an erosional channel visible in the bottom-left corner of the satellite picture in Fig. 4a. For scale: the trees on top of the profile are on average about 7 m tall. **(b)** Detail of the profile illustrating stratification and borders between Units II, III, IV, and V. Also, it is shown that accumulations of organic material in Unit III occur at isolated places but not as a recurring pattern as would be assumed for fills of ice wedge casts penetrating Unit IV. Instead, they might represent ancient depressions such as transects of channels resembling the modern one in Fig. 8a.

4.5 Unit IV

Unit IV, which reaches a thickness of ≈ 25 m, almost reaches to the bottom of the exposure in most places. Unit IV is composed of distinct horizontally layered frozen sediments (Fig. 6a, e) that are traceable without interruption over large distances along the steepest part of the outcrop (Fig. 6b). Unit IV is separated sharply from the overlying Unit III (Fig. 6e). The border to Unit V is distinct in colour: brown in Unit IV and dark grey in Unit V. In contrast to the YIC, Unit IV is neither penetrated by wide ice wedges, nor does it contain regular ice wedge casts. Its cryostructure is layered: sediment beds are 5–20 cm thick and separated by ice layers. Exposed exclusively at the steepest part of the profile, Unit IV was not accessible for orderly sampling due to the danger of objects frequently falling from the > 60 m high, intensely thawing and eroding, partly overhanging permafrost wall. Only one sample was collected in situ from a ridge of frozen deposits in 50 m b.g.s. for OSL dating and sedimentological analyses. According to the sedimentological characteristics of this material, Unit IV clearly differs from the

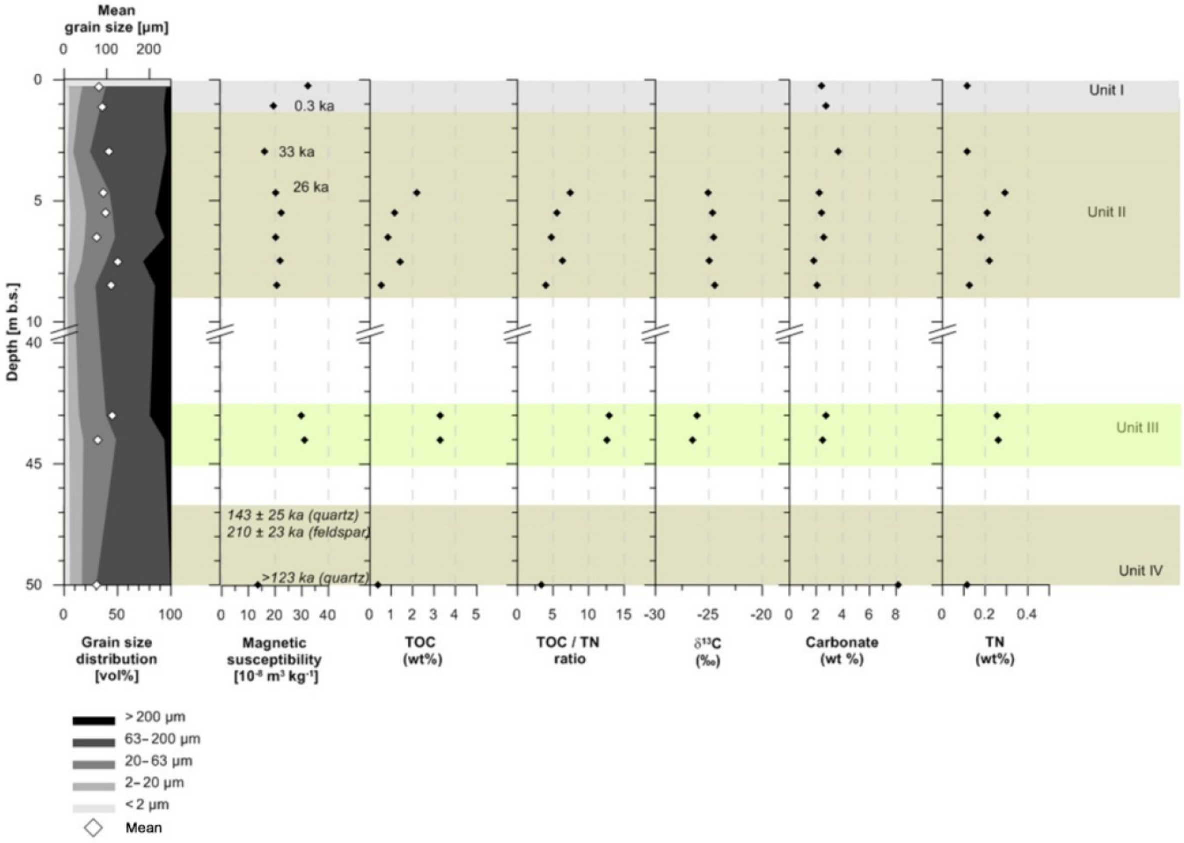


Figure 9. Diagram presenting grain size distribution, MS, TOC and TOC / TN, δ^{13}C, and carbonate records for section A.

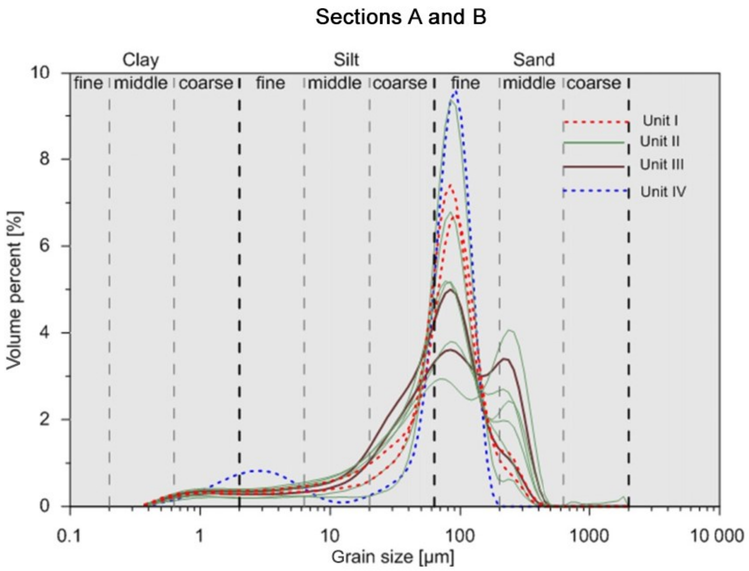


Figure 10. Grain size distribution plot for sections A and B of the Batagay permafrost outcrop.

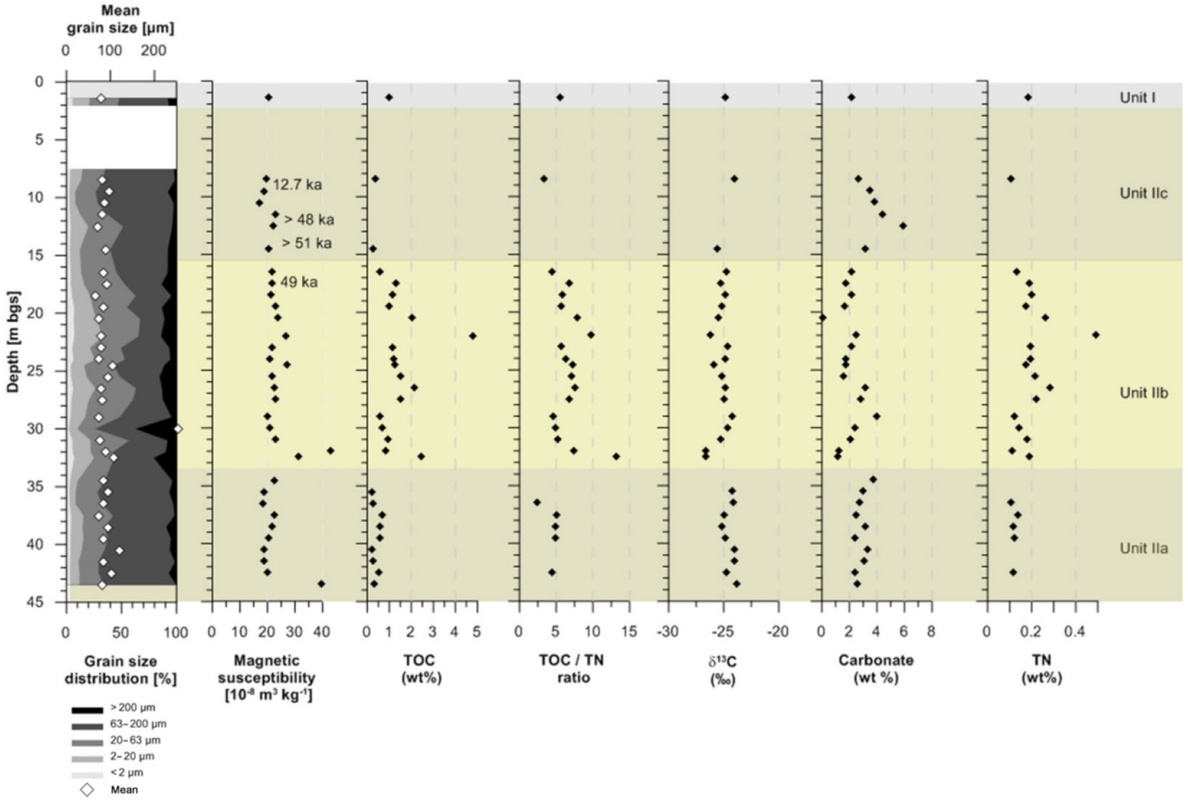


Figure 11. Diagram presenting grain size distribution, MS, radiocarbon ages, TOC, TOC / TN, δ^{13}C, and carbonate records for section C.

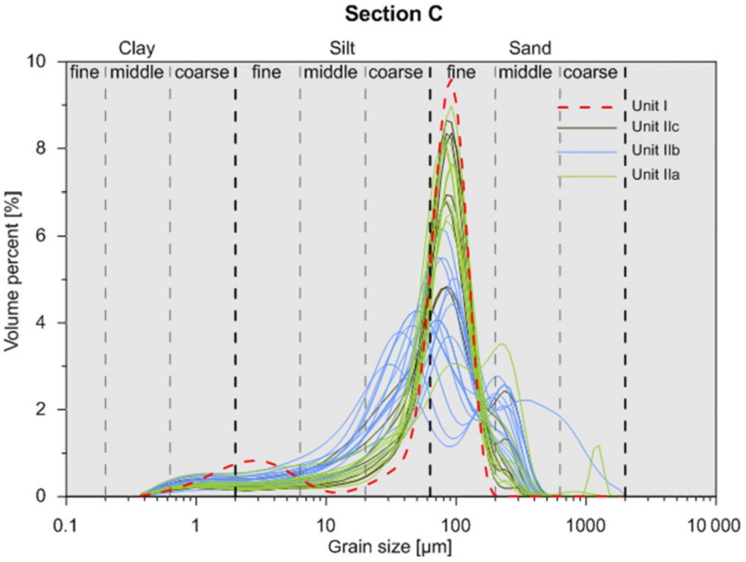


Figure 12. Grain size distribution plot for section C of the Batagay exposure.

Table 3. OSL and IRSL measurement data and respective dating results for the luminescence samples from Unit IV of the Batagay permafrost exposure Dose rate is the effective dose rate calculated based on results from gamma spectrometry and cosmic dose rate and corrected for mineral density, sediment density, grain sizes, and water content. Water is the in situ water content and saturation water content. N is the number of aliquots. PD is the palaeo-dose based on central age model, CAM, according to Galbraith et al. (1999). OD is the overdispersion. Age is the calculated ages according to CAM using the in situ water content. The $>$ sign indicates that minimum age signals were close to saturation and hence tend to underestimate luminescence ages.

Sampling site	67°39′18″ N, 134°38′30″ E, 280 m a.s.l.							
Sample name	Depth [m]	Water [%]	Dose rate [Gy ka^{-1}]	Grain size [µm]	N	PD (CAM) [Gy]	OD [%]	Age [ka]
QUARTZ								
2.7/B/1/47	47	30.1/49.6	1.3	90–160	26	123.8 ± 6.2	26.5	> 93.6
			1.4	63–100	19	129.0 ± 6.1	17.1	> 95.2
2.7/B/2/47	47	34.3/51.6	1.3	90–160	11	127.1 ± 5.1	6.6	> 100.2
			1.3	63–100	11	185.3 ± 26.1	42.9	142.8 ± 25.3[a]
2.7/A/2/50	50	25.1/37.4	1.4	63–100	12	174.4 ± 14.4	23.7	> 123.2
FELDSPAR								
2.7/B/2/47	47	34.3/51.6		63–100	25	274.2 ± 3.32	3.9	210.0 ± 23.0[b]

[a] The CAM age using the saturation water content yields 160.9 ± 27.7 ka. [b] The age using the saturation water content yields 236.6 ± 24.0 ka.

overlying Units I–III. This sample is characterized by the largest sand fraction (70 %) and the highest carbonate content (8.2 wt %) of the studied sample set as well as the lowest MS value (13.7 SI).

OSL measurements for Unit IV in section B show that luminescence signals of quartz already reach the saturation level. For the two duplicate samples at 47 m b.g.s. (samples 2.7/B/1/47 and 2.7/B/2/47) and the one at 50 m b.g.s. (sample 2.7/A/2/50) only 11–26 out of 20–40 measured aliquots yielded equivalent doses and met the quality criteria of a recycling ratio within 10 % and a recuperation of below 5 %. Because of no significant skewness (below 1.5), age modelling was based on the central age model (CAM) according to Galbraith et al. (1999). However, the determined equivalent doses for several aliquots were still above the linear range of growth curves indicated by values above 2 times the D0 value and also by underestimation of applied doses during dose recovery tests. Hence, for the two measured grain sizes of the three samples, only minimum ages could be determined (see Table 3). Only for the sample 2.7/B/2/47 in the grain size 63–100 µm could an OSL age of 142.8 ± 25.3 ka be calculated. A note of caution concerns the water content. OSL ages were based on in situ water contents, for this sample 34.3 %, but samples were taken from unfrozen sediments, while the palaeo-water content of the frozen section remains unknown. To give an upper boundary condition, the saturation water content was used as well, and then the age of this sample yielded 160.9 ± 27.7 ka. Both age estimates lie at the common dating limits of OSL quartz techniques. For the same sample 2.7/B/2/47, feldspar was also available for luminescence dating. The feldspar grains of 63–100 µm showed bright IRSL signals and all 25 aliquots met the quality criteria. Equivalent doses that were determined were within the linear part of the growth curves and showed low errors and an extremely small data scatter, resulting in low overdispersion values of 3.9 % and no significant skewness (−0.32). The CAM yielded an IRSL age for feldspar grains of 210.0 ± 23.0 ka. If regarding the saturation water content as an upper boundary condition of the palaeo-water content, the IRSL age would increase by about 26 kyr (see Table 3 and respective notes).

According to the sedimentological characteristics of this material, Unit IV clearly differs from the overlying Units I–III. This sample is characterized by the largest sand fraction (70 %) and the highest carbonate content (8.2 wt %) of the studied sample set as well as the lowest MS value (13.7 SI).

4.6 Unit V

Unit V is exposed only at the deepest part of the thaw slump near the bottom of the profile (Fig. 6). The main part of this unit is not outcropping but buried. Even though only the truncated heads of ice wedges were exposed, the general composition of Unit V was easily observable and revealed ice-rich deposits in a layered cryostructure similar to the deposits of the YIC (Unit II), embedded in syngenetic ice wedges ≤ 4 m wide (Fig. 7g). Since Unit V exhibits distinct, separate ice wedges several metres wide beneath the layered Unit IV, it can be assumed to be a second ice complex older than the YIC. Unfortunately, Unit V was not accessible for sampling.

5 Discussion

5.1 Lithostratigraphy

According to field observations as well as geochronological and sedimentological data, the permafrost sequence of the Batagay mega-slump consists of five distinct stratigraphic units (Fig. 6a). No gradual transitions were observed between the units; thus, erosional events or strong changes of accumulation conditions can be expected to have occurred.

Unit I represents the active layer or, as we call it, the Holocene cover. The presence of a Holocene layer is typical of the majority of permafrost exposures, although it differs in thickness and age. For example, at Cape Mamontov Klyk it is 3 m thick and covers the time span from 9.5 to 2.2 ka (Schirrmeister et al., 2011b). The dating result from 1.15 m b.g.s. yielded an age of 0.295 ka, which suggests that much of the Holocene layer was eroded. The thickness is not constant along the Batagay outcrop and reaches a maximum observed depth of 1.4 m.

Unit II corresponds to the YIC. YIC deposits can form only under extremely cold winter conditions. They are thus indicative of cold stage climate in a continental setting. Our dating results confirm the assumption that the YIC was deposited from at least >51 to 12 ka BP, thus during the last cold stage and including the Marine Isotope Stage (MIS) 3 (Kargin) interstadial period. Huge syngenetic ice wedges and high segregation ice contents are the most typical features of YIC sequences. The structure of ice wedges intersecting sediment columns is evidence for the syngenetic freezing of the ice wedge polygon deposits. The ice wedges were 4.5 to 6.5 m wide, which indicates the impact of an extremely cold climate during their formation and also indicates aridity (Kudryavtseva, 1978). The thermokarst mounds (*baidzherakhs*) appearing in staggered order 4.5–6.5 m apart on the upper southeastern part of the YIC support this hypothesis.

The structural differences of the Unit II ice wedges suggest that they represent three generations of past ice wedge growth. Also, the threefold division of Unit II, as visible in its contour in the profile and in grain size parameters and TOC content in section C, may reflect three different climate stages, e.g. MIS 4, 3, and 2 during YIC formation. In this case, the MIS 4 and MIS 2 cold stadial phases were characterized by relatively uniform landscape conditions with fine sand accumulation and low bioproductivity, whereas the MIS 3 interstadial was characterized by changing accumulation conditions and higher bioproductivity. Unfortunately, the geochronological data do not support such subdivision since most dates are beyond the limit of the radiocarbon method. The coarse dating hence does not imply continuous sedimentation during the last 51 kyr; thus, we cannot exclude interruptions in the sedimentation record. Also, we could not take samples directly from the visually different subunits in the western part near section A (Fig. 6d) to verify if sedimentological characteristics confirm the apparent visual differences. The YIC at parts of section A differed from the YIC in other parts of the exposure in having considerably smaller outcropping ice wedges. We considered the absence of visible large ice wedges due to exposed intra-polygonal sediment sequences concealing the ice wedges at this place. Owing to the lack of large exposed ice wedges, this part of the sequence was, however, separated from the YIC and regarded as its own unit by Murton et al. (2016).

Dating results may indicate that parts of the YIC could have been eroded. Taken at a depth of 2.05 m b.g.s., the uppermost dated sample of Unit II in section A has an age of ca. 33 ka BP. The dating of the next overlying sample with a position in Unit I only about 1 m above resulted in an age of ca. 0.3 ka BP. This young age might be the result of contamination with modern material. No features of cryoturbation were observed but the horizon included roots of modern plants. Cryoturbation is very unlikely since the ground is not wet enough for cryoturbation due to inclination and fast drainage. No Holocene sediments older than the 0.3 ka BP sample at 1.15 m b.g.s. in section A have yet been found in the Batagay mega-slump, but this could be due to the difficulty of accessing the upper parts of the profile. The youngest YIC age in section A of about 26.2 ka BP originates from plant material amassed in a ground squirrel nest 4.6 m b.g.s. The age inversion between 2.05 and 4.6 m might be the result of younger material actively transported by arctic ground squirrels deep into their subterranean burrows for food storage. Together with the fault tolerance of the radiocarbon dating, this might explain the inversion. The assumption of plant material transport by ground squirrels is reasonable for depths of up to 1 m below ground, which is an average depth for the permafrost table. The permafrost table as a natural barrier for ground squirrel penetration can be even deeper, when the soil substrate is coarse-grained and dry as is often the case for sandy deposits. Larionov (1943) reported on a ground squirrel nest found in Siberia at 2 m depth.

Due to the uncertainty of the age–height relation, we re-dated material from the ground squirrel nest and obtained an age of about 25 ka BP, which confirms the original dating (Table 2). The substrate at the site is sandy and, during the lifetime of the ground squirrel, it was probably dry due to the inclination at this slope. The eventuality that the overlying older age originates from redeposited material from further uphill must however be taken into account as well.

The youngest YIC age from the Batagay thaw slump of about 12.7 ka BP was determined in section C (southeastern part) at 8.5 m b.g.s. This result stresses the difference between southeastern and northwestern parts of the outcrop. An age gap of several tens of thousands of years could be expected between the infinite age of >48 ka BP at 12.5 m b.g.s. and 12.7 ka at 8.5 m in section C. It is implausible that only 4 m of YIC deposits were formed during more than 35 kyr.

The observed stratigraphic hiatus of up to 12 kyr atop the YIC was likely caused by post-depositional erosional events, such as widespread thermo-denudation or local thermal erosion of early Holocene deposits. A sudden shift from deposition to erosion as a consequence of intense warming during the late glacial–early Holocene transition (e.g. Bølling–Allerød) and also during other warm phases such as the middle Weichselian interstadial is a characteristic feature of many YIC sequences in Yakutia (e.g. Fradkina et al., 2005; Wetterich et al., 2014; Schirrmeister et al., 2011b) and can also be readily assumed for the Batagay thaw slump. The uppermost boundary of YIC sequences as dated with the AMS radiocarbon method differs between 28 ka BP on the New Siberian Islands and 17–13 ka BP at various other sites. Available radiocarbon dates from mature *alas* depressions in central Yakutia reported to have an age of 12 ka BP (Katasonov et al., 1979; Kostyukevich, 1993).

The organic layer of Unit III below the base of the YIC (Unit II) is characterized by a high abundance of macroscopic plant material including woody remains. Plant macrofossil analyses reveal taxa characteristic of northern taiga forests with larch (*Larix gmelinii*), birch (*Betula* spp.), shrub alder (*Alnus fruticosa*), and indicators of dry and open habitats (Ashastina et al., 2015). The palaeobotanical results clearly indicate warm climate conditions during the formation of this layer. High values of TOC and C / N and low δ^{13}C values reflecting increased bioproductivity and moderate organic-matter decomposition confirm this suggestion. These proxy records together with the position of Unit III below the base of the YIC, the infinite AMS date of >44 ka BP of the sample, and the OSL quartz date of 142.8 ± 25.3 ka of the sample taken from Unit IV indicate that Unit III probably formed during the MIS 5e interglacial. This assumption is in good agreement with data from Lake El’gygytgyn (Tarasov et al., 2013), where the Eemian interglacial from 127 to 123 ka was the warmest period in the last 200 kyr. The organic layer of the Batagay Unit III is continuous throughout the outcrop and shows a uniform thickness of about 1.5 m, reaching up to 3.5 m in thickness in palaeo-depressions. Such a distribution might indicate the presence of a continuous palaeosol that developed under stable interglacial conditions.

The uniformly occurring Unit IV with its characteristic horizontal bedding was observed over large distances along the lower and very steep segment of the exposure wall. The lack of wide ice wedges or ice wedge casts indicates that the conditions during deposition of Unit IV were inappropriate for the formation of a pronounced ice complex directly below the last interglacial Unit III. Unit IV instead represents sediments that, in contrast to YIC deposits, consistently accumulated under uniform depositional environments. We did not find any evidence for the presence of lacustrine or fluvial deposition in the sediments along the whole permafrost sequence. We detected neither pebbles, other coarse material, nor freshwater mollusc remains. Fluvial or lacustrine deposition can be excluded because of the topographical setting: the area around the Batagay mega-slump is northeastwardly inclined. This would prevent water stagnation and would not result in clear horizontally layered structures. Instead, laminar slope deposition as the result of ablation or aeolian activity can be assumed to be the main sedimentation processes that formed Unit IV. The assumed laminar slope deposition can be related to cryoplanation and other nivation processes during cold phases, with perennial snow accumulations further uphill. Detailed sedimentological results are not available for Unit IV since it was not accessible for sampling during our field stay. A detailed description of this unit was presented by Murton et al. (2016).

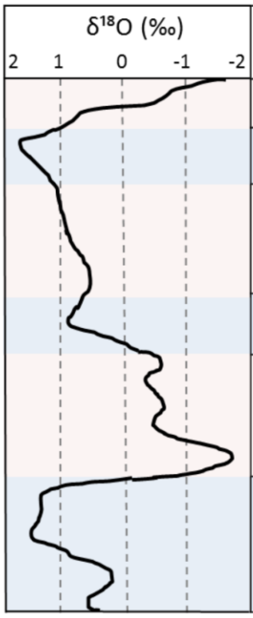
The lowermost Unit V was observed in the field at the bottom part of the thaw slump wall (Figs. 6, 7g). The existence of truncated ice wedges several metres in width and their position more than 20 m below Unit III, which represents the last interglacial period, allow the interpretation that this unit represents an ice complex indicating a continental cold-stage climate with extremely cold winters already occurring during the Middle Pleistocene. The symmetric ice wedges contained in the unit point to the syngenetic formation of Unit V. The finding of such ancient ice wedges also demonstrates that ice-rich permafrost survived at least two glacial–interglacial cycles (MIS 5 and MIS 1). Similar observations of ice complex deposits older than the last interglacial were made on Bol’shoy Lyakhovsky Island by Andreev et al. (2004) and Tumskoy (2012) and were dated by Schirrmeister et al. (2002) to MIS 7. On the basis of the stratigraphical position of this ice complex below Unit III, which is thought to be deposited during the last interglacial, we assume that Unit V is older than MIS 5e, thus of the Middle Pleistocene age.

An overview of changes in palaeoclimatic conditions and the response to these changes reflected in the sediment sequence of the Batagay mega-thaw slump is available in Table 4. The shifts in sedimentation characteristics of the Batagay sequence are in good agreement with global climatic events, such as glacial and interglacial phases recorded by oxygen isotope data, and regional climatic changes, identified by stadial–interstadial phases in Siberia and Europe.

5.2 Sedimentation processes of the Batagay YIC

Our reconstruction of YIC formation is based on the analysis of GSD as discussed in Sect. 4. Additional studies on the mineralogical composition as well as micromorphological analysis would be useful to identify the sources more precisely. The radiocarbon dating results of the YIC in the Batagay mega-slump from >51 to 12 ka BP with large gaps in between suggest that the sedimentation experienced interruptions or parts of the sequence were eroded. In addition to post-depositional erosion, the gaps within Unit II might also be the result of temporarily and spatially shifted local deposition. Sediments were deposited during given periods and at a particular part of today’s outcrop mainly from a certain source area, such as Mt. Kirgillyakh northeast of the outcrop; during earlier or later periods, sedimentation might have stopped there and instead taken place mainly at another

Table 4. Overview of permafrost dynamics recorded in the Batagay sequence in presumable correlation with global and regional climate histories. Due to the sparse dating resolution, the correlation is mainly based on the chronostratigraphic comparison of Batagay and lowland exposures. Global climate history is represented by marine isotope stages (MISs; Aitken and Stokes, 1997) derived from the $\delta^{18}O$ curve (modified from Pisias et al., 1984), reflecting global temperature changes studied in deep sea cores. Negative $\delta^{18}O$ ‰ values reflect warm climate stages, while positive values identify cold phases. The regional Siberian climate phases are given according to Sachs (1953). The European regional climate events for comparison are named according to Litt et al. (2007).

$\delta^{18}O$ (‰)	Date BP, ka	MIS	Siberian classification	European classification	Unit	Permafrost dynamics
	< 11.5	1	Holocene	Holocene	I	Permafrost degradation, erosional processes
	28 – 11.5	2	Sartan stadial	Late Weichselian	IIc	Yedoma Ice Complex, thickest ice wedges - coldest climatic conditions
	50 - 28	3	Kargin interstadial	Middle Weichselian	IIb	Yedoma Ice Complex with warm phase signals – TOC values higher than in Unit IIc and IIa
	73 - 54	4	Zyryan stadial	Early Weichselian	IIa	Yedoma Ice Complex agradation – thick ice wedges, low organic content
	120 - 127	5	Kazantsevo interglacial	Eemian	III	Thick organic layer, warmest period within the sequence
	> 130	6	Taz stadial	Late Saalian	IV	Cessation of ice complex formation, increased sedimentation rates, shift in climatic conditions
				?	V	Middle Pleistocene Ice Complex, thick ice wedges, cold stage climate

part of the foothill and from a different local source area, e.g. Mt. Khatyngnakh southwest of the outcrop (Fig. 1c). Due to varying discharge directions, locally restricted denudation phases might also have occurred. As a result, the entire YIC sequence might not have formed simultaneously, but may have formed piecewise and successively.

We assume that the sediment material was subaerially exposed and was incorporated into the permafrost syngenetically, e.g. at the same time as the deposition. The final accumulation occurred within small depressions of low-centre polygons, which existed between the ice wedges. The exposed YIC wall is a cross section through the former landscape with polygonal patterned ground.

According to the general scheme of landscape types introduced in Schirrmeister et al. (2011b), the Batagay YIC is related to the second landscape type, which represents cryoplanation terraces occurring on foothill slopes. The first landscape type is low-elevation coastal mountains and foreland accumulation plains; the third landscape type is extended lowland at a great distance from mountain ranges. After 60 ka BP, local mountain glaciers no longer reached the highlands (as was true during the Middle Pleistocene), but glaciation covered only the western and southwestern Verkhoyansky Mountains (Siegert et al., 2007). Hence, the bedrock in the study area could have been affected by strong frost weathering providing fine-grained material for aeolian transport and YIC formation. Such bedrock weathering is also typical of the permafrost sequences at Bol’shoy Lyakhovsky Island, Cape Svyatoy Nos, and the Stolbovoy and Kotel’ny islands (Siegert et al., 2009).

A possible sediment supplier is located 20 km south of the Batagay thaw slump: Mat’ Gora, a 1622 m high massif (Fig. 1b). We suggest however that Mt. Kirgillyakh and Mt. Khatyngnakh, situated just 2 km away (Fig. 1c), mainly provided substantial input to the sediment composition of the Batagay deposits. YIC subunit IIa and IIc are characterized by a unimodal distribution curve made up by a > 50 % fine-grained sand fraction; this can be explained as a result of periglacial, proluvial, or nival processes (Kunitsky et al., 2002). We suggest that subunit IIc correlates to the MIS 2 (Sartan) stadial and subunit IIa correlates to the MIS 4 (Zyryan) stadial.

According to Kunitskiy et al. (2013), nival processes were highly significant here during the late Pleistocene. They proposed that nival (snow-filled) depressions existed at this time; thus, cryohydro-weathering, as discussed by Konishchev (1981), took place. The material trapped on top of the snow was, during snow melt, incorporated into downslope sediments.

In addition to the nival genesis of the sediments, the material trapped by snow could have been transported there by local aeolian processes, as the coarse-silt fraction of 30–50 µm suggests. Some horizons are characterized by less than 40 % of silt in the GSD, thus indicating that aeolian input, although it is significant, might not have been the main and only deposition process. The Batagay mega-slump is located within 10 km of the Yana River and 30 km from the Adycha River floodplains. The meandering pattern of both river systems and the adjacent sandy terraces ≤ 50 m high (Fig. 1c, upper left) suggest that, during the Late Pleistocene, when the continentality and wind velocities were higher than today, the wide, braided floodplains could have provided material for local aeolian input. Local aeolian input could originate from the Batagay river floodplain as well (Murton et al., 2016). Even though the substrate is stabilized almost everywhere by vegetation, today the sandy terraces of the Yana River also provide large amounts of material available for local dust storms in summer. The results of MS measurements did not display, however, any changes in the content of magnetic or magnetizable minerals within the studied sequence as would be expected from shifts in the main source areas, e.g. from local slope deposits to more regional, redeposited alluvial material from the Yana River.

The GSD curves for Units IIb and III indicate a polygenetic sediment origin; this is indicated by the bimodal distribution in fraction sizes, from silt and coarse silt – a possible aeolian transport indicator – to sand, a possible hint of proluvial and nival genesis, as was discussed for subunit IIa and IIc. Nevertheless, the high percentage of the silt fraction in the GSD of subunit IIb cannot be interpreted as an exclusive indicator of aeolian deposition because high silt content in the sediment composition can also result from cryogenic disintegration of quartz due to repeated thawing and freezing cycles (Konishchev and Rogov, 1993; Schwamborn et al., 2012). The predominance of silt in the GSD might be a result of the combination of both processes, frost weathering and aeolian deposition.

However, the Batagay source material certainly differs from that in the coastal outcrops. Bykovsky was fed by the Khara-Ulakh Mountains, a low-elevation coastal mountain ridge. In contrast, Batagay was supplied with sediments from the hillside of the Kirgillyakh–Khatyngnakh eminence. Another possible material source for Batagay is windblown material from the Yana River valley and Adycha River valley; this is suggested by the occurrence of sandy terraces adjacent to the Yana floodplain 7 km west of the Batagay outcrop (Fig. 1c, upper left part).

A certain proportion of local aeolian deposition in the formation of the Batagay YIC is indicated by its sedimentological characteristics. Despite similarities in the general YIC (Unit II) structure, the Batagay sequence is distinct from other permafrost exposures. All coastal outcrops are characterized by polymodal grain size curves, a dominance of fine-grained sediments, and relatively high concentrations of silt in their structure. The Batagay YIC, in contrast, is dominated by fine-grained sand in a unimodal GSD curve (Unit IIa and c) and by bimodal coarse-silt and fine-sand curves (Unit IIb). Higher concentrations of sand in the YIC exposures of Kurungnakh Island and Diring Yuriakh (Lena River delta) are interpreted to be of aeolian origin (Siegert et al., 2009; Waters et al., 1997).

The characteristics of the Batagay YIC profile could be assumed to be close to the Mus-Khaya or Mamontova Gora outcrops because the first is located along the Yana River bank and is in a comparable hydrological location, while the second, from the Aldan River in Central Yakutia, is another example of an inland YIC that never experienced maritime influence. Although also situated in the catchment area of the Yana–Adycha river system, the Mus-Khaya ice complex (Katasonov, 1954) is hardly comparable to the Batagay YIC. In contrast to Batagay, the Mus-Khaya ice complex is affected by fluvial deposition resulting in a cyclic facial-lithological structure represented by dark-brown, organic-rich, loess-like loam alternating with dark-grey, ice-rich loam. This alternation of organic-rich and ice-rich sediments of different composition is the basis of the cyclic YIC structure theory because the deposits are believed to be of predominantly alluvial origin (Katasonov, 1954; Lavrushin, 1963; Popov, 1967). This theory can be well implemented for floodplain settings because the cycles represent changes governed by shifts in the river course, from riverbed to oxbow lake and floodplain deposits. Such cyclic structure is not detectable at the Batagay outcrop because this site was not affected by river influence as it is distant from a river floodplain. On the contrary, the absence of such cyclic structure indicates the slope genesis of the studied YIC.

Seasonally controlled processes under the influence of a continental climate might have governed the deposition of Unit II; during the cold winter, nival deposition could have been dominant, whereas proluvial and aeolian deposition could have prevailed during the snowmelt period and the dry summer season. Aeolian deposition was thus locally restricted and was one of several processes that formed the Batagay ice complex sequence.

5.3 Climatic implications in comparison with other ice complex sequences (inland versus coastal ice complex)

The Batagay mega-slump studied here shows a general structure comparable to coastal permafrost exposures of Quaternary deposits in northeastern Siberia, as described by Schirrmeister (2011a), as follows: (i) late Saalian ice-rich deposits (ancient ice complex), (ii) pre-Eemian floodplain deposits, (iii) Eemian thermokarst deposits, (iv) alluvial deposits from the Eemian–Weichselian transition, (v) early, middle, and late Weichselian ice-rich deposits (YIC), and (vi) late glacial and Holocene thermokarst deposits.

Using the abovementioned general structure of permafrost sequences in the coastal lowlands, we subsequently compare the Batagay units with other Quaternary sediment records in northeastern Siberia.

The Holocene unit at the Batagay outcrop is represented by a thin cover of up to 1.4 m. The only available date reveals an age of 300 years BP. Further dating along the upper edge of the exposure is necessary for the differentiation of late glacial and Holocene deposits. During the late glacial and the Holocene, the YIC and more recent sediments were often eroded due to climatic warming. Thermo-erosion of the upper YIC layer is typical for most of the known permafrost exposures. For example, thermokarst depressions filled with organic deposits are observed at Cape Mamontov Klyk. At the New Siberian Archipelago, the Holocene cover is still partly present (Schirrmeister et al., 2011b).

The YIC, corresponding to Unit II in the Batagay profile, is the most-accessible and best-studied Quaternary permafrost sediment type in Siberia. The YIC developed during MIS 4–MIS 2. Kaplina (1981) estimated the MAGT during YIC aggradation on the basis of such parameters as the width of ice wedges, typical polygon sizes, the temperature coefficient of rock contraction, and values of −20 to −25 °C obtained for the late Pleistocene (today −7.7 °C). Similar values can be assumed for the time of formation of the Middle Pleistocene ice complex – Unit V in the Batagay profile. Ice complex characteristics such as spacing and width of ice wedges cannot reliably be used to estimate mean annual air or even mean winter palaeotemperatures (Kaplina, 1981; Plug and Werner, 2008). However, Romanovskii et al. (2000b) indicated a MAGT 8 °C lower than today during MIS 4 and MIS 3 and 10 °C lower than today during MIS 2 for the coastal lowlands. Siegert et al. (2009) summarized the results of the Russian–German decadal cooperation on the investigation of coastal YIC in northeastern Russia with special attention to sites at Cape Mamotov Klyk, the Lena Delta, Bykovsky Peninsula, Bol'shoy Lyakhovsky Island, and the northern islands of the New Siberian Archipelago. According to the dating results, coastal ice complexes were preserved until 27 ka BP at the New Siberian Archipelago, while along the mainland Laptev Sea coast, younger deposits are also available. Konishchev (2013) suggested a YIC formation time frame from 50 to 11 ka BP. The youngest dates of Batagay YIC deposits have an age of 12 ka BP. The cessation of YIC formation might explain the hiatus in the sedimentation record from 12 to 0.3 ka BP in the Batagay sequence. Such gaps, even though not of such magnitude, also exist in exposures at Kurungnakh Island, the Lena Delta (Wetterich et al., 2008), Molotkovsky Kamen, and Malyj Anjuy River (Tomirdiaro and Chernenky, 1987). Gaps in sediment preservation might also be explained by locally increased erosion triggered by changes in climatic conditions. According to Kaplina (1981), sedimentation gaps are possibly connected to large-scale thermokarst processes as well as an increase in humidity and forest cover. The moister Holocene climate of this area was governed by changes in the hydrological regime, which was triggered by the transgression of the Laptev and East Siberian seas. Peatland deposits as indicators for thermokarst processes as they are characteristic for early Holocene sites in the circum-Arctic (MacDonald et al., 2006) were not detected at the Batagay outcrop. This might be due to the absence of intense thermal degradation or due to the topographical setting preventing meltwater from accumulating. In the Batagay profile, we detected neither lacustrine nor palustrine deposits, which might be indication of thermokarst processes.

Based on detailed studies of YIC in Siberia, Katasonov (1954) detected a cyclic structure of sediments in the Mus-Khaya outcrop. This concept was further developed by Lavrushin (1963) and Romanovskii (1993) and summarized by Konishchev (2013). The identified lithogenetic cycles depict changes in climate conditions that occurred from MIS 4 to MIS 2, e.g. two stadial stages (Zyryan and Sartan) and one interstadial stage (Kargin) with several thermochrones within. On the basis of sedimentological and TOC analyses, we also distinguished three subhorizons in the YIC structure (subunit IIa to IIc). Konishchev (2013) described such cyclic sediment cryostructures as consisting of alternating layers of heavily deformed greenish-grey ice-rich loam, peat inclusions, less ice-rich non-deformed strata, and brown loam with a fine layered cryostructure. Such sedimentation cycles, governed by a floodplain setting, are mentioned, e.g. for the Mus-Khaya, Duvanny Yar, and Chukochiy Yar outcrops (Kondratjeva, 1974; Kaplina et al., 1978; Konishchev, 2013). In Batagay, such cyclicity could not be detected partly due to the specific cross section of the steep southwestern permafrost wall (this wall was mostly cut along the wide ice wedges), partly owing to the lack of accessibility of the unit II along the whole exposure. However, at the more gentle southeastern part of the outcrop, such structures also did not occur, possibly due to a different geomorphological setting as discussed below.

The subdivision of the Batagay YIC is similar to that of Mamontovy Khayata at the Bykovsky Peninsula (Schirrmeister et al., 2011b). Accordingly, the middle parts of both YIC sequences contain MIS 3 peat horizons, indicating warm phases. In Unit IIb of the Batagay sequence, two horizons rich in organic carbon were identified (Fig. 12). The upper part of Mamontovy Khayata is composed of proluvial MIS 2 (Sartan) deposits resembling Unit IIa in Batagay.

Mamontova Gora is situated along the Aldan River in central Yakutia, outcropping in a 50 m high terrace (Markov, 1973). It was stratigraphically subdivided into three units covering the time span from the Holocene to presumably the last interglacial (Péwé et. al., 1977). The middle unit of the Aldan River outcrop revealed radiocarbon ages from 26 ka BP to > 56 ka BP, which correlate to Unit II in the Batagay sequence and supports the assumption that an erosional event took place in central Yakutia on a similar temporal scale as in the Yana Highlands. The Mamontova Gora sequence in contrast to the Batagay profile is composed of 60 % of well-sorted silt with grain size values of 0.005–0.5 mm, which was explained by distant aeolian particle transport from wide, braided, unvegetated flood plains of rivers draining nearby glaciers (Péwé et. al., 1977).

Most of the coastal permafrost exposures in Siberia are characterized by bimodal or polymodal GSD curves (Schirrmeister et al., 2008, 2011b), which indicate a variety of transport, accumulation, and resedimentation processes occurring there. Unimodal and bimodal curves, as were revealed for both Mamontova Gora and the Batagay megathaw slump, could reflect more stable accumulation and sedimentation processes under continental conditions.

Unit III in the Batagay outcrop might be equivalent to part III of the general permafrost sequence structure (i.e. MIS 5e) with a few differences. Its structure is referred to as a lake thermokarst complex (Tomirdiaro, 1982) or as ancient Achchagyisky and Krest Yuryakhsky *alas* deposits (Kaplina, 2011) and is displayed in peat layers ≤ 10 m thick filling former ground depressions, e.g. ice wedge casts. This horizon formed as a result of permafrost thaw processes during the last interglacial (MIS 5e) warming and is present with variable thicknesses in all permafrost exposures from the coastal zone, e.g. from Duvanny Yar, the Kolyma River (Kaplina et al., 1978) and Mus-Khaya, and the Yana River (Katasonov, 1954; Kondratjeva, 1974) to exposures further inland, e.g. the Allaikha and Sypnoy Yar outcrops, the Indigirka River (Lavrushin, 1962; Kaplina and Sher, 1977; Tomirdiaro et al., 1983), Mamontova Gora, and the Aldan River (Péwé et al., 1977). The peat horizon can occur continuously or only in scattered peat lenses as is the case in the Allaikha profile. At the Batagay profile, we noticed a rather thin (about 1 m thick) layer with pronounced lenses ≤ 5 m thick filling former ground depressions. Gubin (1999) and Zanina (2006) studied the palaeosols of the ancient *alas* complex at Duvanny Yar and suggested that two types of soil occurred there: peat bog soils and peaty floodplain soils, both indicating wet ground conditions. Preliminary palaeobotanical analyses of Unit III deposits at the Batagay profile revealed exclusively terrestrial plant remains, no aquatic or wetland plants. Our data accordingly suggest that northern taiga with dry open-ground vegetation existed at Batagay during the MIS 5e interglacial (Ashastina et al., 2015). The presence of larch, birch, and alder in the species composition suggest that climatic features, such as temperature, precipitation, and snow cover thickness, were suitable for forest establishment in the continental part of inland Siberia during the Eemian. The tree species in light taiga forests require a mean temperature of the warmest month of at least 12 °C (Andreev, 1980). Coarse woody fossils are absent at Bol'shoy Lyakhovsky Island (Wetterich et al., 2009) and are sparsely present in records from coastal permafrost exposures, e.g. Oyogos Yar, and Allaikha River exposures (Kaplina et al., 1980; Kienast et al., 2011). The pronounced continentality in Batagay provided suitable climatic conditions for a forest development more intense than in coastal settings during the Eemian. Dry ground conditions with limited peat accumulation during the formation of Unit III might also be due to the relatively low ice content of the underlying Unit IV, which, when the MIS 5e warming started, resulted in less available meltwater from thawing permafrost.

Pre-Eemian deposits (as described for part II of the general classification) were detected on Bol'shoy Lyakhovsky Island (Schirrmeister et al., 2011b) and Oyogos Yar (Kienast et al., 2011). The position of Unit IV in the Batagay outcrop stratigraphically matches the abovementioned pre-Eemian floodplain deposits in the general classification of coastal permafrost exposures from Schirrmeister et al. (2011a). Unfortunately, we could not sample and analyse enough material from Unit IV to reconstruct its genesis, but according to our field observations (appearance and structure of the unit), it is unlikely that the material is of subaquatic origin. The main reason for the absence of temporary and permanent water bodies at the site might be the relief gradient and associated rapid drainage of surplus waters after snowmelt and permafrost thawing. In this setting, intensified rates of frost weathering of the surrounding mountains' bedrocks and increased slope deposition of alluvial material are regarded as the main deposition sources. Ice wedges as prevailing in the underlying Unit V or ice wedge casts are absent in Unit IV. The abrupt transition between both strata suggests a cessation of ice complex formation owing to a sudden climate shift. We assume that ice wedge growth ceased because of boosted sedimentation disrupting frost cracks. Also, milder winter temperatures and/or higher snow accumulation preventing thermal contraction and frost cracking are conceivable.

Unit V of the Batagay outcrop is represented by the truncated heads of wide ice wedges indicating ice complex deposits older than the MIS 5e. Similar structures with a comparable stratigraphic position, corresponding to part I of the general structure of coastal permafrost exposures, were observed on Bol'shoy Lyakhovsky Island and dated back to 200 ka BP (Schirrmeister et al., 2002; Andreev et al., 2004; Tumskoy, 2012). Ice complex is syngenetically frozen sediment containing a grid-like system of large ice wedges resulting in a ground surface pattern of polygonal ridges encircling small depressions, which during ice complex genesis, act as sediment traps. Polygonal ice wedges form due to repeated thermal contraction of the frozen ground, resulting in netlike arranged cracks that are filled in the spring by snow meltwater, which immediately freezes and forms ice veins. A mean annual air temperature lower than −8 °C is regarded as the threshold for ice complex formation (Plug and Werner, 2008). Polygonal ice wedge systems are indicative for continental cold stage climate with very cold winter air temperatures and annual ground temperatures. Ice wedge growth is not only influenced by climate but also by local factors such as ice content, grain size distribution, vegetation, and snow depth. However, ice complex deposits clearly indicate climate conditions much colder than present.

The Batagay outcrop is one of the few permafrost profiles accessible in interior Yakutia. The present study offers rare insights into the evolution of northern environments under the conditions of the most severe climatic continentality in the Northern Hemisphere. We suppose that differences in continentality between inland and coastal sites were more crucial during warm intervals, when sea levels were high and coastlines shifted southward. This is supported by the presence of forest plant taxa in the inland exposure (Batagay) and their absence in coastal lowlands (e.g. New Siberian Islands) during the Eemian interglacial. The influence of continentality is greater than the effect of latitude as can be observed by the southward shift of the tree line in coastal areas of Chukotka and Alaska with a more oceanic climate. Summer temperature is more crucial for the vegetation than winter or mean annual temperature. More detailed climate reconstructions should be conducted for the Batagay site using palaeoecological methods in order to test this assumption in the future. Further studies should also be focused on cryolithological analyses of material from Units IV and V to fill the current gaps in knowledge about the formation of these units. Furthermore, studies on ice wedge stable isotope composition will provide valuable information on past winter climate (e.g. Meyer et al., 2002, 2015) necessary for the reconstruction of the palaeoclimatic seasonality at the highly continental site of Batagay. Sedimentological, cryolithological, and stable isotope analyses and the study of fossil bioindicators (plant macrofossils, pollen, insects, and mammal bones) will contribute to the reconstruction of Quaternary palaeoenvironments in western Beringia.

6 Conclusions

- The Batagay mega-thaw slump is one of the few active permafrost outcrops in interior Yakutia, which provides rare insights into sedimentation processes and climate and environmental evolution under the conditions of the most severe climatic continentality in the Northern Hemisphere.

- As indicated by OSL dates, the exposed sequence has been deposited over a large time span, at least since the Middle Pleistocene.

- Altogether, five distinct sedimentological units, representing different accumulation phases, were detected (top to bottom): a Holocene cover layer; the Late Pleistocene YIC; an organic horizon deposited during the last interglacial; a thick, banded, uniform unit without visible ice wedges; and another ice complex older than the last interglacial.

- The detected five cryolithological units reveal distinct phases in the climate history of interior Yakutia: the existence of a Middle Pleistocene ice complex indicates cold stage climate conditions at the time of deposition of Unit V resulting in a MAGT at least 8 °C lower than today.

- A climate shift during deposition of Unit IV caused cessation of ice wedge growth due to highly increased sedimentation rates and eventually a rise in temperature.

- Full interglacial climate conditions existed during accumulation of the organic-rich Unit III. In contrast to other MIS 5e deposits in Yakutia, e.g. in the coastal lowlands, no plant or mollusc remains indicating aquatic or palustrine environments could be detected. On the contrary, plant macrofossils reflected open forest vegetation existing under dry conditions during the last interglacial.

- The late Pleistocene YIC (MIS 4–MIS 2) occurring in Unit II proves the presence of severe cold-stage climate conditions with a MAGT 8 to 10 °C lower than today.

- Peatland deposits as indicators for thermokarst processes, as they are characteristic for early Holocene sites in the circum-Arctic, were not detected at the Batagay outcrop. This might be due to the absence of intense thermal degradation or due to the topographical setting preventing meltwater from accumulating.

- As is indicated by radiocarbon AMS dating, gaps in the sedimentological record likely exist as a result of erosional events or of spatially and temporarily differential small-scale deposition.

- Compared to other YIC sites in Yakutia, Unit II of the Batagay profile could be classified as a highland type of YIC, which is characterized by its geographical position distant from rivers and sea coasts and in proximity to hills and mountains more inland. Whereas fluvial and lacustrine influence is common for certain depositional periods in the majority of permafrost exposures on the Yakutian coastal lowlands, it has to be excluded for the Batagay sequence.

- We suggest that the prevailing sedimentation processes and the sources for the deposited material varied seasonally during the formation of the YIC in the Batagay profile.

Data availability. The sedimentological data sets and the age determination (OSL method) runs of the samples reported in this paper were uploaded to PANGEA (https://doi.pangaea.de/; Ashastina et al., 2017).

Author contributions. FK designed the study conception and arranged the expedition. FK and KA carried out field description and sampling. LS accomplished the sedimentological analysis and plotted the graphs. MF designed and performed the OSL dating procedure and interpretation. KA, LS, FK, and MF participated in drafting the article. KA and FK prepared the paper with contributions from all co-authors. FK, LS, and KA revised the draft.

Competing interests. The authors declare that they have no conflict of interest.

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Chapter 3:

Warm stage woodlands and cold stage steppes: Pleistocene palaeovegetation in North Yakutia's most continental part recorded in the Batagay permafrost sequence

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Abstract

Based on fossil organism remains including plant macrofossils, charcoal, pollen, and invertebrates preserved in syngenetic permafrost deposits of the Batagay sequence in the Siberian Yana Highlands, we reconstructed the environmental history during marine isotope stages (MIS) 6 to 2. Two fossil assemblages, exceptionally rich in plant remains, allowed for a detailed description of the palaeo-vegetation during the two climate extremes of the Late Pleistocene, the onset of the Last Glacial Maximum (LGM) and the Last Interglacial. In addition, altogether 41 assemblages were used to outline the vegetation history since the penultimate cold stage of MIS 6. Accordingly, meadow steppes resembling modern communities of the phytosociological order *Festucetalia lenensis*, occurring today in the Central Siberian steppe belt and in extrazonal relict steppe patches in Northeast Siberia, formed the primary vegetation during the Saalian and Weichselian cold stages. Cold-resistant tundra-steppe communities (*Carici rupestris-Kobresietea bellardii)* as they occur north of the treeline today were in contrast to more northern locations mostly lacking. The local presence of larch (*Larix gmelinii*), proven by macrofossils nearly over the whole studied period including the onset of the LGM, suggests that northern tree refugia existed at the study site possibly throughout several glacial cycles. During the Last Interglacial, open coniferous woodland similar to modern larch taiga was the primary vegetation at the site. Abundant charcoal indicates wildfire events during the Last Interglacial. Zoogenic disturbances of the local vegetation were indicated by the presence of ruderal plants, especially by abundant *Urtica dioica,* suggesting that the area was an interglacial refugium for large herbivores. Meadow steppes, which formed the primary vegetation during cold stages and provided potentially suitable pastures for herbivores, were a significant constituent of the plant cover in the Yana Highlands also under the full warm stage conditions of the Last Interglacial. Consequently, both, meadow steppes and larch stands occurred in the Yana Highlands during the entire investigated timespan from MIS 6 to MIS 2 documenting a remarkable environmental stability. Thus, the proportion of these two major plant communities merely shifted in response to the respectively prevailing climatic conditions. Their persistence indicates both low precipitation and a relatively warm growing season throughout and beyond the late Pleistocene. The studied fossil record also proves that modern steppe occurrences in the Yana Highlands did not establish as late as in the Holocene but instead are relicts of a formerly continuous steppe belt extending from Central Siberia to Northeast Yakutia during the Pleistocene. The persistence of plants and invertebrates characteristic of meadow steppe vegetation in interior Yakutia throughout all climatic fluctuations of the late Quaternary documents the former suitability of this region as a refugium also for other organisms of the Pleistocene mammoth steppe including the iconic large herbivores.

Key words: palaeo-vegetation, plant macrofossils, invertebrates, charcoal, pollen, ground squirrel nest, LGM, Eemian

1. Introduction

Climatic and associated vegetation changes are considered possible drivers for the extinction of Pleistocene mammoth fauna (Campos *et al.*, 2010; MacDonald *et al.*, 2012; Prescott *et al.*, 2012). In high latitudes, rising temperature and increased humidity triggered, according to this interpretation, the transformation of the Pleistocene nutritious grassland vegetation into birch shrubland, coniferous forest tundra and finally into low-diverse taiga and tundra wetlands (Binney *et al.*, 2009;

Edwards *et al*., 2005; Kienast, 2013). Correspondingly, the demise of mainland mammoth populations coincided with the expansion of coniferous forests and the formation of extensive northern peatlands (MacDonald *et al*., 2012). The question remains, however, as to why the Pleistocene mammoth fauna survived several warm pulses during the Pleistocene, including full interglacials such as MIS 5e, but became extinct in particular in the course of the Holocene. Also, it is not fully clear whether the restructuring of late Quaternary vegetation was the cause or, due to herbivore - vegetation interactions, the consequence of the demise of megafauna.

A key region for understanding the mechanisms underlying the late Quaternary biotic impoverishment in northern latitudes is Beringia (Hulten, 1937; Tugarinov, 1929). The sector between the mouths of the Siberian Khatanga River and the Canadian Mackenzie River including entire Yakutia remained free of continental ice sheets during the late Quaternary (Barr and Clark, 2012; Svendsen *et al*., 2004). Due to its relative environmental stability, Beringia, and NE-Siberia in particular, is regarded the last refuge of mammoth fauna (Yurtsev, 1982; Boeskorov, 2006). The dominance of grazers among Beringian megaherbivores has been taken as evidence for productive, cold-adapted grassland, the tundra-steppe or mammoth steppe being the key vegetation type in the Pleistocene Arctic (Guthrie, 1990). Based on vegetation studies at currently isolated relict steppe stands in Northeast Siberia and Chukotka, Yurtsev (2001) suggested that the Pleistocene palaeo-landscape were analogously characterized by a codominance of steppe and arcto-alpine plant species. He also showed that modern relict steppe vegetation forms patchy mosaics in response to local environmental conditions such as topography, exposition, disturbances and soil. In recent years, palaeobotanical studies confirmed Yurtsev's assumption (Kienast *et al*., 2005; Kienast, 2013). Palaeontological records from permafrost sections in Northeast Siberia revealed the mosaic-like character of Pleistocene vegetation with a coexistence of steppe, meadow and arcto-alpine plant communities (Kienast *et al*., 2005, 2008), which is in line with the descriptions of modern tundra-steppe relict vegetation in Yakutia (Reinecke *et al*., 2017; Yurtsev, 1982, 2001).

In the present paper, the term mammoth steppe is accepted as an ecosystem (or palaeo-biome) supposedly dominating during Pleistocene cold stages as suggested by Guthrie (1990). Tundra steppe, in contrast, is henceforth regarded here as a certain plant community occurring at dry exposed places in the alpine belt of mountains and subsumed in the plant-sociological class *Carici rupestris-Kobresietea bellardii* (Kucherov and Daniels, 2005). Tundra steppe vegetation is thus regarded part of the Pleistocene mammoth steppe and no longer as a synonym. It corresponds to plant communities formerly designated *Kobresia*-meadows (Kienast *et al*., 2005; Wetterich *et al*., 2008) or dry arctic upland vegetation (Kienast *et al*., 2008). We implement this sharp distinction to make palaeo-vegetation reconstructed on the base of diagnostic species comparable with modern vegetation that is analogously classified using diagnostic species.

Several palaeontological methods can be used for the reconstruction of the Quaternary palaeo-vegetation. Palynological analyses are a widespread tool, but the relevance of pollen analyses alone for the reconstruction of local vegetation in northern latitudes is limited (e.g. Birks and Birks, 1980). Macro-remains, conversely, are a superior tool for the reconstruction of local palaeo-vegetation but are less valuable for the regional picture. A relatively novel approach is the identification of taxa using ancient DNA preserved in permafrost deposits (e.g. Zimmermann *et al*., 2017). Comparative studies have shown that the identification of plant macro fossils is comparable to the usage of ancient DNA (Jørgensen *et al*., 2012; Willerslev *et al*., 2014). It is recognised that entomological approaches are also suitable tools for the reconstruction of palaeo-vegetation (e.g. Elias, 1994, 2001, 2006; Kiselev, 1982; Kiselev, Nazarov, 2009; Sher *et al*., 2005). Frozen remains of mammals, insects, mollusks, as well as plant macrofossils give unique insights into arctic terrestrial ecosystems of the

Pleistocene (Berman *et al*., 2011; Fisher *et al*., 2012; Guthrie, 1990; Harington, 2007; Kienast *et al*., 2011; Zanina *et al*., 2011). Using a multi-proxy approach could help to overcome the constraints of individual approach (Kienast *et al*., 2011).

Most of the known fossil vegetation records are situated in the coastal lowlands of Yakutia. Due to Quaternary sea level fluctuations, Yakutia's coastal lowlands and the adjacent shelves were intermittently hit by tremendous coast line shifts (Bauch *et al*., 2001; Romanovskii *et al*., 2004) and correspondingly fluctuating maritime influence on climate. However, inland sections unaffected by maritime climate but with constantly continental climate throughout the Quaternary, were scarcely available so far. A newly formed permafrost exposure near Batagay, Verkhoyansk district, Yakutia, is one of the few active inland permafrost outcrops in Siberia (Fig. 1; Ashastina *et al*., 2017; Murton *et al*., 2017). As a result of intense thermo-denudation, the megaslump formed in the Yana Highlands within 40 years only (Günther *et al*., 2015; Kunitsky *et al*., 2013). The region can be considered as a benchmark for northern inland climate as Verkhoyansk is a town situated in the Yana Highlands with the lowest measured winter air temperature and the greatest seasonal temperature gradient, e.g. the most severe climatic continentality in the Northern Hemisphere (USSR Climate Digest, 1989). Previous studies on the Batagay permafrost exposure dealt with structure, composition, chronology, cryostratigraphical and sedimentological characteristics of the permafrost sequence (Kunitsky *et al*., 2013; Ashastina *et al*., 2017; Murton *et al*., 2017) and expansion rates of the outcrop (Günther *et al*., 2015) or described megafauna findings, including frozen carcasses of horses (*Equus* sp.) and bison (*Bison priscus*), as well as bone remains of cave lions (*Panthera leo spelaea*), woolly rhinoceroses (*Coelodonta antiquitatis*), mammoths (*Mammuthus primigenius*), and other extinct Pleistocene animals (Novgorodov *et al*., 2013). These findings indicate that the Yana Highlands, due to their climatic stability, were among the last refuges for now extinct mammoth fauna. Data on fossil plant and insect remains and on ancient vegetation were lacking so far from the Batagay exposure.

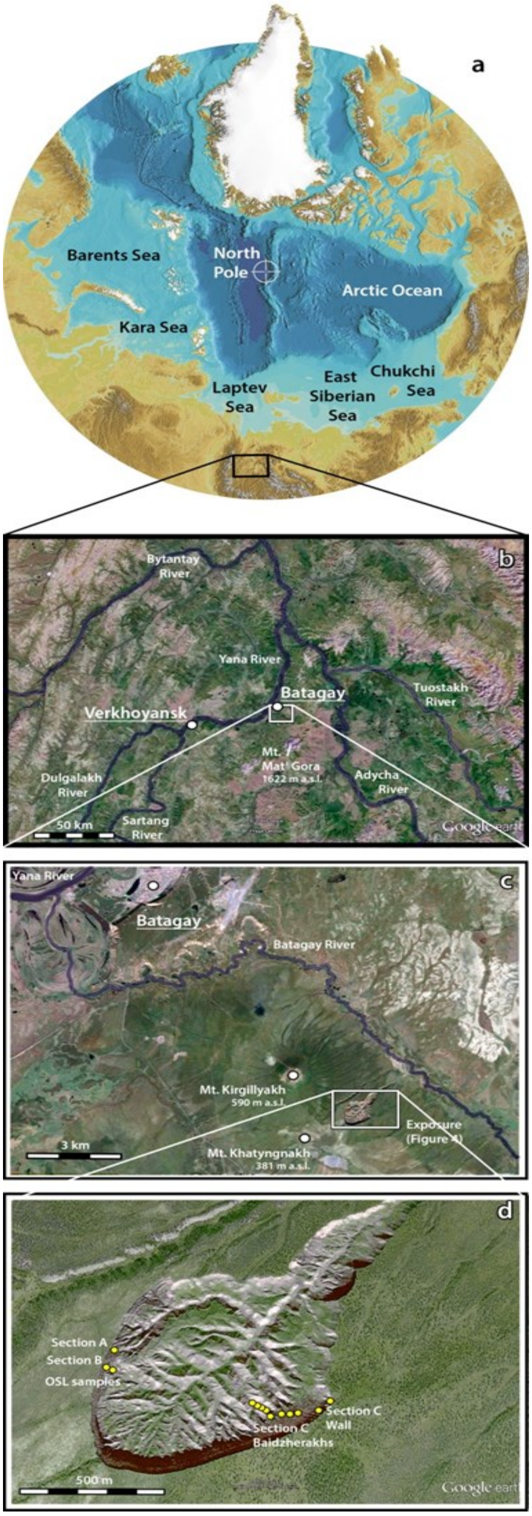

Figure 1: (a) Location of the Yana Highlands in northeastern Siberia. Map modified from Jakobsson *et al*., 2012. (b) Situation of the study area on the right southeastern bank of the Yana River valley. (c) Location of the Batagay mega slump (framed) at the northeastern slope of Mt. Khatyngnakh, left bank of the Batagay River. (d), Location of the studied sections in the Batagay mega slump. (b), (c), and (d) modified from satellite pictures, Google Earth V. 7.1.2.2041. (July 4th, 2013), Batagay Region, Russia 67°34'41.83"N, 134°45'46.91"E, Digital Globe 2016, CNES Astrium 2016, http://www.earth.google.com (accessed April 25th 2016).

In this paper, we present first results of the analyses of plant macro-fossils, charcoal, pollen and invertebrates obtained from permafrost deposits accessible at the Batagay mega-thaw slump. We provide a reconstruction of palaeo-vegetation from MIS 6 to 2 with a focus on the Last Interglacial (LIG) and the onset of the Last Glacial Maximum (LGM), and compare the results with modern vegetation in the area as well as with palaeo-records available from coastal sites. Environmental conditions associated with the reconstructed palaeo-vegetation are inferred from the respective macro -and microclimatic conditions of comparable modern vegetation types in Yakutia. We aim at ascertaining the macro-climatic impacts on ecosystems in Beringia's most continental region and in one of the last refugia of the Pleistocene megafauna during warm and cold extremes of the Pleistocene. Furthermore, we reveal non-climatic impacts on palaeo-vegetation such as disturbances and eutrophication potentially related to the presence of megaherbivores.

2. Regional setting

The Batagay outcrop (67° 34'41.83" N, 134° 45'46.91" E) is located 10 km southeast of Batagay, the municipal centre of the Verkhoyansk district, Sakha Republic (Yakutia, Russian Federation). The study site is 2.300 m northeast from the left bank of the Batagay River, a tributary to the Yana River. The outcrop slopes down between 300 and 240 m a.s.l. into the foothills of Mt. Khatyngnakh (Fig. 1c).

The Yana Highlands are bordered by the Verkhoyansky and Chersky Mountains, which are primarily composed of volcanic intrusive rocks, siltstone and argillite of the Permian, Jurassic, Cretaceous and Palaeogene Periods. The Neogene period is represented by clay deposits interspersed with pebbles and gravel, loam, sandy loam, and sands (Vdovina, 2002). The Highlands with the Yana River valley are covered with thick Quaternary deposits (Katasonov, 1954). According to Popp *et al*. (2007) and Siegert *et al*. (2009), the Highland territory was not glaciated at least during the last 60 ka, whereas both the Verkhoyansk Mountains and Chersky Ridge were influenced by alpine glaciers during Pleistocene cold stages (Glushkova, 2011; Stauch and Lehmkuhl, 2010).

The climate of the Yana Highlands is continental subarctic (Dfd; Köppen, 1884), it is characterized by low precipitation rates and by the globally largest seasonal temperature gradient exceeding 100 K. Climate data are available from Verkhoyansk (USSR Climate Digest, 1989), 50 km north-east from the study site (Fig. 1b). The mean annual precipitation amounts to only 181 mm with a maximum falling in summer. Within generally dry Yakutia, the upper reaches of the Yana drainage system exhibit the lowest precipitation resulting in a relatively high percentage of modern steppe vegetation in the study area (Yurtsev, 1982).

The degree of climatic continentality oscillated in the course of the Quaternary. But the Batagay outcrop has been always exposed to the continental climate: it is located 410 km from the coast to the Laptev Sea today, 535 km at 10 ka BP, 1040 km at 18 ka BP, and 450 km during the Eemian (Robertson Group and Geological Institute, 1991). Continental climate with warm summers and dry conditions fostered grassland vegetation and large grazing mammals.

Due to low ground temperatures associated with extremely continental climate and lacking inland ice cover, thick permafrost deposits formed in the Yana Highlands comparable to those in the coastal lowlands of Yakutia and on the shelves (Romanovskii *et al*., 2004). The ice-bonded permafrost (Ice Complex) deposits are penetrated by thick ice wedges and consist of up to 90 vol % of ice (Romanovskii *et al*., 2004). Ice Complex deposits formed syngenetically, i.e. sediments passed immediately into permafrost synchronous with their deposition (Schirrmeister *et al*., 2013). Since they preserve fossils in excellent condition, these deposits are an exceptional palaeoenvironmental archive.

The modern vegetation in the study region is built up of light coniferous forest dominated by *Larix gmelinii* (Isaev and Timofeyev, 2010). The study site is situated within the subzone of northern taiga in the Verkhoyansk district, i.e. upper Yana floral district (Isaev *et al*., 2010). In contrast to the neighbouring western districts, *Pinus sylvestris* is absent here, as the Verkhoyansk mountain range seems to be an effective migration barrier for that species. Instead, *Pinus pumila* is a common constituent of mountainous taiga in the Yana Highlands.

In addition to *L. gmelinii* and Siberian dwarf pine (*Pinus pumila*), the modern vegetation is composed of *Alnus alnobetula* subsp*. fruticosa, Betula divaricata, B. nana* subsp*. exilis* and *Salix* spp. in the shrub layer, and the dwarf shrubs *Ledum palustre, Vaccinium vitis-idaea, Arctous alpina* and *Empetrum nigrum*. The ground is mostly wet and densely covered with a thick layer of lichens (*Cladonia stellaris, C. rangiferina, C. arbuscula, Cetraria isl*and*ica, Stereocaulon paschale*) and mosses (*Polytrichum piliferum, Dicranum congestum*); only few grasses and herbs occur (e.g. *Polygonum tripterocarpum*, *Corydalis sibirica, Pedicularis lapponica*).

The Verkhoyansk district is characterized in places by mountain tundra and cryophilic steppes as the climate there is the most continental within Yakutia and represents the closest existing analogue of the Beringian cold stage climate. Modern relict steppe occurrences in Verkhoyansk and Ust-Nera are described by Yurtsev (1981, 1982, 2001). Also modern Coleopteran assemblages, resembling Pleistocene tundra-steppe environments, have been collected in the Yana Highlands (Berman *et al*., 2001).

3. Material and methods

3.1. Material

The Batagay outcrop represents the worldwide biggest thaw slump reaching dimensions of 800m in diameter and forming a steep headwall of up to 80m (Günther *et al*., 2015). The total height of the erosional cirque is estimated to be 110m from the topmost edge to the bottommost point, where the bedrock is exposed (L. Vdovina, Yana Geological Service, 2014, personal communication). Sediment loaded meltwater constantly flows off the headwall and the steep slopes forming drainage channels. These channels dissect a number of up to 30m high ridges (Fig. 2c) of frozen sediments on the bottom of the slump, forming a fan that is visible in satellite photos. Due to a slight northeastern inclination, the sediment-loaded meltwaters stream down to the Batagaika River.

In summer 2014, we sampled the exposure for palaeo-ecological studies. We distinguished five units in the sequence from top to bottom (Fig. 2b). The samples were taken from three different sections (A, B, C) according to accessibility of the deposits (Fig. 1d). At section A, in the western part of the cirque, the upper part of the sequence was accessible. In the central part of the cirque, in section B, organic-rich deposits assumedly from the Last Interglacial were outcropping. At section C in the southeastern part of the outcrop, the upper, central and lower parts of the sequence were sampled. A detailed description of the studied sediment succession is given in Ashastina (2017). The described stratigraphy corresponds with that of Murton *et al*. (2017) although different terminology is used. A brief outline of the sequence and provide dating results is In Appendix A.1.

According to stratigraphy and absolute dating, based on nine Accelerator Mass Spectrometry (AMS) ^{14}C and two Optical stimulated Luminescence (OSL) samples, the Batagay permafrost (sediments have been deposited since the late Middle Pleistocene and experienced erosional events during the Late Pleistocene and the Holocene (Appendix A.1, tables; Ashastina *et al*., 2017).

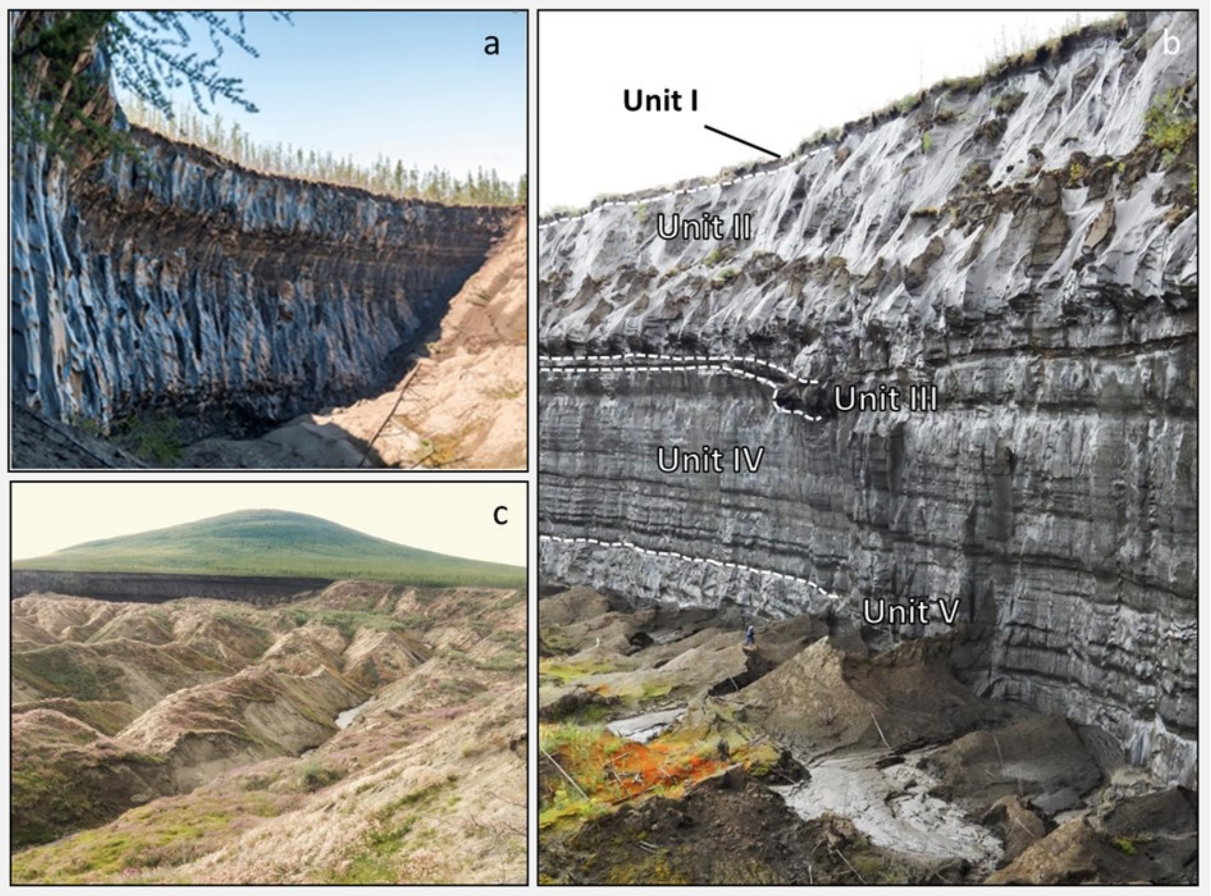

Figure 2. The Batagay thaw slump: a – view on the Ice Complex of north-western part of the slump; b – 5 units of the headwall according to Ashastina *et al*., 2017; c - view from the northern rim of the Batagay thaw slump over ca. 30 m high ridges of frozen sediments intersected with outflows.

3.2. Sampling and preparation

According to accessibility of the permafrost exposure, we took bulk samples of frozen material with a volume of two to ten litres about every 1 meter in vertical direction for multi-disciplinary analyses using a hammer and a chisel. In case an organic rich horizon was detected, it was sampled additionally. We obtained 45 samples in total. In the field, the samples have been split for sedimentological and palaeo-ecological analyses. Samples for sedimentological and palynological analyses were air-dried and remained otherwise unprocessed. Samples for plant macrofossil, charcoal, and insect analyses were wet-sieved with standard test sieves from Rentsch GmbH with mesh sizes of 2 and, to ensure that also small seeds and other remains are caught, 0.25mm then and air-dried.

3.2.1. Macrofossil preparation and identification

At the laboratory of Senckenberg Research Station of Quaternary Palaeontology, Weimar, we screened the samples using an Olympus SZX 16 stereomicroscope and hand-picked material suitable for macrofossil and insect identification. Plant remains, mainly seeds, fruits, inflorescences, scales, and leaf fragments, were identified to the lowest taxonomic level using a reference collection at the Senckenberg Research Station of Quaternary Palaeontology, Weimar, Germany (IQW, 2017), seed atlases, and identification keys (Anderberg, 1994; Berggren, 1969, 1981; Kats *et al*., 1965). The taxa nomenclature follows The Plant List (2017). The identification of the cryptogamic plants was conducted in the Senckenberg Museum of Natural History, Görlitz.

3.2.2. Charcoal

Charcoal identification was performed for two samples from Unit III rich in charcoal. Microscopic wood anatomy is used to identify the wood species (Huber, 1951; Schweingruber, 1978, 1990; Schoch *et al*., 2004). The size of analyzed material ranged from 1 to 12 mm. Each specimen was picked under the stereomicroscope and split with a razor along tangential and radial planes. A reflected-light microscope was used to examine the cellular details of fragments in order to identify taxa. The charcoal was compared to the reference collection available at the Laboratory for Ancient wood, Langnau, Switzerland.

3.2.3. Palynology preparation

A total amount of 40 samples, each consists ca. 10 g of dry material, were used for the palynological analyses. The samples were chemically treated according to the methodology suggested by Faegri and Iversen (1989), including treatment with a 10% solution of hydrochloric acid for dissolving carbonates, 10% solution of potassium hydroxide for removing humic acids, and high-concentration hydrofluoric acid for removing silicates. Acetolysis was not performed. A Lycopodium spore tablet (batch 483216) was added to each sample for calculating the total pollen and spore concentration. Pollen grains mounted in glycerine were analysed under a transmitted light microscope AxioImagerD2 with 400× magnification. In addition to pollen and spores, coniferous stomata and other non-pollen palynomorphs (NPPs) were counted. Only 19 samples contain palynomorphs, other are palynologically ‘sterile’ (Table with counts in Appendix A.2). Pollen percentages and pollen concentrations were calculated only for samples with >100 grains, based on a pollen sum of all detected taxa, taken as 100%. The results of pollen analysis are illustrated by the pollen diagram (Appendix A.3) made in Tilia software for four richest pollen samples (pollen sum >100); pie chart is constructed for the sample from the ground squirrel nest (Appendix A.3).

3.2.4. Invertebrate sampling

Numerous chitin fragments of different size found in the studied material, were picked using an Olympus SZX 16 reflected light microscope. In case the sediment stuck to the chitin and could not be removed with a wet brush, the specimen was suspended in water again and the minerals were then mechanically removed. The fragments were counted for each detected taxon and the minimal number of individuals (MNI) was calculated (Kuzmina, 2015; Sher and Kuzmina, 2007). Identified taxa were combined to 13 ecological groups following the methods of Sher *et al*. (2005), Kuzmina and Sher (2006), Sher and Kuzmina, (2007), and Kuzmina (2015). Identification has been conducted by comparison of the chitin fragments with a database of modern and fossil insect images (Kuzmina, 2014).

3.2.5. Reconstruction of palaeo-vegetation

The ancient vegetation was reconstructed in a number of ways depending on the used proxies, pollen and palynomorphs, invertebrates or plant macrofossils. Pollen and palynomorphs have a low taxonomic resolution and are transported over greater distances and therefore rather provide information on the general character of vegetation on a larger regional scale, e.g. indicating the dominance of forest or rather open ground vegetation in the region. Macrofossils, in contrast, indicate the local conditions and allow for the precise identification of plant taxa mostly down to the species level. They are therefore comparable with the recording of modern vegetation even though the original species assemblage is fragmentary owing to incomplete preservation. Insects have often a very distinct ecological niche with a narrow tolerance range. The ecological preferences of identified insects give thus a valuable complementary indication and were taken into account for the reconstruction of ancient vegetation.

For vegetation reconstruction, we considered primarily the presence/absence of plant taxa as the quantity of identified remains does not necessarily reflect the actual abundance of the taxa in the palaeo-vegetation. The fossil number is also affected by taphonomy, preservation and reproductive strategy of the plant species. Despite such restrictions, past vegetation units can be effectively reconstructed on the basis of few identified species that are characteristic, or diagnostic, for certain plant communities. Following the methodology of Kienast *et al*. (2005, 2008, 2011) for the reconstruction of palaeo-vegetation, the identified vascular plant taxa were grouped into plant communities (syntaxa) in line with their ecological preferences and present-day occurrences (Dierßen, 1996; Hilbig, 1995; Reinecke *et al*., 2017). The phytosociological nomenclature of syntaxa follows the Braun-Blanquet classification (Weber *et al*., 2000).

We used data on actual vegetation composition from Reinecke *et al*. (2017) and Reinecke *et al*. (in preparation) to characterize recent vegetation types for comparison with palaeo-vegetation (in total 210 vegetation relevés, 10 x 10m, species abundances). Vegetation types were classified using TWINSPAN (Hill, 1979) as implemented in JUICE (Tichy, 2002) and similarity of plots based on species composition was visualized in an ordination (DCA) using CANOCO (ter Braak and Šmilaue, 2012). Only relevés of most relevant vegetation types for the palaeobotanic comparison were chosen for display in the ordination (thus excluding 19 wetland relevés). Current environmental conditions for each plot, including microclimatic as well as macroclimatic variables, were added to the ordination. Slope inclination, northerness, easterness, and heat load (derived from slope aspect; following McCune, 2007) were recorded in the field. Macroclimatic variables (mean annual temperature, annual precipitation, summer temperature, summer precipitation, winter precipitation, (temperature) continentality, precipitation seasonality) were downloaded from Worldclim (Hijmans *et al*., 2005). We then added only those species of the recent vegetation, which were also found in the palaeo-record (separately for warm and cold stage species) to display, how vegetation of the late Pleistocene relates to modern vegetation types.

4. Results and interpretation

The macrofossil analysis of several thousands of identifiable plant remains revealed 61 vascular plant taxa from 23 families (Appendix A.4). The analysis of charcoal remains yielded five species. Pollen analysis accounted for 20 taxa from 1892 identified pollen and spores. Among invertebrates, 102 taxa were identified (Appendix A.5).

Most of the identified macro- and microfossils were found in two organic-rich accumulations – the ground squirrel nest at a depth of 4.6 m bgs and the organic layer representing Unit III, sampled in a depth of 43-44 m bgs (Fig. 3). These two fossil assemblages give us a clear and comprehensive picture on composition and structure of the vegetation at the time of deposition and allow for major conclusions about habitats, climate and other environmental factors. The ground squirrel nest was built, according to the AMS radiocarbon dating, during the onset of LGM. Unit III was deposited during MIS 5. Thus, the assemblages represent two major climate stages and are therefore regarded as references for cold or warm stage conditions. All other samples were poor in fossils or, partly, lacking any identifiable remains. This applies to all proxies and is obviously the result of generally poor preservation of organic material in the studied sediments. The poor preservation or, respectively, the highly corroded state of the organic material in our samples is probably owed to mechanical forces, microbial decomposition and, primarily, oxidation associated with the sediment composition, which is dominated by sand. Sandy deposits are well aerated and are therefore a good environment for the rapid decay of organic matter.

Figure 3. Reference samples position in the outcrop and view through the microscope. a – sample of Eemian Interglacial age; b – sample of Last Glacial Maximum age enclosed in the ground squirrel nest, the nest is about 12 cm x 20 cm; c – macrofossil assemblage of Eemian age; d – macrofossil assemblage of pre-LGM age.

We exemplarily contrast local palaeo-vegetation and environmental setting for both climate extremes and compare them to modern plant communities and their respective environmental conditions. Based on the reconstruction of the palaeo-vegetation from these reference assemblages, we then extrapolate the results on the remaining, fossil poor samples to provide more generalized information on the history of vegetation throughout the sequence.

4.1. Vegetation of the last cold stage

4.1.1 Dating

The ancient nest preserved cold stage material in excellent condition. The accessible part of the den had a size of about 12 x 20 cm and represented winter storage for hibernation of the ground squirrel (Fig. 3b). Accordingly, it was stuffed with plant material, mainly with inflorescences, fruits and seeds actively gathered in the territory surrounding the den during the life time of the rodent. The AMS ^{14}C-dating of identified terrestrial herb remains (*Plantago* sp., *Artemisia* sp.) and ground squirrel droppings resulted in an age of 26,180±122 a BP (Poz-77152). The nest was accordingly built during the onset of the LGM (Clark *et al*., 2009; Lambeck *et al*., 2014; Hughes and Gibbard, 2015). It is therefore a unique archive of northern environments out of the range of glaciations at this time.

4.1.2 Pollen

Palynological analyses of material from the nest revealed, with 321 pollen grains, the highest recorded concentration of microfossils in the whole sequence. More than half of the counted pollen (51.4%) falls on Caryophyllaceae. Furthermore, we found a high proportion of *Artemisia* (28.7%), other Asteraceae (11.0%), and a lower amount of Cyperaceae, Poaceae (4.0%), Ranunculaceae, Brassicaceae and ferns (0.3%). The pollen spectrum indicates open vegetation, dominated by insect pollinated herbs. Since the pollen was obtained from the cache, it probably originated largely from the gathered inflorescences. Thus, it cannot be ruled out that the pollen spectrum is biased and does not reflect the actual regional vegetation at the lifetime of the ground squirrels. The high proportion of Caryophyllaceae is reflected by macrofossils, which consist to a large degree of Caryophyllaceae species like *Silene samojedorum, Stellaria* sp. and *Eremogone capillaris.*

4.1.3 Macrofossils

The identification of several thousand macrofossils in the ground squirrel nest resulted in altogether 20 vascular plant taxa (Fig. 4). This number is relatively low but it is in line with observations of modern arctic ground squirrels, which cache plant material selectively. Modern ground squirrels in the Yukon cache only 24 of more than 100 vascular plant species growing in the proximity of the nest (Gillis *et al*., 2005). On the other hand, plant species that are abundant in the nest do not necessarily reflect the dominance of those plants in the local vegetation (Zazula *et al*., 2007). The high proportion of nutritious inflorescences and fruits in the Batagay sample (*Plantago canescens*, *Artemisia* and *Silene samojedorum* (syn. *Lychnis sibirica*)) confirms the assumption of selective harvesting by the ancient ground squirrels. Since only the presence of diagnostic species and not abundances and completeness of the species spectra was considered, the potentially biased gathering of rodents does not foil the reconstruction of local vegetation.

In Table 1, the identified plant taxa are listed according to their synecological preferences, i.e. arranged in plant communities (syntaxa) consistent with their present-day occurrences. Following these results, the local plant cover during the last cold stage was composed almost exclusively of grassland vegetation. The most abundant remains originated from dicotyledonous steppe plants such as *Silene samojedorum* (syn. *Lychnis sibirica*), *Plantago canescens*, *Artemisia* sp., *Alyssum obovatum*, *Tephroseris integrifolia*, *Eritrichium villosum* and *Eremogone capillaris. Phlox sibirica* and *Potentilla arenosa* were present in low abundance. Grasses were also present, however in lower quantity than dicots. We found *Agropyron cristatum*, *Festuca* cf. *lenensis*., *Koeleria* cf. *pyramidata*, and *Poa* sp. All of the listed plant taxa are characteristic of steppes. The arctic ground squirrel (*Urocitellus parryii*) in itself is an indicator of Pleistocene steppe like vegetation (Zazula *et al*., 2006).

Figure 4. Macrofossils of vascular plants characteristic for cold stage vegetation at Batagay, the Yana Highlands. (1) *Selaginella sibirica* megaspore; (2) *Agropyron cristatum* floret; (3) *Koeleria* sp. floret; (4) *Festuca* sp. floret; (5) and (6) *Festuca* sp. spikelet fragments; (7) *Carex duriuscula* nutlet; (8) *Stellaria* sp. seed; (9) *Stellaria* sp. calyx with opened capsule; (10) *Eremogone capillaris* open capsule; (11) *Eremogone capillaris* capsule fragment with unripe seeds attached; (12) *Eremogone capillaris* seeds; (13) *Silene samojedorum* calyx with closed capsule; (14) *Silene samojedorum* seed; (15) *Ranunculus pedatifidus* ssp. *affinis* nutlet; (16) *Alyssum obovatum* leaf with characteristic stellate hair; (17) *Alyssum obovatum* seed; (18) *Smelovskia* sp. seed fragment; (19) *Empetrum nigrum* leaf; (20) *Phlox sibirica* capsule valve; (21) *Myosotis asiatica* flower; (22) *Myosotis asiatica* mericarp; (23) *Eritrichium villosum* mericarp; (24) *Plantago canescens* seed; (25) *Plantago canescens* capsule; (26) *Artemisia* sp. flower; (27) *Artemisia* sp. cypsela; (28) *Tephroseris integrifolia* cypsela.

Table 1. List of identified plant macrofossils and their grouping into plant communities (syntaxa) in line with their ecological preferences and present day occurrences.

		Depth, m bgs																																	
Plant communities	Plant taxa	1.1	2.0	3.0	3.5	4.6	5.5	6.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	16.5	17.5	18.5	19.5	25.5	32.5	33.5	34.5	35.5	36.5	36.7	37.5	38.5	40.5	41.5	42.5	43.0	43.5	44.0	50.0
forest and forest tundra (Vaccinio-Piceetea)	*Ledum palustre*												+																			+			+
	Equisetum scirpoides			+					+		+					+			+													+	+	+	
	Moehringia laterifolia																															+		+	
	Larix gmelinii	+		+		+	+	+			+	+		+							+	+	+						+	+		+	+	+	+
	Alnus sp.																															+		+	
	Alnus alnobetula subsp. *fruticosa*																										+					+	+	+	
	Betula Subgenus *Betula*								+															+								+	+	+	
	Betula nana s.l.					+																													
	Empetrum nigrum s.l.	+				+															+														
	Vaccinium vitis-idaea								+				+					+				+	+												
	Rosa acicularis																															+	+	+	
ruderal vegetation (Epilobietea angustifolii and Stellarietea mediae)	*Rubus idaeus*																															+	+	+	
	Urtica dioica																				+											+	+	+	
	Hordeum jubatum																															+			
	Descurainia sophioides					+																			+	+	+								+
	Corispermum crassifolium																																	+	
	Lepidium densiflorum																								+										
	Sonchus arvensis																															+		+	
saline meadows (Asteretea tripolii)	*Chenopodium sp.*			+	+	+																													
	Rumex maritimus						+																												
	Puccinellia sp.			+																														+	
	Puccinellia tenuiflora													+											+										
	Carex duriuscula					+	+											+	+									+			+	+			
steppes (Cleistogenetea squarrosae,	*Erigeron acris*																																	+	
	Agropyron cristatum					+																													
	Alyssum obovatum					+									+			+																	+

Table 1. (Continued) List of identified plant macrofossils and their grouping into plant communities (syntaxa).

Plant communities	Plant taxa	Depth, m bgs																																	
		1.1	2.0	3.0	3.5	4.6	5.5	6.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	16.5	17.5	18.5	19.5	25.5	32.5	33.5	34.5	35.5	36.5	36.7	37.5	38.5	40.5	41.5	42.5	43.0	43.5	44.0	50.0
steppes (Cleistogenetea squarrosae, Festucetalia lenensis)	*Artemisia sp.*		+			+			+						+											+								+	+
	Stellaria sp.					+	+						+		+																				
	Eremogone formosa/capillaris					+																													
	Festuca sp.					+									+																+			+	+
	Koeleria sp.					+																													+
	Silene samojedorum		+			+												+														+			
	Silene repens		+																					+	+							+			
	Thymus serpyllum																																	+	
	Tephroseris integrifolia					+																													
	Phlox sibirica					+																				+			+						
	Plantago canescens					+																													
	Poa sp.				+	+								+	+									+	+	+	+	+	+		+	+	+	+	+
	Potentilla arenosa					+												+										+	+			+			+
	Potentilla tollii													+										+		+		+		+	+	+	+	+	+
tundra steppes (Carici rupestris–Kobresietea)	*Eritrichium villosum*					+																													+
	Selaginella sp.	+	+								+			+		+											+								
	Draba sp.					+																			+	+								+	+
	Smelovskia sp.				+																				+										
	Myosotis asiatica					+																													
	Fabaceae tribe *Galegeae* (cf. *Oxytropis* sp.)									+										+										+					+
	Papaver Sect. Scapiflora				+	+	+				+	+	+	+			+	+	+						+					+		+		+	+
	Stellaria jacutica																															+			
	Minuartia rubella																				+														
	Minuartia verna																																	+	
	Minuartia arctica			+																															
	Ranunculus pedatifidus subsp. *affinis*					+																													
	Saxifraga oppositifolia		+																																
	Saxifraga sp.																				+														
	Juncus sp.																				+	+												+	
	Juncus arcticus													+								+													

4.1.4 Palaeo-vegetation reconstruction

Following Reinecke *et al*. (2017), we integrate our reconstructed palaeo-steppes in the class *Cleistogenetea squarrosae* MIRKIN et. al.,1992. Recently typical steppes of West Eurasia are subsumed under *Festuco-Brometea,* whereas the Eastern steppes belong to *Cleistogenetea squarrosae* (Ermakov *et al*., 2006). Earlier publications (e.g. Kienast *et al*., 2005) assigned reconstructed Yakutian palaeo-steppe communities to the classes *Festuco-Brometea* and *Koelerio-Corynephoretea* following the European phytosociological nomenclature. This is erroneous given that Eastern steppes of Mongolia and Transbaikalia, and their Yakutian outposts, differ in floristic composition from European and West Siberian steppes and therefore belong to another floristic region - the Central Siberian or Mongolian-Daurian floristic region and its vegetation (Hilbig, 1995; Meusel *et al*., 1965).

The results of the ordination analysis provide an overview of the patterns in modern vegetation samples. The two main axes of the DCA (Fig. 5a) separate steppes in the lower right corner from meadows in the top left, and from taiga as well as tundra steppe in the lower left corner. These differentiations can be attributed to differences in continentality, slope inclination and SW-exposition, which were higher in steppes, and to differences in annual and summer precipitation, summer temperature and heat load, which increase towards meadows and steppes. Figure 5b gives the same ordination, but additionally shows axis 3 that separates taiga from tundra steppe plots. The ordination thus displays two divergent gradients from steppes (yellow) to light taiga (dark green) and from steppes over meadows (light green) to tundra steppe (blue). This roughly reflects a gradient of increasing moisture availability from the right to the left and increasing temperature from the top to the bottom. We also overlaid the corresponding species data. Species names corresponding to the LGM sample of the palaeo-record are coloured in blue. In today's vegetation these species clustered mostly in the area of actual steppes (*Koeleria pyramidata* [KoelPyr], *Agropyron cristatum* [AgroCri], *Alyssym obovatum* [AlysObo], *Eritrichium villosum* [EritVil], *Plantago canescens* [PlantCan], *Eremogone capillaris* [EremCap], *Myosotis* sp. [MyosSpe], *Phlox sibirica* [PhloSib]) as well as in the actual tundra steppe (*Tephroseris integrifolia* [TephInt], *Myosotis asiatica* [MyosAsi]). However, single species of modern light taiga occurred in the palaeorecord of the cold stage as well (*Empetrum nigrum* [EmpNig], *Ranunculus pedatifidus* subsp. *affinis* [RanuPet]). Names of the species of the warm stage of the palaeo-record species are coloured in red. Today these species are associated with samples of modern light taiga (*Moehringia laterifolia* [MoehLat], *Equisetum scirpoides* [EqiSci], *Rosa acicularis* [RosaAci], *Rubus idaea* [RubuIda], *Betula* sp. [Betula sp], *Urtica dioica* [UrtiDio], *Chenopodium album* [ChenAlb]) and meadow vegetation (*Silene repens* [SileRep], *Puccinellia hauptiana* [PuccHaup], *Minuartia verna* [MinuVer], *Chenopodium* sp. [ChenSpe]), although some species of modern steppe (*Carex duriuscula* [CareDur], *Potentilla tollii* [PoteTol], *Stellaria jacutica* [StelJac]) and tundra steppe (*Minuartia rubella* [MinuRub], *Ledum palustre* [LeduPal]) occur in the palaeorecord of the warm stage as well.

Besides the listed steppe plants, we identified few other grassland species that are characteristic of dry arctic or, correspondingly, alpine meadows of the class *Carici rupestris-Kobresietea bellardii* OHBA 1974. Only *Ranunculus pedatifidus* subsp. *affinis* and *Myosotis asiatica* could be detected. Eventually, the dwarf shrub *Empetrum nigrum* might also have occurred in *Kobresietea* vegetation or, alternatively, in the understorey of open light taiga stands. *Kobresietea* communities form the dominant vegetation in the alpine belt of mountains, i.e. the zone above the tree line. In the Arctic, they are today restricted to dry, exposed, well-drained sites and they are absent in zonal lowland habitats, which are characterized by waterlogged ground due to the damming effect of the

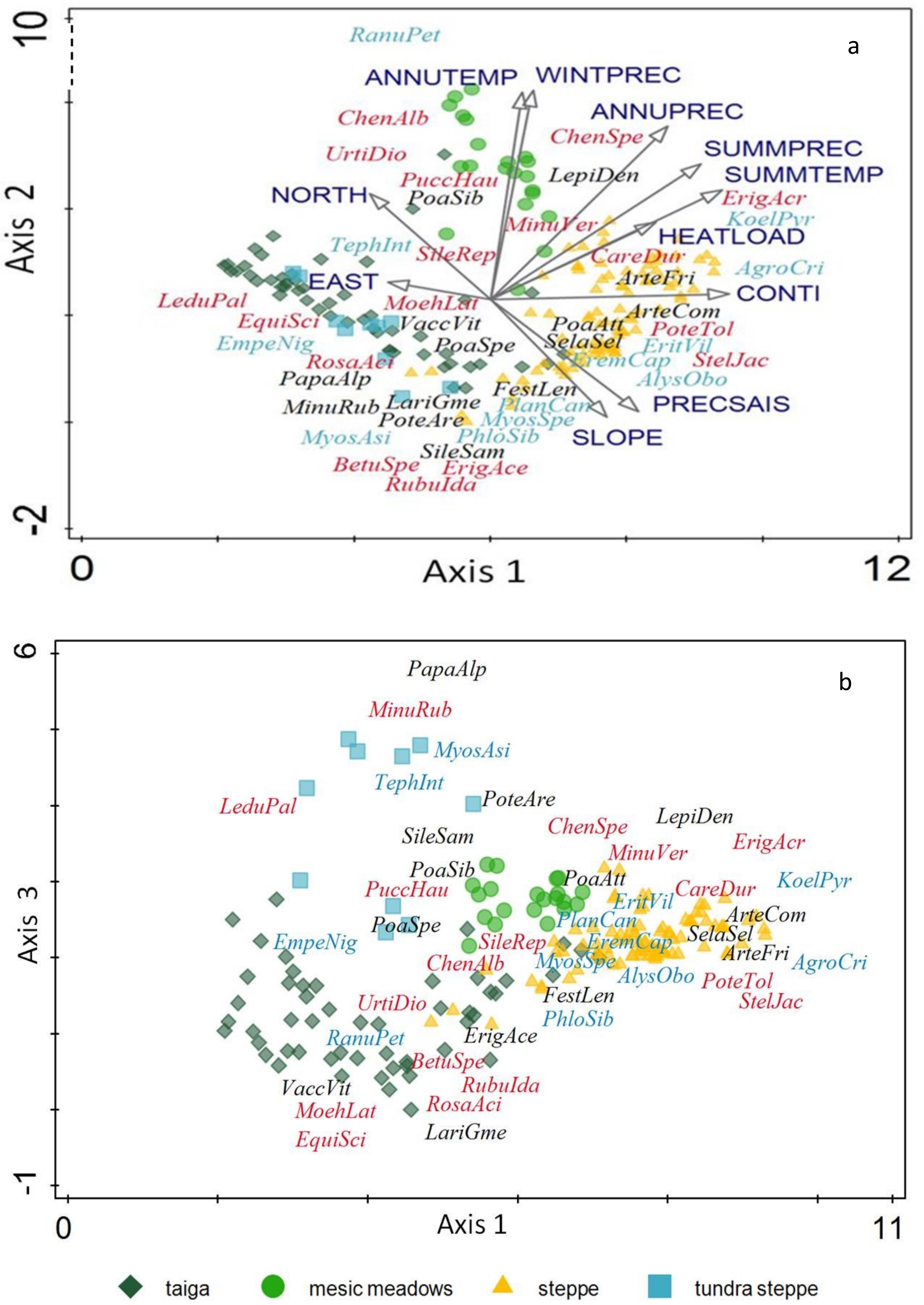

Figure 5. Bi-plot of the DCA ordination (a shows axis 1 and 2; b shows axis 1 and 3) of 210 vegetation plots using recent plant species composition with post hoc-fitting of environmental variables (ANNUTEMP = mean annual temperature; ANNUPREC = annual precipitation; SUMMTEMP = summer temperature; SUMMPREC = summer precipitation; WINTPREC = winter precipitation; CONTI = continentality (annual temperature range); PRECSAIS = precipitation seasonality; all macroclimatic variables from WORLDCLIM. NORTH = northern ess (aspect); EAST= easterness (aspect); SLOPE= slope inclination; HEATLOAD = Heat load). Only plots of the most relevant vegetation types for the palaeobotanic comparison are shown (taiga, mesic meadows, steppe and tundra steppe. Species are coloured according to their respective occurrence in the palaeo-botanic record: last cold stage (blue), last warm stage (red) or both cold and warm stages (black).

permafrost table. *Kobresietea* vegetation is regarded as a modern analogue of Pleistocene palaeo-vegetation (Walker *et al*., 2001) and it is equated with tundra steppes (Yurtsev, 1982; Reinecke *et al*. 2017) – a designation that is accepted also in the present paper. In earlier descriptions of reconstructed palaeo-vegetation, tundra-steppe was described simply as *Kobresia*-meadows or *Kobresia*-mats (Kienast *et al*. 2005, 2011).

The finding of larch remains dated to the time of the LGM proves the local occurrence of trees in interior Yakutia north of the Arctic Circle throughout the last cold stage. As visible in the dominance of light demanding herbs in the fossil assemblage, trees did not play a significant role in the plant cover at this time. But the finds prove that the Yana Highlands were a full glacial refugium for trees. According to the macrofossil database on woody taxa in Northern Eurasia (Binney *et al.*, 2009), larch was so far not detected in that area before 13 ka BP. The existence of tree populations in northern refugia throughout the last glacial cycle might explain the rapid reoccupation of their former territory at the advent of the Holocene. The presence of *Larix gmelinii* during the rapid cooling phase is in accordance with its capacity to withstand extremely low winter temperatures in the continental climate.

4.1.5 Insects

The insect species composition in the nest suggests that the detected insects were not purposely gathered by the ground squirrels as their prey but came into the den actively by themselves or by chance (Fig. 6). Few more or less complete specimens of lace bug (Tingidae), the weevil *Phyllobius kolymensis*, and an ant-like beetle *Anthicus ater*, as well as fragments of flies and parasitic wasps were detected. We assume that they were occasional visitors, which might have used the den as a shelter. Some of them might also be randomly collected by the ground squirrels together with plant material. *Anthicus ater* occurs in meadows within the forest zone and *Phyllobius kolymensis* is an indicator of meadow-steppe vegetation (Sher and Kuzmina 2007). The detection of both species supports the palaeobotanical results.

In addition, there were numerous tiny larva heads probably from small round fungus beetles (Leiodidae), which can be considered as regular nest inhabitants. Many of the so-called nest-beetles in the subfamily Cholevinae within the Leiodidae are typical occupants of mammal nests. Larvae of rove beetles (Staphylinidae) and carrion beetles (Silphidae) were present as well and can also be regarded as nest occupants.

In summary, the palaeontological results suggest that steppe grassland dominated the vegetation indicating dry conditions during the cold stage. The scattered occurrence of larch was proven as well. The scarcity of woody plants might be not only the result of climate but it might also be caused by frequent disturbances of vegetation due to grazing and trampling by herbivores. Grazing supports grassland vegetation. *Plantago canescens* has a certain affinity to open, disturbed ground. Its abundance in the record might be a clue of frequent disturbances. *Papaver* sect. *Scapiflora* is another plant characteristic of barren or disturbed ground. Both taxa were recorded in the sample, *Plantago canescens* was even among the most abundant plant species in the record.

Figure 6. Insects from the Batagay site: 1-87 beetles: 1-3 - head, pronotum, elytron of *Cymindis arctica*; 4 – pronotum of *Poecilus nearcticus*; 5 - elytron of *Pterostichus montanus*; 6-10: head, pronotum, left and right elytra, male genitalia of *Harpalus amputatus obtusus*; 11 – elytra of *Pterostichus pinguedineus*; 12, 13 – pronotum, elytra of *P. brevicornis*; 14-16 – head, pronotum, elytra of *Dyschiriodes melancholicus*; 17 - elytron of *Bembidion umiatense*; 18 - elytron of *Dicheirotrichus mannerheimi*; 19, 20 - pronotum, elytra of *Cyrtoplastus irregularis*; 21 – pronotum of *Cholevinus sibiricus*; 22 – elytron of *Colon* sp.; 23 – head of Aleocharinae gen. indet.; 24 – elytra of *Phosphuga atrata*; 25-27 - head, pronotum, elytron of *Atheta* sp.; 28, 29 – pronotum, elytra of *Arpedium quadrum*; 30, 31 – pronotum, elytron of *Lathrobium* cf. *longulum*; 32, 33 - pronotum, elytron of *Tachyporus* sp.; 34-39 - meso and metasternum, elytron, head, pronotum, thorax and abdomen, elytron of two or three species of *Stenus* sp.; 40, 41 – pronotum, leg of *Aphodius* sp.; 42-51 – head, mandible, prosternum, meso and metasternum, pronotum, metacoxa, leg, abdominal sternites, elytron of *Morychus viridis*; 52 – elytron of *Simplocaria elongata*; 53 – head and pronotum of *Ptinus* sp.; 54 – elytron of *Stephanopachys substriatus*; 55 – pronotum of *Troglocollops arcticus*; 56 – pronotum of *Atomaria kamtschatica*; 57 – elytron of *Cryptophagus acutangulus*; 58 - elytron of *Caenoscelis ferruginea*; 59 – pronotum of *Scymnus* sp.; 60 – elytron of *Nephus bipunctatus*; 61 - elytron of *Heterocerus* sp.; 62 – elytron of *Anthicus ater*; 63 - elytron of *Meligethes* sp.; 64, 65 - pronotum, elytron of *Corticaria ferruginea*; 66, 67 – head and pronotum, elytron of C. rubripes; 68 - elytron of *Leptophloeus angustulus*; 69 - elytron of *Altica engstromi*; 70, 71 - head and pronotum, elytron of *Bromius obscurus*; 72 - elytron of *Chrysolina arctica*; 73 - elytron of *Liophloeus tessulatus*; 74-77 – head, pronotum, meso, metasternum and abominal sternites, leg of *Stephanocleonus eruditus*; 78 – head of *S. incertus*; 79, 80 – head, pronotum of *Phyllobius virideaeris*; 81 - head with deciduous mandible of *Phyllobius* (*Angarophyllobius*) sp.; 82, 83 – head, elytron of *P. kolymensis*; 84 - head of *Rhynchaenus* sp.; 85, 86 – head, pronotum of *Hypera diversipunctata*; 87 – elytron of *Dorytomus rufulus amplipennis*. 88-92: hemipterans: 88 – pronotum of *Eurygaster* sp.; 89 - scutellum of *Aelia* sp.; 90 – whole body of Tingidae gen. indet; 91 – elytron of Saldula sp.; 92 – head of Cicadellidae gen. indet. 93-102: ants: 93, 94 – head, thorax of *Leptothorax acervorum*; 95-102 – thorax, pronotum, femur, coxa, tergite, head of major worker, mandible of major worker, head of minor worker of *Camponotus herculeanus*. 104-106 dipterans: 104-106 – two pupae, leg, head of Diptera gen. indet.; head of Tipulidae gen. indet. (larvae). 108 - wing pad of Ephemeroptera gen. indet. 109-114: non-insect invertebrates: 109-111 – cephalothorax with leg, cephalothorax, leg of Araneae gen. indet.; 112 – whole body of *Daphnia* sp.; 113 – cocoon of earthworm Lumbricidae gen. indet.; 114 – egg of worm Nematode gen. indet.

4.2. Vegetation of the warm stage

Three samples attributed to MIS 5 are available from the Batagay outcrop at section B. These reference samples were taken from Unit III in the lower part of an organic accumulation representing the fill of a former depression, in a depth of 43-44 m bgs. Direct radiocarbon dating of the sampled material resulted in a non-finite age of > 44 ka BP. A finite OSL date of 142,800±25,300 a was obtained from sediments of Unit IV underlying the sampled deposits (Ashastina *et al*., 2017). Unit III is located directly below the Yedoma Ice Complex (YIC) - deposits of the last cold stage. Its position between the YIC (MIS 4-2) and deposits OSL-dated to about 143 ka BP (MIS 6), Unit III is likely to be of the Last Interglacial origin (MIS 5).

Since the three samples of organic debris appeared in a fine bedding alternating with silty fine sand beds, they might reflect a vegetational succession. The sampled material was very rich in macroscopic plant remains (Fig. 7). Remarkably, the samples were, however, nearly devoid of pollen. Just three andfive grains, respectively, were detected at depths of 43.5 and 44 m bgs.

4.2.1 Plant macrofossils

The identification of plant macrofossils resulted in 34 taxa. The most abundant remains originate from woody plants characteristic for northern taiga forests. Accordingly, the stand-forming trees were larch as well as tree birches. Beside several fruit scales unambiguously from *Betula pendula*, there were hundreds of *Betula* fruits with eroded wings, which could not be assigned with certainty to a definite species. A large part of them probably originated from shrub birches as they were detected in deposits of the Last Interglacial along the coast (Kienast *et al*., 2008, 2011). Shrub alder (*Alnus alnobetula* subsp*. fruticosa*) could be reliably identified in large quantity. The frequency of shrub alder in the vegetation of the Last Interglacial is corroborated by numerous nodules of the actinomycete bacterium *Frankia alni* that is a nitrogen-fixing symbiont of *Alnus*. *Rubus idaeus* was an abundant element of the shrub layer. Also the former presence of *Rosa acicularis* is verified by macrofossils. Additionally, few leaf fragments and buds from *Salix* sp. were identified. The dwarf shrub *Ledum palustre* and the herb *Moehringia laterifolia* as characteristic components of the understorey in taiga forests were likewise detected. *Pinus pumila* was not found in the rich and well preserved macrofossil assemblage indicating that this species was very likely absent. This is an important difference to the modern vegetation, where the Siberian dwarf pine is very common at the site.

The nitrophytic ruderal plant *Urtica dioica* was found in high abundance. The diversity of ruderal plants including *Hordeum jubatum, Corispermum crassifolium, Sonchus arvensis*, *Chenopodium* sp*., Corydalis sibirica* and *Papaver* sect. *Scapiflora* in the assemblage of MIS 5 is an indication of locally disturbed ground. It thus is in contrast to the recent ground cover at the site with a thick layer of lichens and mosses. Lichens and mosses are not able to withstand disturbances (Zimov *et al*., 1995).

Cryptogams effectively decrease evapotranspiration and thus potentially cause wet ground even under low precipitation. The detection of diverse xerophilous vascular plants such as *Silene repens, S. samojedorum*, *Potentilla arenosa*, *Comastoma tenellum, Erigeron acris*, *Thymus* sp*., Artemisia* sp., *Festuca* sp., *Poa* sp., and the endemic species *Potentilla tollii* indicate open and locally dry habitats existing in the area also during the warm stage. It seems that steppe vegetation continuously existed in the Yana Highlands already before the last cold stage and thus persisted throughout the late Pleistocene. Even potentially productive grasses such as *Festuca* sp., *Poa* sp. and *Puccinellia* sp. possibly serving as forage for large herbivores were present. *Puccinellia* sp. is typical of saline meadows in closed basins with fluctuating moisture, as they occur under arid conditions in continental regions. Beside *Puccinellia* ap., also *Chenopodium* sp., *Erigeron acris* and *Sonchus arvensis* are salt-tolerant.

Figure 7. Macrofossils of vascular plants characteristic for Last Interglacial vegetation at Batagay, the Yana Highlands. (1) *Larix gmelinii* fascicle (short shoot); (2) *Larix gmelinii* needle; (3) *Larix gmelinii* cone; (for 1-3, note the smaller scale bar); (4) *Larix gmelinii* seed; (5) *Puccinellia* sp. caryopsis; (6) *Alnus alnobetula* subsp. *fruticosa* catkin bract; (7) *Alnus alnobetula* subsp. *fruticosa* catkin rachis; (8) *Betula pendula* catkin bract; (9) *Betula* sp. nutlet; (10) *Urtica dioica* seed; (11) *Chenopodium* sp. seed; (12) *Corispermum crassifolium* seed; (13) *Stellaria jacutica* seed; (14) *Moehringia laterifolia* seed; (15) *Silene repens* seed; (16) *Rubus idaeus* inflorescence; (note the smaller scale); (17) *Rubus idaeus* aggregated drupelets forming part of etaerio; (18) *Rubus idaeus* pyrene; (19) *Potentilla tollii* nutlet; (20) *Rosa acicularis* nutlet; (21) *Ledum palustre* leaf; (22) *Vaccinium vitis-idaea* leaf; (23) *Erigeron acris* cypsela; (24) *Sonchus arvensis* cypsela.

As in the pre-LGM ground squirrel nest, we found in the deposits of Unit III numerous droppings of rodents, which were however considerably smaller than those of ground squirrels. We therefore assume that they originate from small rodents of the subfamily Arvicolinae that includes voles and lemmings, both characteristic for taiga habitats.

4.2.2 Charcoal

High amounts of charcoal in the sediment indicate the spread of wild fire events during the Last Interglacial. More than 500 charcoal pieces were found within the sample from 43 m bgs. Their size varied from 1mm to 2cm. The identification of charcoal resulted in typical forest taxa: *Betula* sp., *Larix* sp. (burned needles, cone fragments, fig. 8), *Salix* sp., *Equisetum* sp., Ericaceae cf. *Ledum* sp., as well as stems of herbs. Wildfires might be a reason for the difference in species composition to the modern day taiga at the site. *Betula pendula* does not occur today at the exposure but was common during the Last Interglacial. It is a characteristic pioneer wood whose dispersal is stimulated by wildfires. Also, *Rubus idaeus* does not occur today but was common in the fossil assemblage. It likewise frequently occurs in forest glades after wildfires. It seems that disturbances of the plant cover, e.g. by fire action, played a crucial role for composition, structure and dynamic of the ecosystem at this time. The presence of other disturbance indicators supports this assumption.

Figure 8. Examples of charcoal cellular structures typical for: a – *Larix* sp., b – *Betula* sp. Diameter of both twigs is 1 mm.

4.2.3 Insects

Whereas differences in the percentage of open or forest habitat species within the short sequence of plant assemblages within Unit III are hard to discern, the fossil invertebrate assemblages slightly varied within Unit III. The upper sample in a depth of 43 m bgs comprised 722 fragments of insects, spiders, oribatid mites, and worms (Appendix A.5). The calculated MNI is 198 belonging to 50 species in total. As many as of 32% of the assemblage consists of forest taxa. Mainly carpenter ants *Camponotus herculeanus* (Fig. 6.95-102), which nest inside rotten wood mostly in coniferous forest, were detected. Two other detected species are also directly connected to forest trees. The carrion beetle *Phosphuga atrata* lives under the bark of dead wood and the weevil *Magdalis carbonaria* is limited to coniferous trees. Numerous cocoons of earthworms indicate stable environmental conditions and soil forming processes during the Last Interglacial. Several tiny cocoons, probably originating from soil nematodes, as well as remains of oribatid mites and fly pupae indirectly indicate pedogenesis as well. Abundant remains of plant litter inhabitants including several species of the family Cryptophagidae such as *Atomaria kamtschatica, Cryptophagus acutangulus,* and *Caenoscelis ferruginea* could be identified. These beetles are common faunal elements in forests and were so far rarely detected in Pleistocene deposits. According to the rich and diverse association of forest and plant litter invertebrates, a well-developed forest existed at the time of the Last Interglacial.

Grassland species were by contrast rare in the upper sample of Unit III. We found only a few fragments of weevils of the Cleonini tribe (*Coniocleonus* or *Stephanocleonus*) and a shield bug (*Eurygaster* sp.). These insects are regarded belonging to a group of meadow-steppe species. The low taxonomical resolution of identification is, however, insufficient to give more precise implications. The usually most common steppe-tundra indicators of NE Siberia are absent here.

The fossil arthropod assemblage from the lower sample in Unit III in 43.5 m bgs yielded 324 fragments of insects, spiders and oribatid mites. The estimated MNI is 137 belonging to 37 species. Most of the identified species do not indicate any certain habitat but have broad ecological amplitude. The high percentage of this indifferent group merely indicates that invertebrates were present in relatively high diversity. The high number of oribatid mites and fly pupae indirectly indicate soil formation in this layer as well. Regular forest insects are not preserved in great diversity. The carpenter ant *Camponotus herculeanus*, was present in relatively high abundance. In addition, numerous fossil fragments of the rove beetle genus *Atheta* were detected. Many species of this genus live in mushrooms where they pray on fungus gnat larvae. The deduced presence of mushrooms with their complex of abundant eaters and predators is an indirect indication for a forest setting. As in the upper sample, the insect assemblage comprises various plant litter inhabitants such as several species of the families Leiodidae, Lathridiidae, and Staphylinidae. A well-developed plant litter cover is a characteristic feature of forest environments. Wildfires in taiga are indirectly indicated by the presence of the leaf beetle *Bromius obscurus* who feeds on fireweed (*Epilobium angustifolium*), which is a pioneer plant that regularly occupies wildfire areas.

The presence of open vegetation within the ancient forest is in the lower sample indicated by a number of regular meadow insects such as a fossil leaf-hopper and the weevil *Phyllobius virideaeris*. Some species found in the sample such as the pill beetle *Morychus viridis* (Fig. 6.42-51), the soft-winged flower beetle *Troglocollops arcticus*, the leaf beetle *Chrysolina arctica*, and the weevil *Otiorhynchus cribrosicollis* are characteristic for cold and dry (cryoxerophilous) grassland vegetation, potentially in line with *Kobresietea* communities.

Summarizing the results of plant and invertebrate analyses, we can draw the following conclusions. A dry herb-rich light coniferous taiga with a pronounced plant litter cover existed at the study site during the Last Interglacial. The long-term stability of warm stage conditions resulted in soil-forming processes, which are indicated by geobiontic invertebrates or soil-dwelling larvae. Plant and insect species characteristic for open habitats point toward frequent disturbances of the past vegetation as result of grazing and/ or fires during the Last Interglacial. Charcoal remains indicate that wildfires were an important factor in the dynamics of warm stage forest vegetation.

4.3. History of local vegetation and environment throughout the sequence

The analysis of the two above-described fossil rich assemblages that served as reference for the onset of the LGM and the MIS 5 as climate extremes formed the basis for the interpretation of the other samples. In this way, also the less well-preserved material revealed enough information to reconstruct the history of vegetation and environments for the entire sedimentation period. In contrast to our previous top down approach for the sediment description in the order of sampling, we proceed now chronologically, i.e. we start with the oldest and conclude with the youngest.

Unit IV

The only available sample from the lower sand Unit IV, taken in 50 m bgs, was deposited during the Saalian cold stage (MIS 6). The plant macrofossil composition with numerous remains of drought adapted grasses (*Koeleria* sp., *Festuca* sp., *Poa* sp., *Puccinellia* sp.) and steppe forbs (*Alyssum obovatum, Artemisia* sp., *Eritrichium villosum, Papaver* sp., and *Potentilla* spp.) indicates that meadow steppes predominated at this time. Ruderal vegetation is revealed by *Chenopodium* sp., *Descurainia sophioides* and *Draba* sp. The presence of snow hare (*Lepus timidus*) detected by its dropping is an indirect indication for open landscape. Few needles of larch and a leave of *Ledum palustre* indicate the scattered existence of trees and boreal dwarf shrubs in the Yana Highlands already at the penultimate cold stage suggesting that northern tree refugia possibly persisted throughout several glacial cycles. No pollen grains were found in this sample, probably due to rapid accumulation of aerated sandy matrix. The sample included only three fragments from two insect species: a weevil *Coniocleonus* sp. characteristic of meadow-steppes and a leafhopper, which can live in various types of grassland. Altogether, the plant and insect composition of the only sample in Unit IV indicates that meadow-steppe vegetation existed under dry conditions in the cold stage prior to the Last Interglacial. Generally, the vegetation of the penultimate cold stage resembled the LGM meadow steppe as reconstructed on the basis of the cold stage reference sample from the ground squirrel nest.

Unit III

The vegetation reconstructed for Unit III as a reference for Pleistocene warm stage conditions was already described in detail. Accordingly, light coniferous taiga with evident plant litter and soil formation existed at the study site. Numerous xerophilous plants and invertebrates indicate that patches of steppe vegetation persisted throughout MIS 5 suggesting the existence of a mosaic of woodland and open habitats. This mosaic might have been the result of frequent disturbances of the plant cover due to grazing and/ or wildfires as is indicated by abundant charcoal remains.

Unit II

Unit II represents the YIC. Ice complex deposits form under glacial conditions. The YIC was deposited during the Weichselian cold stage (MIS 4 to 2). The majority of the studied samples, including those from the lower part of the YIC, originate from section C in the eastern portion of the cirque. Only a small number of samples of Unit II were taken from section A in the western part of the exposure. First, we describe the sequence of fossil records in section C. The plant macrofossil records in the lower section of Unit II at depths between 42.5 and 38.5 m bgs are scarce and dominated by few xerophytic forbs and grasses such as *Potentilla tollii, P. arenosa, Papaver* sp. and *Poa* sp. Scattered larch needles were found at depths of 40.5 and 41.5 m bgs. The pollen content was mostly insignificant. Only in the sample at 39.5 m bgs, 91 pollen grains were counted displaying the following composition: Ericales (26.4%), *Artemisia* sp. (14.0%), *Pinus* sp. (14.0%), Caryophyllaceae (9.9%), Cyperaceae (8.8%), Poaceae (2.2%). *Pinus* sp. produces 10-80 kg pollen per hectare annually (Birks and Birks, 1980). This productivity along with its ability to be dispersed over long-distances suggests that the detected pollen don’t represent the local presence of *Pinus* sp. 157 fossils of invertebrates belonging to 50 taxa were found in this section, mainly characteristic of open, dry habitats including typical representatives of the Pleistocene tundra-steppe: the ground beetles *Harpalus amputatus obtusus* and *Cymindis arctica*, the pill beetle *Morychus viridis*, and the weevils *Stephanocleonus eruditus* and *S. incertus*. Forest or shrub inhabitants were not detected. Only a few rove beetles occurring in plant litter could be found. Among the invertebrates of other habitats, leaf-hoppers, spiders, fly pupae, one aquatic beetle and *Daphnia* ephippia were detected. The latter two taxa thus suggest the presence of small water ponds, e.g. ice-wedge polygonal ponds characteristic of YIC. The fossil records display a shift from the more humid warm stage climate with light coniferous woodland and intertwining steppe patches to dryer cold stage conditions with predominating dry open grassland interspersed by scattered woodland.

In the section between 37.5 m bgs, and 35.5 m bgs primarily plant macrofossils from xerophilous forbs like *Potentilla tollii, Artemisia* sp., *Phlox sibirica*, and *Silene repens* as well as the ruderals *Lepidium densiflorum* and *Descurainia sophioides* could be identified. *Descurainia sophioides* is a moist site pioneer that occupies disturbed and overgrazed areas (McKendrick, 2000). At 36.5 m bgs, arctic petrophytic pioneers, e.g. *Papaver* Sect. *Scapiflora* and *Smelovskia* sp. (sensu Al-Shehbaz and Warwick, (2006), who integrated *Gorodkovia, Redowskia* and *Hedinia* into the genus *Smelowskia)* were found. *Smelowskia jacutica* (formerly *Gorodkovia jacutica*) still occurs in the study area today and is therefore most probably represented by fossil seeds. We also identified few grasses like *Poa* sp. and *Puccinellia* sp. The plant species detected in this section indicate arid conditions and constitute steppe and meadow vegetation. Tree birch (*Betula* Subgenus *Betula*) and shrub alder (*Alnus alnobetula* subsp*. fruticosa*) were the only woody plants identified in this section; larch was not detected. Due to the scarcity of the fossils, it is difficult to resolve whether larch was really absent at the time of deposition of this section or whether its remains are merely not preserved in the studied sample. Invertebrates were absent in this section.

The macrofossil assemblage in the section between 34.5 and 32.5 m bgs contained again woody taxa represented by *Larix gmelinii* and dwarf shrubs (*Empetrum nigrum, Vaccinium vitis-idaea*) in the undergrowth as well as petrophytic arctic pioneers. The presence of e.g. *Silene repens, Draba* sp., *Saxifraga* sp., and *Juncus sp.* suggests that there was no continuous taiga but more or less open vegetation intercalated with small groves. The pollen counts of 303-325 grains per sample in the section at 32.0-32.5 m bgs are quite rich. The palynological results show a dominance of taxa characteristic of boreal vegetation: Ericales, Betulaceae, and Pinaceae. However, also the presence of xerophytic and cryophytic taxa are noticeable: *Artemisia* (6.0-12.0%), Caryophyllaceae (5.0-6.1%), Cyperaceae (4.6%). Among woody taxa, pollen of *Picea, Pinus* and *Tsuga* deserve special attention. Pollen of *Picea* sp. (4.0%), *Pinus* sp. (2.1%) and *Abies* sp. are present at 32.5 m bgs. In the sample half a meter above, the percentage of *Pinus* pollen increased up to 7.3%, *Picea* decreases to a single grain and *Abies* pollen is absent. The composition of the woody pollen fraction points to re-deposition of the sediments between 32.5 and 32 m bgs, e.g. due to cryoturbation in the active layer. Also invertebrates indicate forested habitats. The sample from 32.5 m bgs contained 65 fragments (26 individuals) which belong to 11 species of insects and oribatid mites. We found the ground beetle *Pterostichus brevicornis*, which occurs in wet tundra and boggy forests, the riparian ladybird *Hippodamia arctica*, several plant litter species such as *Arpedium quadrum* and *Corticaria* sp. as well as the auger beetle *Stephanopachys substriatus* and the ant *Camponotus herculeanus*, which are strictly bound to forest environments. Steppe insects were not found in this section, what makes the assemblage remarkably different from the interval in 42-38.5 m bgs, which was assumedly deposited during the Early Weichselian. The entomological results indicate a northern forest or forest-tundra environment. In view of the scarce fossil content, this reconstruction must be treated with caution.

In the long section from 31.5 to 20.5 m bgs, the studied deposits were poor in all kinds of fossil material and almost devoid of plant remains. A single seed of the Fabaceae tribe Galegeae (cf. *Oxytropis* sp.) could be identified; a macrofossil-based vegetation reconstruction is therefore not possible for this depth interval. There are, however, two samples in 29 m and 27.5 m depths that yielded a sufficient number of invertebrate remains. The insect assemblage in the sample in 29.0 m bgs contains forest species like the lined flat bark beetle *Leptophloeus angustulus* and plant litter species (*Cryptophagus* sp.) and, at the same time, the steppe weevil *Stephanocleonus eruditus*. The sample from 27.5 m bgs yielded only 14 fragments exclusively of steppe species (*Cymindis arctica)* and the cryo-steppes species *Morychus viridis*. Pollen are largely absent at the lower part of the interval. The only sample with reliable pollen counts in 22 m depth yielded a spectrum of 314 pollen grains composed of *Artemisia* (20.0%), Caryophyllaceae (18.8%), other herbs and grasses (14.6%), Cyperaceae (12.4%), *Selaginella rupestris* (5.4%), Asteraceae (4.1%), Ranunculaceae, *Saxifraga* sp., Poaceae (2.2%), *Larix* sp. (less than 1.0%), *Salix* sp., *Betula* sp., *Alnus fruticosa*, Ericales, and others. Given the small amount of tree pine pollen (less than 1.0%) it is unlikely that *Pinus* sp. occurred in this area, its pollen was likely wind-transported over far distances. At a depth of 20.5 m bgs, only 18 pollen grains were found, reflecting xerophytic vegetation cover. The poorly preserved entomological and pollen analyses in the depth interval from 31.5 to 20.5 m bgs, in summary, yielded inconsistent indications from forest to xerophytic grass-sedge vegetation, possibly reflecting the concurrent presence of woodland and grassland at the transition from late Early to Middle Weichselian.

For the section from 19.5 to 12.5 m bgs, several AMS ^{14}C dates between 48 and 51 ka BP are available; we assume that this narrow age range is a result of the fact that the dates represent the limit of the dating method. The obtained ages thus must be used with care. The studied samples might represent the early Middle Weichselian. According to the identifications of the poorly preserved plant macrofossils, dry open ground indicators like steppe forbs (*Artemisia* sp.*, Potentilla arenosa, P. tollii, Alyssum obovatum, Silene samojedorum, Eremogone capillaris*) and graminoids (*Poa* sp., *Festuca* sp.) dominated the plant cover together with the cryophytic pioneer plant *Papaver* Sect. *Scapiflora.* The steppe sedge *Carex duriuscula* is an indication of overgrazing and heavily disturbed ground (Hilbig, 1995). Megaspores of *Selaginella rupestris* confirm the indication of dry and exposed ground. Scattered dwarf shrubs such as *Vaccinium vitis-idea*, *Ledum palustre* and the boreal dwarf horsetail *Equisetum scirpoides* occurred at this time as well.

The pollen analysis of this depth interval is based on grain counts from 24 to 216 per sample. The upper palynological spectra (19.5 m bgs) is dominated by spores from bryophytes, *Selaginella rupestris* (32.6%), ferns (7.3%), as well as pollen of Cyperaceae (6.3%) and *Artemisia*, pointing to a mixture of pioneer vegetation and dry grassland vegetation. The spectrum at 18.5 m bgs is dominated by pollen of Caryophyllaceae (47.0%) and other herbs (18.0%) along with 8,8% pollen of woody taxa: *Betula* sp., *Salix* sp., *Alnus alnobetula* subsp*. fruticosa* and *Pinus* sp. indicating an open drought adapted vegetation with scattered groves. At 16.5 m bgs, *Selaginella rupestris* becomes dominant in the palynological complex (43.5%), along with Cyperaceae 17.6%, *Salix* sp., Caryophyllaceae, and Asteraceae, which share together 9.3%, reflecting again an open steppe-like environment.

Invertebrate remains were found in several depths of this section. The insect assemblage from 19.5 m depth bgs sharply differs from all other samples of the sequence as it contains the highest number of chitin fragments (513). However, MNI is only 60 and the species diversity is with only 9 species very poor. We could identify numerous sclerites including legs and mandibles of only a single species – *Morychus viridis* (Fig. 6.42-51). *Morychus viridis* occurs today in relictic, cold, very dry, exposed and snow-less 'sedge-steppes', mainly composed of *Carex argunensis* (an East Siberian vicariant of *C. rupestris*) exclusively in NE-Siberia (Berman, 1990; Sher and Kuzmina, 2007). This species can therefore be regarded characteristic of *Carici rupestris - Kobresietea* communities. Found in the majority of Northeast Siberian fossil assemblages, often in very high numbers, this pill beetle is a symbol of the Pleistocene mammoth steppe in Western Beringia (Sher and Kuzmina, 2007). Most of the other detected species are also typical for the Pleistocene mammoth steppe: the steppe species *Stephanocleonus eruditus* and *Cymindis arctica*; the xerophilous tundra weevil *Hypera diversipunctata*, the ground beetle *Poecilus nearcticus* and the dung beetle *Aphodius* sp. The abundance of plant litter insects and oribatid mites is an unusual feature of the assemblage as it is inconsistent with dry, exposed ground indicated by the mammoth-steppe representatives. The taphocenosis thus represents a mosaic of several different habitats.

The assemblages from the samples between 19.5 and 12.5 m bgs consisted, beside scattered terrestrial steppe-tundra species, almost exclusively of aquatic invertebrates, such as caddisfly larvae and *Daphnia*, indicating the presence of an ephemeral small water body. Altogether, the combined proxy data of plant macrofossils, pollen and insects indicate predominating steppe and *Kobresietea* vegetation on very dry, exposed, open ground. The relative portion of dry grassland, open-ground pioneer vegetation and small ponds, probably in centres of polygons, changed in association with the local topographic conditions in this interval of the Middle Weichselian.

The uppermost part of unit II at section C in depths of 11.5-8.5 m bgs, provided three fossil assemblages suitable for vegetation reconstruction. Only scattered plant macrofossils are present in the samples at 11.5 and 10.5 m bgs. They prove the presence of boreal taxa, e.g. *Larix gmelinii* and *Vaccinium vitis-idaea*, as well as *Equisetum scirpoides*. The Arctic pioneer *Papaver* Sect. *Scapiflora* and the spike moss *Selaginella rupestris* indicate the presence of dry and exposed sites. The sample in 8.5 m depth bgs was AMS ^{14}C-dated to about 12.6 ka BP and comprised very few plant macrofossils of shrubs and dwarf shrubs, i.e. *Salix* sp. and *Vaccinium vitis-idaea,* as well as *Equisetum scirpoides* and the moss *Aulacomnium turgidum*. According to the radiocarbon date, the assemblage was deposited at the very end of the last glacial period, more specifically during the Allerød Interstadial and is therefore regarded the youngest fossil assemblage of the entire profile. The four identified plant taxa are all representative of northern boreal woodland vegetation. The palynological complex from this sample embodies only 52 spore and pollen grains. The dominance of *Selaginella rupestris* spores and the scattered presence of Cyperaceae, Caryophyllaceae, and Asteraceae pollen suggest open, exposed ground.

The remaining samples were taken from the upper part of the YIC in section A, located in the western part of the slump (Fig. 1d). The sample depths between sections A and C are not directly comparable because the elevation of the ground surface as reference point differs between the sampled sections. The same is true for the age of the sediments; e.g. the youngest sample in section C dated to the end of the last glacial, the Allerød, was taken at a greater distance from the ground surface than the older pre-LGM reference sample from the ground squirrel nest in section A. The difference in elevation of the scarp at the opposite sections might be due to uneven inclination of the ground surface as well as differing sedimentological facies and erosional events. Ashastina *et al*. (2017) pointed out that, in order to understand the nature of these unconformities, additional sedimentological and dating analyses are necessary.

The composition of the scarce plant macrofossil assemblage about 1m below the pre-LGM reference sample in 5.5 m bgs includes the steppe species *Silene samojedorum, Carex duriuscula* and the halophyte *Rumex maritimus* as well as several needles of *Larix gmelinii*. The palynological composition of the sample in 5.5 m bgs, represented by only 84 spores and pollen, contains one single pollen grain of *Pinus* subgen. *Diploxylon* (tree pine), which might have been transported over far distances. More than two thirds of the spore and pollen sum is represented by the open ground indicator *Selaginella rupestris*. In addition, pollen of Caryophyllaceae and Asteraceae were detected indicating open meadow-like vegetation.

The invertebrate assemblages in this depth interval are again composed almost exclusively of aquatic invertebrates, such as caddisfly larvae and *Daphnia*. Only scattered steppe-tundra insects were detected. In summary, the combination of fossil indicators reveals open vegetation with meadow-steppes and exposed disturbed ground. The presence of small ephemeral ponds or paddles is indicated by aquatic invertebrates and by the halophytic nitrophilous pioneer *Rumex maritimus*, which is characteristic of muddy sites in ponds and at lake shores periodically inundated and drying out in summer due to high evaporation under arid climate.

The next upper sample is the fossil ground squirrel nest in 4.6 m bgs, which is, as reference assemblage for cold stage conditions, described above in detail. According to the comprehensive palaeontological assemblage, grassland composed of meadow-steppes complemented by few tundra-steppe representatives prevailed at the study site indicating dry conditions during the LGM. The scattered occurrence of larch is also indicted by plant macrofossils.

The YIC samples of unit II, with depths of 3.5-2m closest to the ground surface at section A, revealed only plant remains and no further fossils. As in the samples discussed above, the assemblages comprised a mixture of xerophytic, ruderal and dry arctic grassland species as well as scattered remains of larch. Dominant species in the assemblages in 3.5 and 3.0 m depth bgs are *Chenopodium* sp. and *Poa* sp.; a scanty amount of *Papaver* sp. and scattered seeds or seed fragments of *Minuartia arctica, Puccinellia* sp., and *Smelovskia* sp. are present as well.

The uppermost sample in 2.05 m depth bgs was AMS ^{14}C-dated to about 33 ka BP (Lab Nrs. Poz-79751 and Poz-80390). Thus, the sample has an age older than the underlying ground squirrel nest suggesting an age inversion and a possible re-deposition of this material. Alternatively, the inversion might be the result of plant transport by the ground squirrels deep into their subterranean burrows beneath considerably older layers. Depending on the thickness of the active layer, arctic ground squirrels can burrow their dens deeper than 1m, when the soil substrate is coarse-grained and dry as in sandy deposits. Larionov (1943) reported on a ground squirrel nest found in Siberia at 2m depth. The assumed inversion might be also the result of erosional events associated with repeated climate shifts at the transition from the late glacial period to the early Holocene. We could not find any Holocene deposits older than 300 years BP at the exposure, suggesting that denudation rather than deposition occurred during the Holocene perhaps as result of thawing and destabilisation of permafrost near surface. The poor assemblage of plant macrofossils in 2.05 m depth was dominated by steppe species like *Silene repens, S. samojedorum* and *Artemisia* sp. as well as *Saxifraga* sp. and the spikemoss *Selaginella rupestris*.

5. Discussion

Different bioindicator groups including pollen, invertebrates, plant remains and charcoal from the Batagay permafrost sequence were used to reconstruct the history of vegetation and environments in the Yana Highlands during the penultimate cold stage, the Last Interglacial and the last cold stage including the LGM and the late glacial. The vegetation existing during the two climate extremes of the late Pleistocene, the warm stage (MIS 5) and the onset of the cold stage (MIS 2), could be reconstructed in very detail.

5.1. Steppes and larch groves persistent throughout the investigated timespan

The vegetation during cold-stages was, according to our results, dominated by meadow steppes resembling modern communities of *Festucetalia lenensis.* During MIS 5 in contrast, the zonal vegetation mainly consisted of open taiga forest corresponding to today's phytosociological class *Vaccinio-Piceetea.* Primary tree species were *Larix gmelinii* and *Betula pendula*. Palynological data already revealed before that open *Larix-Betula* forests with *Pinus pumila* and *Betula* shrubs existed at the middle course of the Yana River during the Last Interglacial (Lozhkin and Anderson, 1995). Based on the new data presented here, we can specify the composition of the warm stage vegetation. According to our results (table 2), the woodlands were interspersed with ruderal and, in particular, meadow steppe vegetation, which constituted the zonal vegetation during cold stages prior to and after the Last Interglacial.

Within the investigated timespan from MIS 6 to MIS 2, no substitution in the floristic composition was detectable but only shifts in the percentages of the respective plant communities as well as in the abundances and diversity of their representatives. The studied assemblages rather showed that the study area was covered with meadow-steppes along with groves of cold-deciduous trees (mainly larch) throughout most of the reconstructed period. The respective percentages of woodland and open vegetation assumedly changed through time in accordance with the predominating climate conditions and degree of disturbances.

The few samples in the record without larch remains were in general very poor in macrofossils. Therefore, it is difficult to resolve whether larch was really absent at the time of their deposition or whether larch remains are merely not preserved in the studied material. Cold stage larch macrofossils from the time before and during the LGM are reported so far only from West Siberia and the Russian Far East (Binney *et al*., 2009). The closest known glacial larch occurrence, dated to the Younger Dryas, is reported from the Dyanyshka peat profile situated west of the Verkhoyansk Mountain range at the edge of the Central Yakutian Plain about 170km south of the Arctic Circle and 520km southwest from the Batagay site (Werner *et al*., 2009). The existence of larches at the western foreland of the Verkhoyansk Mountains during the Younger Dryas was regarded as proof for their survival during late Pleistocene cold stages (Werner *et al*., 2009). This assumption is confirmed by the nearly continuous presence of larch in the 50-ka pollen record from Lake Billyakh about 85km east of the Dyanyshka section (Müller *et al*., 2010). The here-presented macrofossil evidence of larch in the Yana Highlands north of the Arctic Circle even during the LGM is all the more noteworthy as the climate is (and was) there much less favourable than in Central Yakutia. The palaeobotanical results from the Batagay profile suggest that larch groves existed in the area already during the penultimate cold stage and survived throughout the entire late Pleistocene.

On the other hand, grassland vegetation, primarily meadow-steppe, also persisted at the site throughout the studied timespan even under the relatively moist, full warm stage conditions of MIS 5. Wildfires might be the reason for the persistence of steppe vegetation in glades within the ancient forest. Wildfires might also have resulted in the abundance of pioneer wood species such as *Betula pendula, Alnus alnobetula* subsp*. fruticosa* and *Rubus idaeus*, which are partly more restricted or absent at this site today. The leaf beetle *Bromius obscurus*, which is restricted to *Epilobium angustifolium*, likewise indicates indirectly disturbances of forest vegetation possibly by fire.

Wildfires were, however, not the only factor of disturbance, likely during the Last Interglacial and certainly during cold stages. A high amount of ruderal taxa is characteristic of disturbed ground and is often considered to be related to overgrazing (Yurtsev, 2001). Steppe vegetation and grasslands in general are fostered by grazing (Johnson, 2009; Zimov *et al*., 1995). The absence of charcoal in the cold stage samples of Units IV and II virtually excludes fire as a disturbance factor suggesting that the territory was instead heavily grazed during cold stages. Ground squirrels, a typical steppe species, depending on open vegetation, in turn can strongly affect the vegetation and are regarded landscape engineers. The average home-range of *Urocitellus paryyii* is up to 200 metres surrounding the burrow (Hubbs and Boonstra, 1998). A sufficiently dense ground squirrel population could have affected the vegetation heavily within this range. An even more severe impact on vegetation can be expected from large herbivores. Numerous fossils of Pleistocene megaherbivores including mammoth, woolly rhino, horse and bison were found in the Batagay exposure (Novgorodov *et al*., 2013; Murton *et al*., 2017; and personal observations). The nitrophytic ruderal plant *Urtica dioica*, characteristic for resting or dung places (Walter, 1974), was found in high abundance together with other ruderals in deposits of the Last Interglacial suggesting the presence of megaherbivores also during this time. Zoogenic disturbances like grazing, trampling and wallowing by herbivores have in general a great impact on vegetation resulting in a mosaic-like structure, more openness and higher diversity (Johnson, 2009) stimulating the spread of pioneer plants. Meadow steppe vegetation

Table 2. Environmental reconstruction for the Yana Highlands since MIS 6. Results and interpretation produced by plant macrofossil, pollen, charcoal, and insect analyses.

Stratigraphy	MIS*	Depth, m bgs	Geology	Plant macrofossils	Pollen	Invertebrates	Palaeoenvironment
Active layer, Unit I	modern		fine sand of modern origin	none	none	none	modern
Late Weichselian (Sartan), Unit IIc	MIS 2	2.0-8.5	Yedoma Ice complex, mainly fine-grained sand with thick ice wedges, evenly distributed organic material and occasional layers and chunks of higher organic content	Abundant meadow-steppe species, few tundra-steppe taxa, scattered larch remains, few ruderal species	Caryophyllaceae *Artemisia,* Cyperaceae, Asteraceae, *Selaginella rupestris*	open grassland species, aquatic invertebrates, mammal nest inhabitants	Meadow-steppe vegetation with largely open, exposed ground and scattered larch stands, sporadic ponds or paddles, ground squirrels and large herbivores
Middle Weichselian (Karginsky), Unit IIb	MIS 3	10.5-19.5		Meadow-steppe forbs and grasses, *Selaginella rupestris* few light taiga species	*Selaginella rupestris* open ground, steppe, grassland, sparse boreal taxa	*Morychus viridis*, and other tundra-steppe taxa, plant litter species, aquatic species	Mainly meadow-steppe vegetation with tundra-steppe inclusions, mostly dry and exposed ground, likely small woods, ephemeral small ponds
Early Weichselian (Zyryan), Unit IIa	MIS 4	25.5-40.5		Meadow steppe taxa, few ruderals and halophytic grass, few light taiga species	*Artemisia*, various meadow herbs, Selaginella, Ericales, Betulaceae, Pinaceae	Steppe and tundra-steppe species, also forest taxa, few plant litter inhabitants, few aquatic invertebrates	Meadow-steppe interspersed by tundra-steppe patches and scattered woodland, sporadic ponds
Eemian (?), Unit III	MIS 5	43-44	Continuous organic layer merging at places into accumulations of large macros-copic plant remains	Open, herb-rich northern taiga forests with larch, tree and shrub birches, shrub alder, raspberry, wild rose; steppe and ruderal herbs with abundant *Urtica*, high amount of charcoal	Not enough pollen	Mostly forest species, plant litter inhabitants, cocoons of earthworms indicate pedogenesis, few meadow and tundra-steppe beetles,	Dry, herb-rich light coniferous taiga with a pronounced plant litter cover, widespread wildfires, stability of warm stage conditions resulted in soil-forming processes, patches of meadow-steppe vegetation persisted, probable presence of megaherbivores (existence of ruderal nitrophytes)
Unit IV	MIS 6		horizontally layered frozen fine sand sediments, thin ice wedges only	Mainly meadow steppe taxa, few ruderals, larch and *Ledum palustre* remains	Not enough pollen	One meadow-steppe indicator and another grassland species	meadow-steppe vegetation with scattered woods

*Preliminary age division based on geochronology, radiocarbon, and OSL dates during the Last Interglacial, as detected in the present study, is a suitable pasture for large herbivores. The availability of such grassland vegetation is, in combination with thin snow cover, a crucial factor for the survival of herbivores during severe winters (Formozov, 1990).

5.2. Steppes in Northeast Siberia: Pleistocene survivors or Holocene immigrants?

The palaeontological record of the Batagay section contributes to the understanding of the phylogeography of Yakutian plants and animals. The site is situated in the Yana Highlands, where steppe communities are still being well developed and play a notable role in the landscapes (Yurtsev, 1982; Berman *et al*., 2001). The question whether plants and invertebrates of modern steppes persisted in Yakutia throughout the Pleistocene or whether they immigrated to Yakutia only during the Holocene was contentious for a long time (Yurtsev, 1982; Kozhevnikov and Ukraintseva, 1997). Almost all plant and invertebrate species detected as fossil remains in Pleistocene deposits are known from modern relict occurrences in Northern Yakutia (Kiselev, 1981; Kiselev and, Nazarov, 2009; Kuzmina, 2015; Yurtsev, 1982, 2001) even though these steppes are restricted in extent and species diversity. The results in the present paper support the assumption that the occurrences of disjunct taxa in modern steppes of Yakutia are relicts of a formerly continuous range extending from Central Siberia and Mongolia during the cold and dry glacial climate phases.

Formerly, there was only one section known from the Ust’-Nera region at the upper Indigirka River, from where fossil insects were analysed (Kiselev and Nazarov, 2009). The Ust’-Nera record resulted in the reconstruction of forest and riparian habitats without contribution of steppes. The fossil invertebrate record of Ust’-Nera originates, however, from deposits, whose geological origin is poorly studied and so far unpublished and whose age is problematic (probably the Middle Pleistocene). The exploration of the Batagay section and its new palaeontological record provides important arguments to this discussion.

The statement of Berman *et al*. (2001, 2011), the areas at the middle courses of Yana and Indigirka Rivers were refuges for steppe insects throughout long periods of the Pleistocene is confirmed by the results of this study. The Pleistocene entomological complex in former studies consisted of two relevant components: steppe and tundra. Tundra insects are, however, not well presented in the Batagay sequence. The Arctic tundra group is absent here, the wet tundra group has a percentage of less than 2%, and the portion of the dry tundra group ranges between 1 and 7%. In more northern sites, the percentage of the tundra groups is much higher even in interglacial faunas. For example, the Last Interglacial forest assemblage from the Alazeya River (Kuzmina, 2015) comprises 10% of dry tundra and 20% of wet tundra insect species. Mammoth-steppe invertebrate assemblages in northern regions might include even up to 80% of tundra species (Kuzmina, 2015).

According to the entomological results, the Yana Highlands provided refugia mainly to steppe species but not to the whole mammoth-steppe complex. Similar observations were made in modern occurrences – relict steppes are occupied exclusively by xerophilous components of the regular Pleistocene community, while hygrophylous and mesophilous tundra insects are absent there (Berman *et al*., 2001, 2011).

An analogous situation is observable in the assemblage of plant macrofossils. Whereas plants characteristic of steppes are preserved in high diversity and abundance, true indicators of tundra meadows - *Kobresietea* communities - are largely absent. The only true representative of the class is *Ranunculus pedatifidus* subsp. *affinis.* Plants diagnostic for the vegetation class *Carici rupestris-Kobresietea bellardii* such as *Kobresia myosuroides* or *Dryas* sp. are absent in the Batagay assemblages but were relatively common in previously studied palaeobotanical records of the northern lowlands (Kienast *et al*., 2005, 2008, 2011; Wetterich *et al*., 2008; Schirrmeister *et al*., 2011).

The Eastern steppes of Yakutia (*Cleistogenetea squarrosae)* comprise two orders – the true steppes *Stipetalia krylovii* and the meadow steppes *Festucetalia lenensis*. True steppes (*Stipetalia krylovii*) are dominated by steppe grasses. Meadow steppes (*Festucetalia lenensis*) in contrast are dominated by forbs. The fossil assemblage of the ancient ground squirrel nest was clearly dominated by herbaceous dicotyledons, i.e. forbs. Consequently, the pre-LGM palaeo-steppe community around the den can be interpreted as meadow steppes of the order *Festucetalia lenensis*. This classification is in accordance with the northern location of the study site and also with larch remains found within the den, which indicate the proximity to larch groves. Modern meadow steppes within the zonal steppe belt primarily occur in northern or elevated areas that are not as dry as true steppes and are often interspersed by herb-rich larch groves (Hilbig, 2000). True steppes (*Stipetalia*) have today their northernmost occurrence in Central Yakutia. The new results suggest that the Pleistocene grassland vegetation in the study area was mainly composed of meadow-steppes (*Festucetalia*) and that *Kobresia*-meadows were possibly restricted to higher elevations.

5.3. Climatic implications

The lack of *Kobresietea* representatives in the Batagay record even during cold stages might be the result of summer temperatures warmer than in the coastal lowlands. Warm summers are also indicated by the persistence of larch. *Larix gmelinii* requires a mean temperature of the warmest month (MTWA) of minimum about 10 °C and a growing season length of more than 60 days (Abaimov, 2010). The presence of arctic ground squirrels in itself points to an active layer depth of more than 1 meter because for successful hibernation, ground squirrels need to burrow deep enough to ensure a constant temperature throughout the winter (Buck and Barnes, 1999; Mayer, 1953). The ground squirrel nest of the pre-LGM suggests therefore that the active layer must have been thicker than 1m, which indicates warm and sufficiently long summers. Beside deeply thawed, the ground during the Last Glacial must have been drained better than at present - an indication for low precipitation. Arctic ground squirrel nests were also detected in the lower sand unit below the YIC in the Batagay profile (Murton *et al*., 2017) and thus seem to be relatively common in this sequence occurring also in deposits associated with the penultimate cold stage.

From the Duvanny Yar outcrop in the Kolyma lowland, numerous Arctic ground squirrel nests, radiocarbon dated from 33 ka BP to 27 ka BP, were described and analyzed by Gubin *et al*. (2001, 2003) and Zanina *et al*. (2005, 2011). The composition of plant species gathered in the dens differed from those at Batagay at this site despite analogous habitat requirements of ground squirrels, to wit dry open areas or tundra steppe with well-drained substrates (Buck and Barnes, 1999). *Polygonum viviparum*, a forb species occupying cold, moist and exposed tundra soils, was the most abundant taxon among the cached plants in the Kolyma lowland (Gubin *et al*., 2001; Zanina *et al*., 2011). The strict preference of this particular species (up to 90% of a sample), even when the closely related *P. bistorta* was also available, is documented for Arctic ground squirrels in the Yukon as well and might be due to this plant's high starch content and aggregated distribution (Gillis *et al*., 2005). The absence of *P. viviparum* and most other representatives of tundra meadows in the cache of the Batagay nest likewise suggests the real lack of *Kobresietea* communities displaying climate conditions warmer than in the northern lowland areas during the last cold stage. Corresponding to the plant composition in the Batagay nest described here, representatives of steppe and dry pioneer vegetation like *Plantago canescens, Silene samojedorum, Poa* sp., and *Myosotis asiatica* were common in ground squirrel caches at coastal sites (Maksimovich *et al*., 2004). Steppe and pioneer vegetation was widespread throughout West Beringia during the Weichselian glacial and formed mosaics with meadows, *Kobresietea* communities, aquatic and littoral vegetation in the northern lowlands and with light coniferous forest in inland areas.

Steppe plants are primarily indicators of dry ground. They consequently stand for low precipitation, just as halophytic meadow plants such as *Puccinellia* sp. and salt-tolerant muddy-site-pioneers like *Chenopodium* sp. and *Rumex maritimus* indicate the drying out of ponds and salt accumulation at the ground surface due to high evaporation. Aridity is a characteristic feature of continental climate. Owing to the massive global sea level fall, the degree of continentality and aridity can be assumed to be even more pronounced during cold stages, when e.g. the northern shelf seas as potential source of moisture retreated by several hundred kilometers.

Precipitation was probably lower than today also during the last warm stage. Low precipitation during MIS 5 is indicated by numerous steppe taxa and by the absence of *Pinus pumila* in the palaeorecord. The stone pine requires a snow depth of minimum 40cm (Okitsu and Ito, 1984; Khromentovsky, 2004). Accordingly, the absence of *Pinus pumila* in the record might indicate thin snow cover due to low winter precipitation or possibly high wind exposure during the Last Interglacial.

Lower precipitation and more pronounced continentality during MIS 5 were observed also at more northern sites in Yakutia. Palaeontological records of this time from both coasts of the Dmitrii Laptev Strait, Bolshoi Lyakhovsky Island and Oyogos Yar, revealed the existence of subarctic shrub tundra interspersed by grasslands and shallow lakes in the area that is now Yakutia’s coastal lowlands (Kienast *et al*., 2008, 2011). Macroremains of larch (*Larix gmelinii*) at Oyogos Yar indicate the tree line was shifted to about 270 km north of its current position. Climate reconstructions revealed an MTWA about 10 K warmer than at present in the region, an extended growing season, high evaporation and locally thin snow cover in winter (Kienast *et al*., 2011). Pollen analyses from the Bolshoy Lyakhovsky site (Andreev *et al*., 2004) suggest that the vegetation cover was dominated by open plant associations with Poaceae and *Artemisia.* Shrub tundra with *Betula nana, Salix* sp., and *Alnus alnobetula* subsp*. fruticosa* existed assumedly at moister places. At Oyogos Yar, the palynological spectrum was likewise composed by around the half of taxa of open vegetation with Poaceae, Cyperaceae and *Artemisia* and around 40 % of woody taxa like *Betula* sect. *Nanae, Betula* sect. *Albae*, *Alnus alnobetula* subsp*. fruticosa* and *Larix* indicating open woodland vegetation alternating with grasslands (Andreev *et al*., 2011; Kienast *et al*., 2011).

Comprehensive palynological records and tree macrofossils from Eemian sites in the Yana-Kolyma lowlands suggest that *Larix-Betula* woodlands with a shrub layer consisting of *Betula* spp., *Pinus pumila*, *Salix* sp., and *Alnus alnobetula* subsp*. fruticosa* existed in areas covered today with tundra suggesting an MTWA 4 to 8 K warmer than today in the coastal lowlands (Kaplina, 1981; Lozhkin and Anderson, 1995). The mean temperature of the coldest month was reconstructed 12 K colder than today, indicating a greater seasonal temperature gradient and thus confirming more pronounced continentality.

6. Conclusions

- Meadow steppes resembling modern communities of the phytosociological order *Festucetalia lenensis* within the class *Cleistogenetea squarrosae* in extrazonal relict steppe patches in Northeast Siberia formed the primary vegetation during the Saalian and Weichselian cold stages.

- Cryophilous species diagnostic for tundra-steppe vegetation of the class *Carici rupestris-Kobresietea bellardii* were unexpectedly scarce at the study site yet during the Last Glacial Maximum, which embodies the globally coldest climate phase of at least the last 130 ka.
- Instead, even during the LGM, larch stands existed in the Yana Highlands indicating relatively warm summers with an MTWA higher than 10°C throughout the studied period.
- The macrofossil-proven local presence of larch demonstrates that the study region was a northern tree refugium throughout the late Quaternary and beyond.
- During MIS 5 warm stage, open coniferous woodland was the primary vegetation at the study site resembling modern taiga (class *Vaccinio-Piceetea*) but with birch (*Betula pendula*) as a constituent not present today.
- High amounts of charcoal, the presence of insects feeding on fireweed (*Epilobium angustifolium*) and the finding of plants like *Rubus idaeus,* characteristic of burnt down woodland, indicate wildfire events during the Last Interglacial.
- The presence of other pioneer plants, abundant *Urtica dioica* in particular, indicate zoogenic disturbances of the plant cover during MIS 5 suggesting the study area was an interglacial refugium for large herbivores of the mammoth faunal complex.
- Even under the full warm stage conditions, meadow steppes formed a significant constituent of the plant cover in the Yana Highlands indicating low precipitation and potentially providing suitable pastures for herbivores.
- The studied fossil record proves that modern steppe occurrences in the Yana highlands did not establish recently but that they are relicts of a formerly continuous steppe belt extending from Central Siberia to Northeast Yakutia during the Pleistocene.
- The persistence of plants and invertebrates diagnostic of meadow steppe vegetation in interior Yakutia throughout the late Quaternary indicates climatic continuity and documents the suitability of this region as a refugium also for other characteristic organisms of the Pleistocene mammoth steppe including the iconic large herbivores.

Chapter 4:

Pleistocene refugia in Western Beringia: fossil evidence of a Yakutian endemic plant for the last interglaciation

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Review of Palaeobotany and *Palynology*, draft

Abstract

Quaternary history of northeastern Asia is an intriguing chapter for palaeontologists. The region served as a refugium for flora and fauna of the Pleistocene, characterised by transgressing and regressing sea-levels. Populations isolated in refugia can result in the establishment of new species. Endemics of northeast Asia are understudied from phylogenetic point of view. Here, we report a finding of a fossil seed of an endemic steppe plant. The seed originates from the sample taken from the Batagay permafrost exposure, the Yana Highlands, northeastern Asia. Stratigraphic and chronologic dating attribute the fossil to the Last Interglacial. This new data suggests that the Yana Highlands were already a distribution area of xerophytes at least from the Last Interglacial on. The modern steppes in the region did not establish recently, but are remnants of a former closed steppe belt connecting Mongolia and northeastern Asia.

Introduction

Yakutia, Russian northeast Siberia, remained largely unaffected by glaciations in contrast to the most of other northern regions, as it was constantly characterised by cold and dry continental climate throughout the Quaternary (e.g. Svendsen *et al*., 2004; Barr and Clark, 2012). Here, the formation of arctic vegetation occurred (Yurtsev, 1968), which was accompanied by the spread of steppe taxa into inland Yakutia and northern highlands. These northern areas remained under continental climate influence since the Pleistocene cold phases until present. The level of climatic continentality increased due to global ice sheet growth, regression of arctic shelf seas resulted in the northwards retreat of the coastlines (Velichko, 1975). Due to this relative environmental stability under persistent continental climate, interior northeastern Asia was a refugial area for cold adapted biota (Sher, 1997; Abbott *et al*., 2000). The mountainous regions of Northeast Siberia including Yakutia, the Magadan region and inland parts of Chukotka are considered as a centre of speciation (Nikolin, 2012). Today, 80 endemic vascular plant species exist in northern Yakutia (Zakharova, 2011). Little is known so far about the history of speciation of Yakutian endemics, among which more than a quarter are steppe taxa including species from Caryophyllaceae Family (Zakharova, 2011).

According to Vlasova (2011), 24 *Stellaria* species exist in Yakutia, while 135 accepted species within *Stellaria* exist worldwide (253 unresolved; The Plant List, 2018). High speciation of plant taxa could be a consequence of areal disjunctions and adaptation of taxa to new climatic and environmental conditions. Despite present day occurrence of steppe endemics in northern Yakutia, timing of spread and speed of new species establishment are still remaining unclear. According to an accepted theory, steppe taxa occupied northern latitudes during Pleistocene cold stages (Yurtsev, 1968). Understanding of the exact timing of new endemic species establishment would help to pinpoint the timing of climatic and/or geological events affecting flora distribution and speciation in north eastern Eurasia. Molecular data, e.g. DNA analysis, could provide valuable data on genetic similarities and relative age of species, but the timing could be delivered only by a fossil record (Milne and Abbott, 2002).

In the recent study, we report on a finding of a *Stellaria jacutica* SCHISCHK., an endemic petrophytic steppe plant, sampled from the Batagay permafrost outcrop, the Yana Highlands, northern Russia. The dating result could help to understand the temporal frame and area of Verkhoyansk mountain glaciations, which governed new species establishment.

Study site and methods

The Batagay permafrost outcrop is positioned in the Yana Highlands, 2.5 km northeast from the Batagaika River – a tributary of the Yana River (Fig.1). The Yana Highlands are within the continental subarctic climate (Köppen, 1884). Continentality is indicated by the globally greatest seasonal temperature gradient, exceeding 100 K, and low annual precipitation of only 181 mm (RIHMI-WDC, 2016). The Batagay permafrost sequence is composed of several syngenetically accumulated sediment units (Ashastina *et al*., 2017; Murton *et al*., 2017). Frozen sediment was taken in situ from the outcrop using hammer and chisel. The sample originating from 43 m b.g.s. contained numerous plant macrofossils, e.g. seeds, needles, leaves, and entomological remains. The obtained material was wet-sieved through standard test sieves from Rentsch GmbH with mesh sizes of minimum 0.25 mm and air-dried. From the residue, plant macro-remains were picked using an Olympus SZX 16 stereomicroscope and identified by comparison with reference material from carpological collections at the Senckenberg Research Station of Quaternary Palaeontology, Weimar, Germany (IQW, 2017) and at the Institute of Biological Problems of the North, Far East Branch, Russian Academy of Sciences (IBPN FEB RAS) Magadan (MAG, 2018). The identification of *Stellaria jacutica* was verified with descriptions in various keys (Tolmachev, 1974; Malyshev and Peschkova, 2003; Vlasova, 2011) and finally by the original description from Schischkin (1940).

The identified macrofossils were dated with radiocarbon method at Poznan Radiocarbon Laboratory, Poland. The calibration was made with OxCal software (Bronk Ramsey, 2009) using IntCal 2013; sediments were dated using optical stimulated luminescence (OSL) method at Helmholtz Institute Freiberg for Resource Technology, Germany.

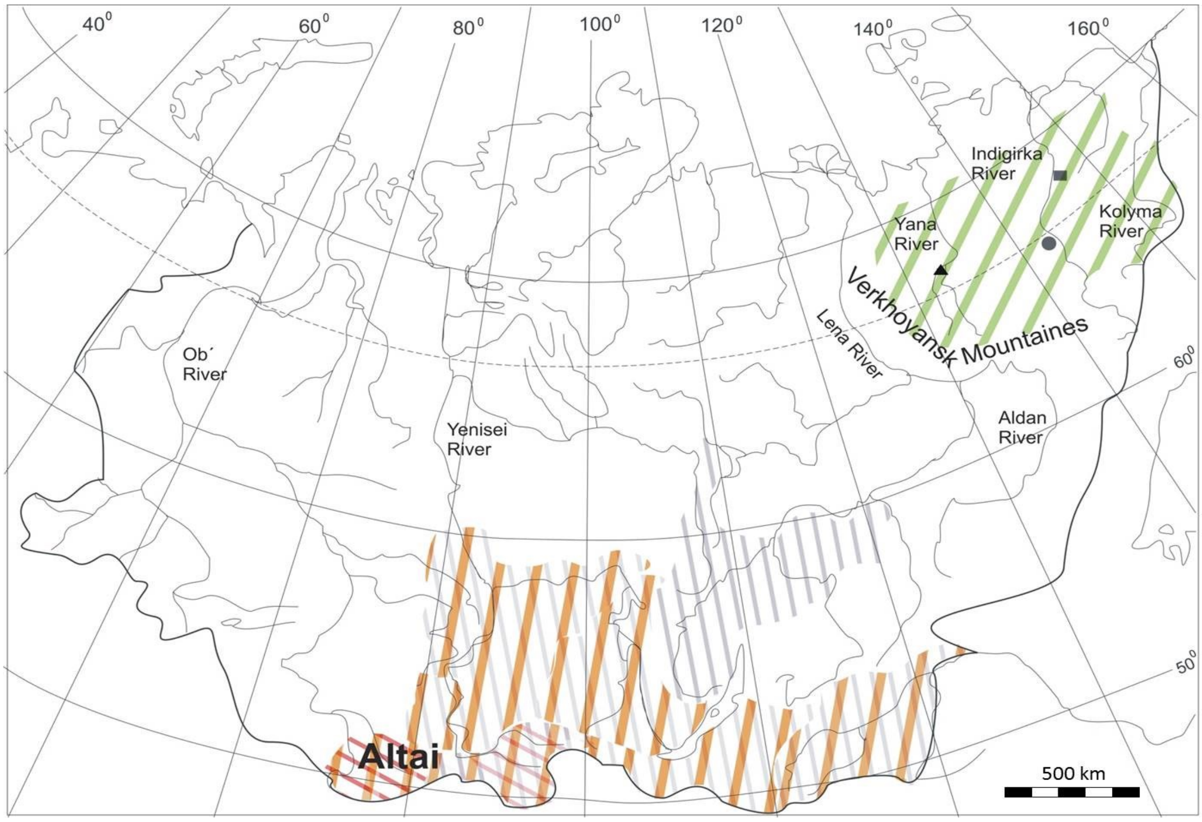

Figure 1. Distribution of extant large-seeded *Stellaria* species in Siberia (excl. the Russian Far East), modified from Malyshev and Peshkova (2003), and pollen fossil finds and references therein). Plant fossils of *Stellaria jacutica*: triangle – seed from the Batagay outcrop (Ashastina *et al*., 2017); circle – pollen from digestive tract of the Cherskij horse (Ukraintseva, 2013); square – pollen from digestive tract of the Mylakhchin bison (Ukraintseva, 2013). Floristic regions with modern occurrence are hatched: *S. petrea* – red; *S. cherleria* – blue; *S. dichotoma* – orange; *S. jacutica* – green.

Results

Sample from 43 m b.g.s. provided a large amount of plant macrofossils for palaeovegetation reconstruction (Ashastina *et al*., submitted). Numerous findings of arboreal and steppe taxa suggest that vegetation cover was a mixture of a dry herb-rich light coniferous taiga and glades inhabited by ruderal and steppe species, such as *Corispermum crassifolium*, *Papaver* sect. Scapiflora, *Silene repens*, *S. samojedorum*, *Potentilla arenosa*, and the endemic species *Potentilla tollii*. This indicates that open and dry habitats existed at the site also during the last interglacial. Among steppe taxa we identified *Stellaria jacutica* (Fig. 2.1) – an endemic that occurs nowadays in basins of the Yana, Indigirka and Kolyma Rivers (Yurtsev, 1981). This is a petrophytic steppe species with main habitat in pebble mountainous areas, river slopes (Tolmachev, 1974). The specimen could be identified with certainty based on a fossil seed displaying the characteristic carpological features of that species. The seed identified as *Stellaria jacutica* is dull blackish-brown, reniform, compressed and is densely covered by conical papillae. The seed has a length of 2.4 mm and a height of 1.8 mm. Such a large seed size is, within the genus *Stellaria*, a rather rare characteristic and can be detected only at a limited number of speciesDirect radiocarbon dating revealed a non-finite age >50 ka BP. In order to determine the age with other dating method, the underlying sediment at 47 m b.g.s. was dated using OSL method and delivered the age of 142,800±25,300 a BP (Ashastina *et al*., 2017). On the basis of palaeovegetation reconstruction (Kienast *et al*., 2016; Ashastina *et al*., submitted) and stratigraphical position, we assume the sample to be of last interglacial origin (MIS 5).

Discussion

There are not many mentions of *Stellaria jacutica* in the palaeo-record. A few identifications of this species are based on pollen (Ukraintseva, 2013) and both originate from the Indigirka River valley. Pollen grains were found within large intestine contents of the Mylakhchin bison (*Bison priscus occidentalis*, Flerov, 1979) and Cherskij horse (*Equus lenensis,* Rusanov, 1968). Radiocarbon dating of the bison reported the date 29,500±1,000 a BP; age termination of the horse resulted in radiocarbon age 38,590±1,120 a BP (Arslanov and Chernov, 1977). Both findings correspond to Karginskiy interstadial. Therefore, we assume that the seed reported within current study is the oldest seed of *Stellaria jacutica* SCHISCHKIN found so far within palaeo-record.

Our identification of Stellaria is based on seed morphology that is a reliable and well-described characteristic. Important traits within the genus Stellaria are seed size and number of seeds per capsule. Such a large seed size is, within the genus Stellaria, a rather rare characteristic and can be detected only at a limited number of species. According to the Flora of Siberia (Malyschev and Peschkova, 2003), there are altogether four large-seeded species, *S. cherleriae*, *S. dichotoma*, *S. jacutica*, and *S. petraea*, present in East Siberia today (Fig. 2). All of them are restricted to dry, exposed habitats in montane steppe areas.

A small-seeded group including the majority of Stellaria species and Cerastium composes another clade within Stellaria (Greenberg and Donoghue, 2011).Two clades are distinguished according to seed characters and in line with the molecular phylogeny. Few seeds (2-3 per capsule) and large seed size are regarded plesiomorphic and ancestral characters (Arabi *et al*., 2017). The small number of large-seeded Stellaria species can therefore be regarded phylogenetically old and conservative. The kinship of *S. jacutica* to other large-seeded Stellaria species such as *S. dichotoma* was already delineated in the original description of the species by Boris Schischkin (1940), who placed *S. jacutica* into the series *Dichotomae*.

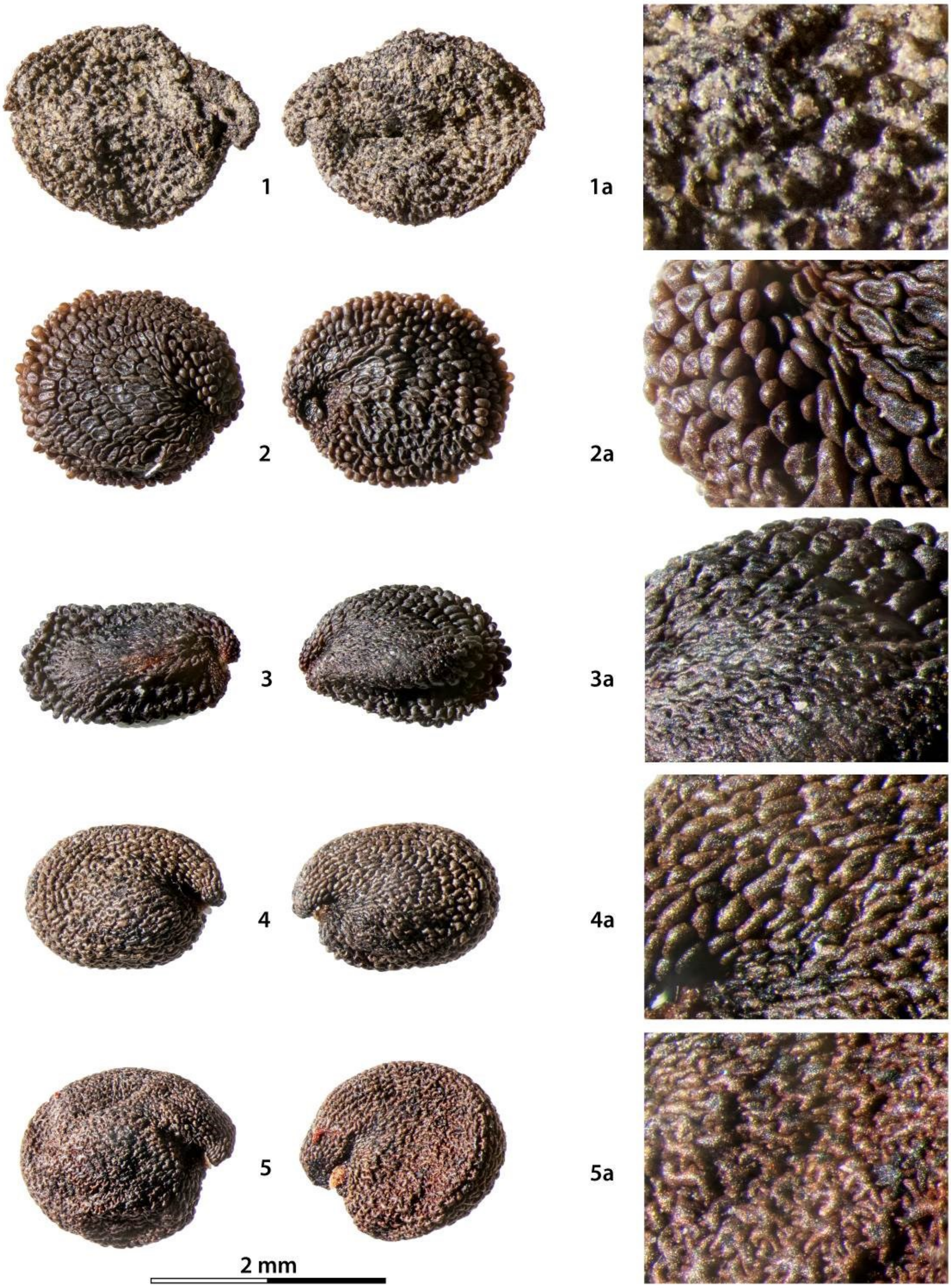

Figure 2. Photographs of seeds from large-seeded Siberian *Stellaria* species. 1. Fossil seed of *S. jacutica* from last interglacial deposits of unit III in the Batagay permafrost exposure (Ashastina *et al*., 2017, submitted). 2. Modern seed of *S. jacutica* collected near the Indigirka River bank in the Chibagalakhskiy Mountains (Cherskiy Range, Yakutia). 3. Modern seed of *S. jacutica* from the Berelyokh River bank in the Magadan Oblast. 4. Modern seed of *S. cherleriae* 5. Modern seed of *S. dichtoma.* a. Detail of seed surfaces.

S. cherleriae, *S. dichotoma* and *S. petraea* occur in South Siberia (Altai-Sayan montane region), Southeast Siberia (Dauria, Transbaikalia) and in Mongolia. *Stellaria jacutica* is occurring exclusively in Yakutia and the Far Eastern Magadan Oblast and might be considered as a vicariant of one of the South-western species. Among the species with a Southern centre of distribution, *S. cherleriae* expands furthest north-eastwards today and is sporadically still (or rather again) occurring in Yakutia (Vlasova, 2011). This species is a periglacial relict of the central Siberian taiga steppes (Antipova 2008). *Stellaria cherleriae* is related to *S. petraea* in mountainous areas. The latter migrated to the north during Saalian glacial, and resulted in a new species of *S. dicranoides* in Alaska, and a new species of *S. pulvinata* on the south Altai Mountains (Kozhevnikov, 1983). So, *S. cherleriae* is distributed geographically closest to *S. jacutica* and might be supposed to be its nearest relative.

The carpological features of both species are, however, regarded quite distinct. The seeds of *S. cherleriae* are described as wrinkled or rugose (Malyschev and Peschkova, 2003; Vlasova, 2011). In our collection (IQW, 2017), they resemble those of *S. dichotoma,* which are described as corrugate, being covered by amoeboid testa cells with sinuate margin (Arabi *et al*., 2017). The seed surface of *S. jacutica,* in contrast, is described as tuberculate and densely covered with conical papillae (Vlasova, 2011). *S. jacutica* seeds might accordingly be considered resembling those of the European *S. holostea*, which are also densely tuberculate. The papillae in *S. holostea* seeds are, however, larger and fewer than those of *S. jacutica* and besides they are arranged in regular rows (Knapp, 2006), which is not the case for *S. jacutica.* In fact, the surface pattern of *S. jacutica* seeds seems to be rather variable as is observable by comparing seeds of different parent plants or different sites. For instance, *S. jacutica* seeds at the Indigirka River bank in the Chibagalakhskiy Mountains (Cherskiy Range, Yakutia) are continuously and densely papillose (Fig. 2.2). But seeds from the Berelyokh River bank in the Magadan Oblast possess papillae only at the back (Fig. 2.3), whereas their lateral sides are covered by amoeboid plates with sinuate margin, which rather corresponds with seeds of *S. cherleriae* and *S. dichotoma*. According to carpological and ecological characteristics, the phylogenetic relationship of *S. jacutica* with the other large-seeded Siberian rock-steppe *Stellaria* (*S. cherleriae* and *S. dichotoma*) is to be presumed.

Given that all Siberian large-seeded *Stellaria* are diagnostic for steppe or tundra-steppe (*Kobresia*-meadows; Kobresietea) vegetation in montane areas, they are characteristic of cool and arid climate. Therefore, it can be conjectured that representatives of that group expanded north-eastwards during the Pleistocene cold stages (Nikitin, 2006). An event of *Stellaria* speciation during the cold stage is reported for northamerican *Stellaria laxmanni* by Böcher (1951) that could be similar to the case of *S. jacutica*.

According to Hernández-Ledesma (2015), the centre of diversity of *Stellaria* is also located in the mountains of central Asia. Nikitin (2006) reports that *Stellaria* sp. appears in the plant macrofossil record of southern part of Asian Russia in eopleistocene. Steppe communities with *Stellaria* sp. spread to the north via the Altai Mountains along the Yenisei, Ob´, and Lena Rivers (Antipova, 2008). During early Quaternary, these rivers were not blocked by ice sheets, while glaciers developed in the mountains and synchronous permafrost started to develop on Siberian plaines (Fradkina, 1995). In middle Pleistocene, Verkhoyansk Mountains experienced uplift to about 2 000 m, intermontane basins deepened, and alpine glaciers evolved (Strelkov *et al*., 1965; Smirnov, 2000). Unglaciated highlands were refugia, where genotypical changes resulting in a loss (extinctions) or gain (speciation) (Böcher, 1951).

The northern Yakutia was a refugium, harbouring the north-eastern subpopulation of large-seeded Stellaria, where it, assumedly, became isolated. This subpopulation became thus disjunctive and could have evolved independently from its south Siberian progenitors via allopatric speciation. *S.*

jacutica is diploid species (2n=26) and has close cytotaxonomic characteristics to *S. dichotoma* (Yurtsev and Zhukova, 1972). The range of *S. dichotoma* in the Altai Mountains reaches 2050 m altitude (Malyshev and Peshkova, 2003), this suggests that the expansion of *Stellaria* range might have occurred via Verkhoyansk mountain range.

S. cherleriea expanded to the north by Saalian glacial (Kozhevnikov, 1983). The Last Interglacial resulted in decreasing of the mountain glaciers and increasing in alpine vegetation cover. The treeline shifted northward to the steppe territories of Yana-Indigirka Highlands, resulting in a mosaic plant cover: *Larix* sp., *Betula* sp., *Rubus* sp., including *S. jacutica* (Kienast *et al*., 2016). At the same time, forest-steppe was flourishing on southern slopes of Verkhoyansk Mountains (Frenzel, 1968). During the next glacial (Weichselian), tundra-steppe covered Yana-Indigirka Highlands (Frenzel, 1968), divided from the Aldan River steppes by small glaciers (Siegert *et al*., 2007). Findings of *S. jacutica* in the Mylakhchin bison and the Cherskij horse at the Indigirka River correspond to Weichselian ice age (Arslanov and Chernov, 1977).

The fossil finding of *S. jacutica* in the sample stratigraphically dated to the last interglacial proves that its speciation happened prior to the late Pleistocene. This finding is thus another proof that there was no glaciation of the Yana Highlands since the middle Pleistocene and that the environmental conditions in this region, north of the Arctic Circle, remained more or less stable since then, i.e. continental and dry.

Conclusions

Presence of a steppe species seed of *S. jacutica* in permafrost sediments stratigraphically dated to the Last Interglacial suggests that speciation occurred earlier and by Eemian this species could have spread to the east – the Indigirka and Kolyma river valleys.

The Yana Highlands were already a distribution area of xerophytes at least from the Last Interglacial on. This implies a high level of warmth, or continentality in the region through the last 120 ka. The finding suggests that modern steppes in the Yana Highlands did not establish in the Holocene, but that they are Pleistocene relicts.

Chapter 5: Concluding discussion

To create a stratigraphical framework of palaeo-ecological studies, this study has outlined the sedimentological structure of the outcrop and described its stratigraphical units and their properties. It also reports the first dating results that suggest that the syngenetic permafrost sequence started to form at least during the Middle Pleistocene (Chapter 2). This supports the assumption that this unique site is of exceptional importance for palaeo-ecological and palaeo-climatological research. A detailed palaeo-vegetation reconstruction (Chapter 3), based on 45 samples processed for multi-proxy analyses, records the vegetation changes from MIS 6 to 2. Finally, analysis of the fossil find of a Yakutian endemic plant reveals that the region served as a refugium for flora and fauna during late Quaternary climatic extremes.

5.1. The Batagay permafrost outcrop – one of a kind (so far)

The Batagay megaslump is unique in several aspects. First, it is one of the few actively growing inland permafrost outcrops in the Yana Highlands. By *inl*and, it is meant that the slump is not only far from the sea coast but also unaffected directly by large rivers or lakes. Therefore, the Batagay sequence provides valuable data on terrestrial climate–vegetation interactions under a strong continental climate. As most permafrost exposures previously studied in Siberia are located along sea coasts and river banks (Chapter 1), their deposits usually include cyclic facial–lithological structures, implying that the sequences experienced changes of the depositional processes that followed the fluvial and marine regime (Katasonov, 1954). Field observations suggest that the Batagay sedimentary sequence accumulated subaerially, as supported by sedimentological and palaeo-ecological studies (Chapters 2 and 3). No aquatic plant remains were found among the macrofossil assemblages, though remains of aquatic invertebrates were identified in the samples, which suggest the former presence of small ponds nearby, but not a subaquatic depositional environment.

The prevailing sedimentary processes changed seasonally at the Batagay site: from nival deposition during winter to eluvial and aeolian deposition in summer (Chapter 2). The exposed syngenetic sequence has been deposited at least since the Middle Pleistocene (Chapter 2). Permafrost sequences of comparable age have been reported from the Arctic sea coast (e.g. Schirrmeister *et al*., 2002; Wetterich *et al*., 2009; Kienast *et al*., 2008, 2011; Tumskoy, 2012). This gives an opportunity to compare the climate history of coastal and inland sites. The general climatic trend seems to be similar over West Beringia: an ice complex of Middle Pleistocene age suggests that climate and, in consequence, mean annual ground temperatures were at least 8 °C lower than those of today (Romanovskii *et al*., 2000b). This assumption is based on the analyses of cryostructures, pollen and macrofossil assemblages in permafrost. Stable oxygen isotope ($\delta^{18}O$) analysis of ice wedges can provide valuable information on winter temperatures (e.g. Meyer *et al*., 2002; Wetterich *et al*., 2011; Opel *et al*., 2017): not an absolute winter temperature (in °C), but relative temperature information (colder/warmer than present). Comparison of $\delta^{18}O$ results of coastal outcrops and the Batagay sequence suggests that Late Pleistocene deposits accumulated under winter temperatures significantly lower than present and reconstructed MIS 3 winter air temperatures at the Batagay study site were extremely low—lower than those of coastal and central Yakutian study sites (Opel *et al*., 2018). The reconstructed LGM winter temperatures differ between coastal outcrops and the Batagay site. For example, winter temperatures at Bol´shoy Lyakhovsky Island were extremely low

(Wetterich *et al.*, 2011), while preliminary data from the Batagay suggest warmer winters than on the coast. However, this might be explained by the resolution of the ice-wedge sampling at the Batagay site, which may have missed the peak LGM wedges and needs to be constrained by additional dating (Opel *et al.*, 2018).

5.2. The Yana Highlands – refugium or not?

Only the mountainous areas of Beringia were glaciated during the late Quaternary, while the majority of the landmass remained non-glaciated and hosted high-latitude biocenoses. Substantial endemism among plants and birds, and persistence of archaic taxa suggest a special position of Beringia (Tugarinov, 1929; Sochava, 1933; Hulten, 1937). The Yana–Kolyma region has a high level of endemism among plants in northeastern Asia (e.g. Zakharova, 2011; Kozhevnikov and Zheleznov-Chukotskij, 2014). These peculiarities were regarded as evidence that several refugia existed for flora and fauna during Pleistocene climatic extremes (e.g. Giterman, 1968; Sher, 1974; Hopkins, 1972). Palynological and plant macrofossil analyses have been used to pinpoint possible refugia locations and their inhabitants (e.g. Grichuk, 1984; Kremenetski *et al.*, 1998; Brubaker *et al.*, 2005; Anderson *et al.*, 2006; Binney *et al.*, 2009). Nevertheless, precise locations of these refugia are still to be found and each fossil enhances the spatial knowledge.

5.2.1. Treeline and *fires*

The results of this study provide valuable data for attempts to detect possible tree refugia in Western Beringia. The concept of refugia originates from the observation of modern Siberian treeline dynamics and tree distribution from the palaeo-records. The modern treeline corresponds to the 10 to 12 °C July air isotherm (MacDonald *et al.*, 2008). This climate–treeline correlation is used for reconstructing past treeline positions: with increasing mean July temperature, the treeline advanced northwards, with decreasing temperature, the treeline retreated southwards. However, treeline expansion is a complex process. Open stands of single trees (often krummholz) disperse, expand and densify under appropriate climatic conditions (Kruse *et al.*, 2016). Infilling of open stands and non-wooded areas is controlled by seed or pollen dispersal and/or by clonal growth (Laberge *et al.*, 2000). Producing viable seeds depends on summer air temperature (Kullman, 2007). The pollen and seeds of Siberian larch species can disperse only short distances (Austerlitz *et al.*, 1997; Ashley, 2010). The proposed speed of modern treeline expansion in Siberia is from 2 to 10 m year^{-1} (Kruse *et al.*, 2016; Kharuk *et al.*, 2006); such slow dispersal suggests that postglacial recolonization of the northern regions was also slow. However, palaeo-records suggest a rapid range expansion. According to Huntley and Birks (1983), the postglacial migration rate of the treeline in Europe is estimated at 1–2 km year^{-1}. Data from Siberia also show rapid expansion (MacDonald *et al.*, 2000; Andreev *et al.*, 2002). The apparent contradiction between the mode and rates of dispersal can be explained by the existence of isolated refugia that served as nuclei for future recolonization (e.g. Sher, 1976; Kremenetski, 1994; Polezhaeva *et al.*, 2010).

Numerous studies based on palaeo-proxies such as pollen, macrofossils and DNA (Anderson and Lozhkin, 2002; Brubaker *et al.*, 2005; Binney *et al.*, 2009; Polezhaeva *et al.*, 2010) suggest that tree refugia were located somewhere in the Russian Far East, western Beringia and Mongolia. The data in the present study support this theory and, moreover, pinpoint one of the refugia to the Yana Highlands. Numerous needles and seeds of larch were found in the Batagay samples (Chapter 3), indicating that the Yana Highlands served as tree refugium at least since the penultimate cold stage

(MIS 6). The LIG is recorded by samples from unit III. During the LIG, annual air temperatures exceeded those at present, setting favourable conditions for establishing well-developed forest interspersed by steppes (Chapter 3). Interestingly, no macroremains of stone pine were observed from unit III. Stone pine, which presently occurs at the study site, requires a snow depth of at least 40 cm to protect itself from winter frost (Khromentovsky, 2004). Its absence in the palaeo-record suggests that winter precipitation here was less than present and/or wind velocities were greater. On the other hand, limited snow cover did not hamper larch, which is strongly cold-resistant. Permafrost limits drainage and provides accessible soil moisture in the overlying active layer, so that vegetation did not suffer from increased summer air temperatures and decreased precipitation.

Charcoal provides direct evidence of fire. Plant macrofossils and chitin remains indicate the presence of plant litter. Under warm summer conditions, dry plant litter could be flammable and ground wildfires could be widely spread by wind. The thickness of the active layer and soil drainage increases in burnt areas (Kharuk *et al*., 2011). As larch is a pyrophitic species (Sofronov *et al*., 2000), larch seedlings together with ruderal plants found in LIG deposits (e.g. *Epilobium angustifolium, Rubus idaeus*) could have benefited from fires. Periodic fires clear tree stands (producing a mosaic of open and wooded habitats), release soil nutrients (accompanied by lush regrowth of early successional stages, including ruderal species), and enhance germination of larch seeds (Kharuk *et al*., 2011). According to Kharuk *et al*. (2011), fires in north Siberia (66° N) occur every 200±51 years on average, constituting an important driver of vegetation diversity.

The shape of unit III varies along the permafrost exposure. It is a prominent thin black layer traceable all across the headwall, but in places it thickens downward to form to 5 m thick v-shaped structures. Such 'organic rich pockets' may have a fire-triggered origin (Sofronov *et al*., 2000). It is proposed that thick organic-rich accumulations correspond to the former v-shaped gullies whose modern counterparts are visible today along the top of the Batagay headwall, while the thin organic-rich layer crossing the headwall is a former ground surface.

Charcoal was less abundant in other samples of the Batagay record, albeit larch macrofossils were persistently present. The climate extreme opposite to the warm last interglacial is the cold Last Glacial Maximum. In the sample dated to pre-LGM (26 ^{14}C ka BP) we also found needles of larch. Pollen analysis showed a low concentration of larch, but such a mismatch can be explained by generally low pollen productivity of larch and poor preservation (Clayden *et al*., 1996). During the LGM, continentality was most likely intensified in Yakutia due to the exposed continental shelf. The Yana Highlands served as refugia for trees, larch in particular due to a combination of increased climatic continentality with relative warm summers, and low precipitation compensated by moisture in the active layer.

5.2.2. Steppes and *mosaic of vegetation*

As discussed above, the Yana Highlands harboured trees during several climatic extremes. According to several studies (e.g. Yurtsev, 1982; Boeskorov, 2006), such refugia also existed for steppe vegetation. The presence of fossils of steppe species within nearly all studied Batagay samples suggests that the Highlands were also refugia and nuclei for the distribution of xerophytic vegetation. The fossil record and, especially, the finding of an endemic steppe plant (Chapter 4) prove that modern extrazonal steppes of Yakutia are relicts of a formerly connected xerophytic belt. The number of endemics in floras of northern Yakutia and Chukotka is rather high (from 30 to 40%) and most of the endemics have south Asian ancestors (Zakharova, 2011; Kozhevnikov and Zheleznov-

Chukotskij, 2014). Additionally, 22 of 80 Yakutian plant endemics are steppe taxa (Zakharova, 2011), suggesting that a steppe component was prominent in the ancient vegetation. The steppe belt was fragmented by glaciers during the Pleistocene cold climatic phases (e.g. Strelkov *et al*., 1965; Velichko, 1984; Fradkina, 1995; Siegert *et al*., 2007). Xerophytic plants survived in isolated refugia, where speciation and adaptation to new environments resulted in the evolution of new species (Chapter 4, Böcher, 1951; Kozhevnikov, 1976; Comes and Kadereit, 1998; Hewitt, 1999; Willis and Whittaker, 2000).

The data from this study indicate that the dominant vegetation component in the Yana Highlands during cold stages was meadow steppe rather than tundra, as was the case on the coast. This may have been induced by climatic continentality of the region—low precipitation and a large annual temperature range during the low sea-level stands. The assemblages of plant macro and microfossils together with invertebrate remains reveal fewer tundra taxa during the Late Pleistocene at the Batagay site than records from the present coastal areas (Kuzmina, 2015; Kienast *et al*., 2005, 2008, 2011; Wetterich *et al*., 2008; Schirrmeister *et al*., 2011). For example, the percentage of tundra invertebrates within Batagay samples varied from 1 to 7%, but reached 80% in the coastal lowlands (Chapter 3). Macrofossil assemblages of the Batagay site almost lack taxa of such tundra-steppe component as *Kobresietea* communities (Reinecke *et al*., 2017), which abound in coastal lowlands (e.g. Kienast *et al*., 2005, 2011). The difference in summer air temperatures between inland and coastal areas (continentality, discussed above) might be an explanation.

To summarise, the new data support the theory of a heterogenic structure of Beringian vegetation (e.g. Yurtsev, 1968; Sher, 1974; Schweger and Habgood, 1976; Giterman *et al*., 1982; Ager, 1982; Kienast *et al*., 2011) that was clearly distinct from the homogeneous wet tundra with sporadic patches of steppe in the present-day coastlands. A mosaic structure of Pleistocene vegetation is revealed by a mixed vegetation signal from pollen, macrofossils and invertebrates and it may reflect varying micro-relief and climate settings. But there is another possible driver that could have impacted the vegetation cover in the Yana Highlands.

5.2.3. Vegetation–herbivore interactions

Herbivores were another possible driver of heterogeneity of the Pleistocene vegetation cover at the Batagay site. This assumption arises from observations of modern herbivore–vegetation interactions in Africa, where high density and large body size of herbivores produce a substantial impact on vegetation (Dublin *et al*. 1990; Owen-Smith, 1999). A similar observation experiment is currently underway in the north-eastern Siberia (Zimov *et al*., 1995).

Direct impacts of herbivores on vegetation may include physical removal of plants and, therefore, decreasing plant density and preventing one plant species from becoming dominant; and utilization of various individual plants/parts of the plants by different herbivores. *Indirect* factors include herbivores consuming dry plants, a boost of nutrient recycling; affecting primary production and dispersing seeds. Such actions arise from herbivore size and population density. Herbivore weight varies from several grams (e.g. pika) up to ton (e.g. bison, musk ox), which is important as the amount of daily herbage consumption (c) relates to the body weight (w): $C=0.09\ W^{0,75}$ (Sinclair, 1975). Hence, the larger the herbivore, the greater the amount of biomass consumed, the greater the distance roamed and the greater the impact on the vegetation. Herbivores heavier than 100 kg are regarded as megaherbivores (1 ton according to Owen-Smith, 1988) and have a tremendous impact on the vegetation. In Africa, they are called *landscape engineers* (Dublin *et al*., 1990; Owen-Smith, 1999).

Figure 5.1. (a) Bison in Ust´-Buotoma Bizonarij enclosure, central Yakutia. Black line highlights the fence of the enclosure. (b) A larch tree trunk with marks produced by bison horns. (c) Bison just before wallowing. The intensively disturbed open-ground pits contrast with the surrounding intact vegetation. (d) Bare ground of the wallowing pit; photograph from F.Kienast. All photographs were taken in July 2015 in Ust´-Buotoma Bizonarij, central Yakutia

Trampling and foraging can physically remove plants. Trampling creates open and/or bare clearings in the vegetation cover. Fragile herbaceous plants can be suppressed by trampling or wallowing. For example, bison wallow several times a day (Knapp *et al*., 1999). Taking a dust bath helps them rid annoying insects and clean their fur. This activity removes plant cover and creates a bare dust bowl 3–5 m in diameter (Knapp *et al*., 1999; personal observation, 2015, central Yakutia). The fringes of wallows are a suitable habitat for ruderal plant species. Disturbances by herbivores help to enrich species diversity (Collins and Barber, 1985). Tree stands are also affected by herbivores. According to observations of this study in central Yakutia, bison can damage trees by horn scratching and bark removal. Trees with weakened insulation and damaged xylems dry off; due to megaherbivore actions, the landscape becomes more open (Fig. 5.1). Small herbivores can also damage vegetation, though their impacts have received less attention than those of large animals. Arctic ground squirrels can effectively change the vegetation around the burrow (Wheeler and Hik, 2013). The average home-range of an arctic ground squirrel is up to 200 m around the burrow (Hubbs and Boonstra, 1998). A dense squirrel population affects the vegetation heavily within this range: caching and trampling lead to establishment of disturbance-tolerant vegetation, while burrowing itself may bury vegetation (Wheeler and Hik, 2013). Price (1971) estimated that a colony of arctic ground squirrels excavates 18 000 kg of soil per hectare per year, which creates ground instability and might affect the drainage of soil (Hall and Lamont, 2003). Hence, it is suggested here that small herbivores should be treated as small-scale landscape engineers. Feeding strategy can also directly influence vegetation patchiness. Herbivores can graze (bison, saiga, ground squirrel), browse (moose) or adopt mixed feeding strategies (musk ox) to use all available food (grasses; herbs; leaves, twigs and bark of trees and shrubs). The food diversity probably resulted in a variety of anatomical specializations of herbivores to exploit a certain food resource. Thus, several herbivore species could coexist within one range (Guthrie, 1982). Guthrie (1982) proposed a model of complementary segregation of Pleistocene herbivores on the basis of herbaceous plant diversity (Fig. 5.2a). According to his theory, small forbs and leafy grasses were consumed by saiga, short and medium grasses by bison, medium grasses by horses, large-stem grasses by mammoth, and leaves and tips of twigs by moose. The plant communities were distributed along a topographical gradient, providing spatial allocation of the herbivores (Fig. 5.2b)

Herbivores alter the vegetation *indirectly* as well. They reduce the amount of detritus and consume dry plants in winter. Therefore, they decrease the probability of ground wildfires by removing potential fuels (Bond and Keeley, 2005). In the absence of herbivores, nutrients are locked in the plants and, therefore, do not contribute to the nitrogen cycle. The digestive systems of herbivores convert plant nutrients into usable form and release them as urine and faeces. These supplementary inputs of nutrients affect plant primary production and boost growth of ruderal plants. This leads us back to the idea (e.g. Redmann, 1982; Guthrie, 1982; Zimov *et al*., 1995; Yurtsev, 2001) that this is a self-sustaining system: open landscapes and mosaic-like vegetation cover are maintained by herbivores; patchy vegetation provides palatable forage; grazing is accompanied by trampling; trampling creates open landscapes and boosts diverse vegetation.

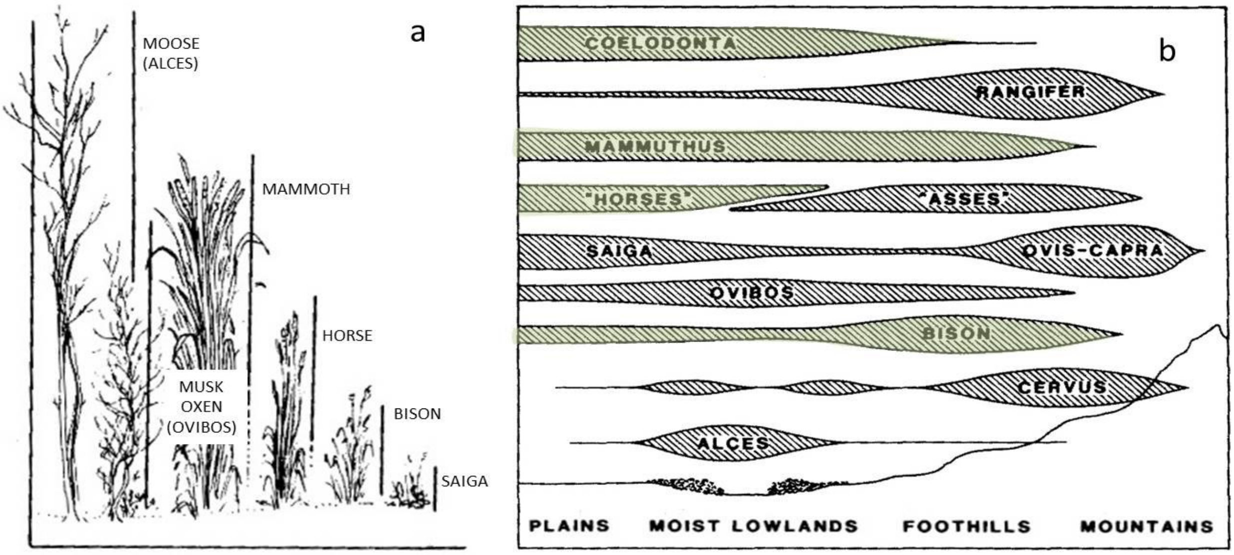

Figure 5.2. (a) Dietary specialization of herbivores on the basis of herbaceous plant diversity. (b) Foraging ranges of herbivores along the topographic gradient. Light green colour illustrates species found at the Batagay site. Pictures from Guthrie, 1982.

Present-day interactions of herbivores and vegetation can be measured, observed and described, and the same interdependencies can be applied to past interactions (Johnson, 2009). This approach requires data about past herbivore density and diversity. For example, based on counts of vertebrate bones, Zimov *et al*. (2012) estimated a herbivore biomass of 10.5 tons km^{-2} in northern Siberia, consisting typically of one mammoth, five bison, 7.5 horses and 15 reindeer per km^2. But it is difficult to obtain accurate estimates of herbivore density and diversity, because the more permafrost thaws, the more data it releases. Most likely, the animal density was spatially heterogeneous and existing calculations are speculative in terms of a minimum number of individuals but valuable in terms of herbivore diversity. Most Pleistocene herbivores were grazers, and this suggests that productive cold-adapted grassland was the key vegetation type (Guthrie, 1990). Species diversity originates from a variety of ecological niches (Whittaker, 1975; Redmann, 1982). Hereby, we have a line of evidence that a vegetation mosaic (Chapter 3) and diverse herbivore populations existed in the Yana Highlands during the Late Pleistocene (Novgorodov *et al*., 2013). One of the main questions is if we can trace the indicators of herbivore presence in the vegetation record lacking animal fossil remains.

One of the new proxies of herbivore presence is dung fungi analysis based on spores of Sordariales (*Sordaria*, *Podospora*, *Gelasinospora*) and Pleosporaleas (*Sporormiella*) (e.g. Burney *et al*., 2003; Robinson *et al*., 2005; Gill *et al*., 2009; Gill, 2014). For example, *Sporormiella* fungi reproduce exclusively in herbivore dung. The presence of these highly distinctive spores in spore–pollen assemblages is inversely proportional to the charcoal abundance in the palaeo-record (Gill, 2014). With a decrease of herbivore populations (decrease of *Sporormiella*), the plant biomass and litter increased, resulting in the intensification of wildfires (increase of charcoal abundance). The dung fungi proxy was tested on a modern bison population (Gill *et al*., 2013). This promising proxy, however, did not show impressive results for the Batagay samples. As reported by Novgorodov *et al*. (2013), the paleontological record indicates herbivore presence at the Batagay site. Nevertheless, altogether 20 spores of dung fungi were detected within four of 45 samples. Most striking was the absolute absence of dung fungi in the ground squirrel sample. The sample that contained the highest number of droppings was expected to be a "hot spot" of dung fungi, but it was not. On the contrary, spores were found in the last interglacial sample, which is rich in charcoal remains. In conclusion, the *Sporormiella* proxy should be treated with caution as the preservation of spores in permafrost sediments and their general taphonomy (e.g. the influence of fire on spore preservation) are not yet well studied and the number of detected spores is too low for quantitative conclusions.

Ruderal plant species are another proxy for herbivore presence. Ruderal plants are often halophytes at moist sites and disturbed eutrophytic habitats (e.g. Grime, 1979; chapters 3 and 5). Fire and herbivores could promote fertilization (Yurtsev, 2001; Chapter 5). Ruderal plants have several features that benefit herbivores: they have a burst of spring growth and are usually not well defended with toxic allelochemical compounds (Janzen, 1975). In order to specify how exactly large herbivores affect the vegetation, Reinecke *et al*. (in prep) performed plot analyses of the vegetation cover within and outside of enclosures in central and northern Yakutia to detect plant species that can be regarded as ruderal plants accompanying large herbivores. In the Batagay palaeo-record *Urtica dioica*, *Plantago canescens*, *Hordeum jubatum*, *Descurainia sophioides*, *Sonchis arvensis* are herbivore indicator species. Therefore, the presence of herbivores at the Batagay site can be assumed for the entire late Quaternary and securely pinpointed at least to the Last Interglacial, MIS3, pre-LGM and LGM(Chapter 3).

Box 2. Grazing at the limit – large herbivore effects on extrazonal steppes and surrounding vegetation in the extreme climate of northeastern Siberia. J. Reinecke, K. Ashastina, F. Kienast, E. Troeva, K. Wesche (in preparation).

The dietary preferences of most herbivores are well recorded in Siberia, but the exact substitution of floristic taxa as an effect of herbivores is still poorly investigated. To fill this knowledge gap, we collected and analyzed data in Yakutia, eastern Siberia. Extra-zonal grasslands there serve as a natural pasture for horses and cattle, and small mammals such as hares and ground squirrels. At the same time, Yakutia harbours two sites dedicated to the projects on rewilding large herbivores—Pleistocene Park (Zimov *et al*., 1995) and Bisonary (Reinecke *et al*., in prep.). Our study region includes five locations (two rewilding enclosures and three sites grazed by domestic livestock) that are spread along the climatic gradient from continental to maritime conditions (Fig. 5.3).

We visited two fenced grazing sites, the Pleistocene Park in northern Yakutia, close to Chersky, and the Ust´-Buotoma Bisonary in central Yakutia, along the Buotoma River mouth. Pleistocene Park was founded in 1996 to run an experiment to convert taiga vegetation to tundra–steppe through impacts of large herbivores. A small enclosure (50 ha) with one European bison and three musk oxen is surrounded by a fenced area (1600 ha) populated in July 2015 by approximately 40 horses and several moose. Pastures include taiga and large areas of floodplain meadows. Animals are fed in winter to secure their survival and built up high-density populations.

The Bisonary was established in 2006 as a part of the governmental program of reintroducing bison to Yakutia. In 2006 the Bisonary had 30 Canadian forest bison grazing in mostly secondary meadows, steppes and dark taiga. By 2015, 35 bison roamed within a 118.5 ha enclosure. Semi-wild horses grazed freely on the meadows and steppes outside the fence.

In order to study the effects of herbivores on vegetation we sampled vegetation plots sized 10 x 10m, using the Londo scale for cover abundance of plant species. The intensity of grazing by bison, horse, cattle and small mammals was calculated based on the density of droppings (in %). To determine the influence of macro- and microclimate within the sites we compiled several BIOCLIM variables (Hijmans *et al*., 2005) and calculated northerness, easterness, and heat load from field observations for each plot. Plant functional traits of the most abundant taxa were measured as well.

We carried out variation partitioning and serial partial canonical correspondence analysis (pCCA) to test the effects of each variable group on species composition: macroclimate (continentality, winter precipitation, mean summer air temperature), microclimate (slope angle and direction, heat load, easternness, northernnes) and grazing (bison, horse, cattle, small mammals). We then carried out a final pCCA with macroclimate as co-variables and microclimate and grazing as environmental variables, using interactive forward selection to find environmental variables that are significant ($p<0.05$) in explaining species composition.

Effects on species composition.

Bison: According to the pCCA (Fig. 5.4) *Chenopodium album*, *Leonurus quinquelobatus*, *Geum aleppicum*, *Plantago depressa*, *Artemisia vulgaris* and *Potentilla longifolia* relate to bison grazing. *Trifolium repens* grows on heavily trampled ground, and *Elymus repens* and *Sibbaldianthe bifurca* are dominant on drier grazed sites. *Carex supina*, *Chamaerhodos erecta*, *Linaria acutiloba, Sibbaldianthe bifurca* and *Potentilla longifolia* indicate intensive grazing in steppes.

Other herbivores: Indicators for horse grazing are more difficult to discern, but *Goniolimon speciosum* and *Koeleria pyramidata* correlate with it. Indicator species for small mammal grazing are also unclear and probably relate to the effect of slope inclination.

Effects on trait composition.

Bison grazing density is correlated with an increasing number of hemicryptophytes and therophytes, and a decreasing number of chamaephytes. Bison disturbance increases the number of defenseless plants and increases the percentage of open ground. The proportion of long-leaved plants also rises under bison grazing pressure, while relative inflorescence height tends to decrease. Slopes grazed by small mammals feature more cushions, fewer dwarf shrubs and more hairy plants.

In overall terms, vegetation, slope inclination and small mammal grazing are positively correlated with taxonomic and functional diversity indices. Heat load and horse grazing are only associated with increasing species richness. Bison grazing is associated with decreased functional diversity, but not with taxonomic diversity.

In conclusion, herbivores have little to moderate effect on vegetation across the study area. The strongest impacts are created by bison through mechanical disturbances of soils (wallowing and trampling) and woody vegetation (shrub destruction and de-barking of trees). As a result, annual weeds occur, indicating the creation of open ground and fertilization through droppings, while other species locally indicate soil compaction. Forest vegetation may locally shift to more light-demanding species. Grasslands may shift to a more xeric character in continental macroclimate and profit from litter reduction in wetter conditions. Despite these local impacts of bison, animal densities today seem to be too low to have significant effects on vegetation on the landscape scale, regardless of livestock species.

Figure 5.3. Map of the Sakha (Yakutia) Republic with five studied locations. Triangles indicate the sites grazed by domestic livestock. Circles pinpoint two rewilding enclosures: a red circle indicates Ust´-Buotoma Bisonary, a blue circle stands for Pleistocene Park. The map of the Yakutia Republic is from https://commons.wikimedia.org/wiki/File:Relief_Yakutia.png, the map of the world is from https://freeclipartimage.com/article/top-78-world-map-clip-art.

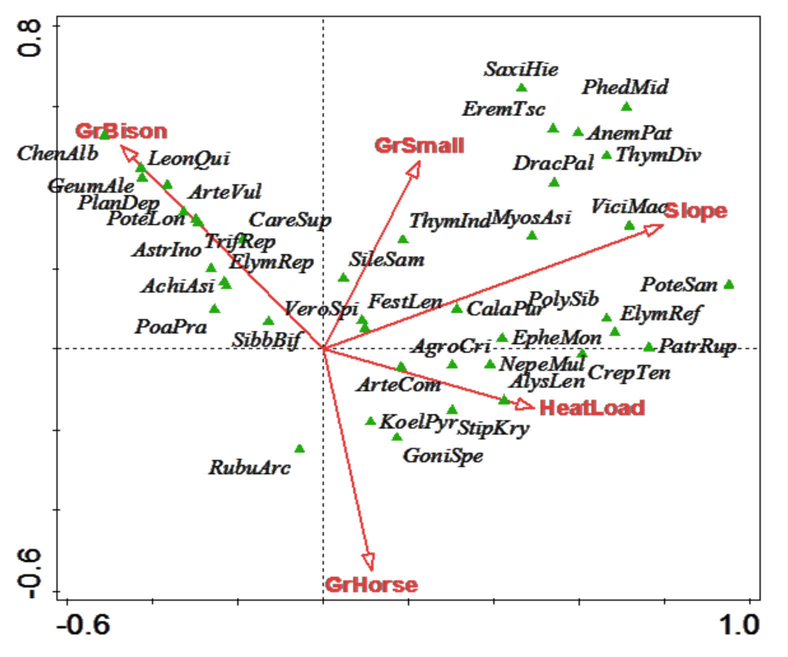

Figure 5.4. Ordination of overall data set: pCCA with macroclimate as co-variable and significant. Microclimate and grazing variables (forward selection, 499 permutations); total variance: 12.9, explained variance: 5.5%, eigenvalues: Axis1: 0.29, Axis2: 0.16; only most abundant species used and 40 best fitted species shown; species square root-transformed. Abbreviations of species names used in a detrended correspondence analysis (DCA) plot are in Appendix A.6.

Indeed, the most pronounced effect was observed in the Bisonary, where animal density was 0.29 individuals/ha. In the enclosures of the Pleistocene Park animal densities are low (0.08 individuals/ha) within the kern fence and only 0.03 individuals/ha within the outer fence. Higher densities of keystone species like the bison, as well as multiherbivore grazing systems might be needed for a more pronounced and consistent effect of large herbivores. The short duration of grazing projects and inappropriate habitats for grazing experiments could also be reasons for the observed moderate effect of herbivores on vegetation.

The Yana Highlands served as a refugium for a variety of Pleistocene herbivores (Novgorodov *et al*., 2013). The results of the current study might be interpreted to draw the following picture. The Batagay site, like most of the former Beringia landmass, is located north of the Arctic Circle, so the onset of the polar day provides enduring sunlight and warmth for plant growth. Rising spring temperatures melted the thin snow cover (Chapters 1, 3), heated the ground and stimulated growth of nutritious plants favoured by herbivores haggard after winter (Guthrie, 1982). Variations in the digestive system and foraging, specialisation on particular plant species and/or plant parts granted diversity among the numerous herbivores. Grazing and trampling actions of animals stimulated and maintained the mosaic-like structure of vegetation that was enhanced by a topographic gradient of the Highlands. Slopes of the hills/river terraces were well-drained and covered by productive meadow–steppe vegetation interspersed by larch stands. Plains and foothills with thermokarst depressions were a suitable environment for halophytic plants preferred by saiga (Guthrie, 1982). Well-drained ground, usually at the foothills in permafrost areas, was a feature important for the existence of ungulates, mammoths and burrowing animals. The small size of ungulate hooves (saiga; Martin, 1982) and great pressure per cm^2 generated by the great body mass of mammoth suggest that those animals would have sunk into moist ground of floodplains (Shilo *et al*., 1983). Polar day conditions and relief provided a variation in the temporal distribution of new growth throughout summer (Guthrie, 1982). The floodplain of the nearby Batagaika and the Yana rivers likely were fringed by forests (with e.g. *Salix*, *Alnus*) and served as a supplementary summer food source. In winter, pasture range in the floodplains were actively visited, as the frozen ground lost its boggy properties and dried floodplain grasses were actively consumed by the herbivores, supplementary food resources as bark and twigs of trees played an increased role in the foraging. Thin snow cover (caused by climatic continentality) on the hill slopes was either removed by winds or easily removed by animals and, therefore, dry meadow–steppe plants were accessible to herbivores. Water demands could be fulfilled by springs (in the Yana Highlands as reported by Shvetsov, 1951), eating snow and/or naled´ ice. Studies on wear of the mammoth tusks (Vereshchagin and Tikchonov, 1986) suggest intensive assisting in breaking river or cleft ice, likely to compensate water demand in winter. Herbivores were successful in enduring drastic continentality - long fur with a thick fat layer were perfect insulators under dry air conditions; small hooves of ungulates were perfect for roaming on firm and dry ground of the Highlands. Snow thickness of > 40 cm is critical for most herbivores (e.g. Formozov, 1990; Vereshchagin and Baryshnikov, 1982). The Yana Highlands might have served as a pasture—all year round or seasonally—for the Pleistocene herbivores due to the benefits of climatic continentality in the region. The vegetation patchiness persisted during all climatic extremes of the Late Pleistocene. Only the proportion of vegetation communities at the site changed.

5.3. Conclusions and Outlook

The Batagay permafrost sequence has a high scientific potential but, to date, has been understudied. This thesis reports sedimentological and palaeo-ecological data, adding valuable information to the environmental history of West Beringia. The perennially frozen material from the Batagay outcrop was used to reconstruct vegetation and climate history since MIS 6; as the lowermost sediments could not be sampled, the beginning of the sequence is older still. According to the data from the coastal lowlands and plant and entomological remains from Batagay, a single mammoth steppe biome existed in north-eastern Asia during the Pleistocene. The percentages of each biocenosis varied according to changes in climatic conditions and local geographical settings.

The Yana Highlands served as a refugium for larch trees and steppe vegetation during climatic extremes of the Last Interglacial and the rapid onset of the LGM. Fossil remains, both floral and faunal, suggest that the Batagay site harboured large and small herbivores. Probably, a suitable topographical gradient from floodplain to hills/high river terraces sustained pasture year-round and met dietary demands of the herbivores of the Pleistocene mammoth steppe. To elucidate the details of the Yana Highlands refugium, it would be helpful to study more permafrost outcrops in the region. Local inhabitants have observed and reported newly exposed permafrost archives in the Yana–Adycha watershed. Analysis of thick ice-rich deposits with multi-disciplinary methods could provide valuable information about environmental conditions of West Beringia.

Obtaining a reliable absolute chronology for all coastal and inland permafrost archives is challenging, as illustrated by dating of unit III at Batagay. The unit—composed of thick organic-rich sediments—is sandwiched between sediments with ages of >50 ^{14}C ka BP and <143 ^{14}C ka BP. Analysis of the organic material suggests that the vegetation cover was a mosaic of steppe vegetation interspersed with well-developed forest that contained several understories of shrubs and forbs, meaning that summers were warmer than at present. Usually, such indirect chronology would lead to the assumption that the age of this layer is the thermal maximum of the last interglacial (MIS 5e), as assumed for Bol'shoy Lyakhovsky and Oyogos Yar, at the Laptev Sea coast (e.g. Kienast *et al.*, 2008, 2011). However, new dating results of the coastal exposure provide an absolute age of 102,400±9,700 a (MIS 5c) to the previously assumed MIS 5e sediments there (Opel *et al.*, 2017). Thus, the indirect age of unit III should be treated with caution. Physical age determination and a higher dating resolution throughout all units are necessary for further investigations to fully exploit the palaeo-ecological potential of the Batagay megaslump. The AMS radiocarbon ages obtained from the site indicate that there are gaps in the sedimentological record. Likely, these gaps are caused by erosional events as a result of thermokarst processes or spatially and/or temporarily various depositional environments. Additionally, it would be useful to date all units of the sequence not only vertically but also transversely.

Wider multi-proxy investigations are needed for a more comprehensive understanding of Beringian palaeo-ecology. Combining several methods would overcome constraints of each single method. Therefore, a complex analysis of host sediments, ice wedges, fossils (macro-, micro-, charcoal, invertebrates, bones etc.) and ancient DNA would amply illustrate the environmental history of the Yana Highlands and west Beringia.

6. Summary

Climate change influences all ecosystems on all levels. Understanding the geological lessons of the Quaternary could provide valuable information for managing future environmental variations. Climatic changes in the past triggered alteration of past environments. The consequences of past alterations are widely documented in palaeontological records.

Permafrost deposits, which underlie vast areas of Asia, provide valuable information for reconstructing past ecological events. Most permafrost exposures studied in Russia are situated in the coastal lowlands of northeastern Siberia, whereas reports of inland archives are scarse. The syngenetic permafrost deposits of the Batagay outcrop preserve valuable data about the palaeo-environment of the Yana Highlands of inland Beringia. The former subcontinent of Beringia connected Eurasia and America during low sea-level stands and hosted a now extinct biome—the mammoth–steppe. To unravel the environmental history of West Beringia, the Batagay permafrost sequence was investigated.

The first part of the thesis (chapter 2) reports the first sedimentological results and provides a stratigraphical and temporal framework of the sequence. The stratigraphy comprises five units, including two ice complexes, two sand units and one woody layer. OSL and AMS dating suggest that the sequence started to accumulate during the late Middle Pleistocene and extends through the Late Pleistocene, with interruptions and erosional events. The depositional processes were climatically and seasonally controlled. Stratigraphical, cryolithological and geochronological data are significant for later palaeontological investigations.

The second part of the thesis (chapter 3) presents the palaeo-environmental reconstruction at the Batagay site during marine isotope stages (MIS) 6–2. Plant macrofossil, palynological, entomological, and charcoal analyses were performed on 41 samples from the Batagay outcrop. The palaeo-vegetation of the two climatic extremes of the Late Pleistocene—the Last Interglacial (LIG) and the onset of the Last Glacial Maximum (LGM)—are described in detail based on exceptionally fossil-rich samples. The palaeo-environmental reconstruction suggests that meadow steppes were a significant vegetation type during the LIG and formed the primary vegetation during pre-LGM. Cold-resistant tundra–steppe communities were mostly lacking at the site during the studied period, whereas larch was locally present in the Yana Highlands throughout the Late Pleistocene. Palaeontological data indicate that the Yana Highlands were a northern refugium for larch, steppe communities, and herbivores. That larch stands and meadow steppes persisted at the site from MIS 6 to 2 indicates environmental stability in the region. The magnitude of climatic continentality changed during the late Quaternary, but warm growing season and low precipitation fluctuations were insufficient to effect fundamental shifts in plant communities in the Yana Highlands.

The third part of the thesis (chapter 4) discusses the phylogeographical history of the endemic steppe plant *Stellaria jacutica* found in the LIG fossil assemblage. A finding of this single seed proves that modern steppes of the Yana Highlands did not establish as late as in the Holocene. Instead, they are relics of a formerly closed central Siberian–northeast Yakutian steppe belt.

Overall, the data obtained from the inland Batagay outcrop differ from those previously reported from coastal permafrost sections. Thus, the results of this thesis provide valuable information about the evolution of vegetation in continental settings of West Beringia.

7. Zusammenfassung

Der Klimawandel beeinflusst alle Ökosysteme der Erde auf sämtlichen Ebenen sowohl jetzt als auch in der geologischen Vergangenheit. Lehren die wir aus der Erforschung des Quartärs ziehen, könnten uns dabei helfen, mit prognostizierten Veränderungen in der Zukunft umzugehen, da Klimawandel die Umwelt der Vergangenheit ebenso geprägt hat. Die Auswirkungen dieser Veränderungen sind in natürlichen Archiven auf der ganzen Welt erhalten und dokumentiert.

Permafrost-Ablagerungen, bedecken weite Teile Nordasiens und sind eine potentiell sehr aufschlussreiche Quelle für die Rekonstruktion früherer Ökosysteme. Die meisten bisher untersuchten Permafrost-Aufschlüsse befinden sich in den küstennahen Tiefländern Nordost-Sibiriens, während Informationen aus dem Inland kaum verfügbar sind. Die syngenetischen Ablagerungen des Batagay Permafrost-Aufschlusses haben wertvolle Informationen über die Paläo-Umwelt des Jana-Hochlandes - das Inlandgebiet der einstigen Landmasse Beringia - konserviert. Beringia verband während der quartären Meeresspiegeltiefstände Eurasien mit Amerika und war Heimat für ein einzigartiges, mittlerweile verschwundenes Biom, die so genannte Mammut-Steppe. Ziel der vorliegenden Arbeit war es, die Umweltgeschichte West-Beringias auf der Basis von Untersuchungen des Batagay Permafrost-Aufschlusses zu entschlüsseln.

Im ersten Teil der Doktorarbeit (Kapitel 2) werden erste sedimentologische Ergebnisse sowie der stratigraphische und zeitliche Rahmen der Umweltgeschichte des Untersuchungsstandortes vorgestellt. Die vorliegenden Datierungen (Optically stimulated luminescence (OSL) und Radiokarbon-Alter) sowie stratigraphische Schlussfolgerungen belegen, dass die untersuchte Permafrost-Abfolge, unterbrochen durch sporadische Erosionsereignisse, seit dem mittleren Pleistozän entstanden ist. Die Ablagerungsprozesse wurden sowohl durch klimatische als auch durch jahreszeitlich bedingte Prozesse beeinflusst. Informationen über die Akkumulationsprozesse, konnten durch stratigraphische, kryolithologische und geochronologische Untersuchungen gewonnen werden und bilden die Grundlage für die paläontologische Erforschung des Permafrost-Aufschlusses.

Im zweiten Teil der Doktorarbeit (Kapitel 3) werden die Ergebnisse der Paläoumwelt-Rekonstruktion für den Zeitraum der Sauerstoff-Isotopenstadien „Marine Isotope stages“ (MIS) 6 bis 2 vorgestellt. Dreiundvierzig Proben aus den verschiedenen stratigrafischen Einheiten des Batagay Aufschlusses wurden auf pflanzliche Makrofossilien, Pollen sowie Käferüberreste und Holzkohlerückstände analysiert. Die Paläo-Vegetation der zwei klimatischen Extreme des späten Pleistozäns – das letzte Interglazial sowie das letzte glaziale Maximum – konnte auf Grundlage außergewöhnlich fossil-reicher Proben im Detail rekonstruiert werden. Die Ergebnisse zeigen, dass Wiesensteppen, analog zu Gesellschaften der heutigen Festucetalia lenensis im Norden der Mongolei und Jakutiens während des letzten glazialen Maximums dominierten und auch während des letzten Interglazials ein bedeutender Vegetationstyp waren. Kälteresistente Pflanzenarten der Tundra-Steppe (Kobresietea) wurden am Fundort für den untersuchten Zeitraum kaum gefunden. Dagegen konnten lokale Lärchenvorkommen im Jana-Hochland für das gesamte Spät-Pleistozän nachgewiesen werden. Unsere paläontologischen Daten belegen, dass das Jana-Hochland ein nördliches Refugium für Lärchen, Steppenpflanzen und Pflanzenfresser war. Die Tatsache, dass sowohl Lärchenbestände als auch Wiesensteppen im Zeitraum von MIS 6 bis MIS 2 existiert haben, belegt die Stabilität der Umweltbedingungen in der Region. Die klimatische Kontinentalität schwankte zwar im Laufe des Spätquartärs, aber aufgrund durchgängig relativ warmer Vegetationsperioden und geringer

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Der dritte Teil der Doktorarbeit behandelt die phylogeographische Geschichte der endemischen Steppenpflanze *Stellaria jacutica*, die in den Ablagerungen des letzten Interglaziales fossil nachgewiesen werden konnte. Der Fund eines einzelnen Samens ist ein weiterer Beleg dafür, dass die heutigen disjunkten Steppen des Jana-Hochlandes nicht erst im Holozän entstanden sind, sondern Relikte eines ehemals geschlossenen zentralsibirisch-nordostjakutischen Steppen Gürtels ist.

Die gewonnenen Daten aus dem jakutischen Binnenland-Aufschluss bei Batagay unterscheiden sich von publizierten Rekonstruktionen der Paläo-Umwelt im Küstenbereich Jakutiens. Die Ergebnisse dieser Doktorarbeit leisten einen wertvollen Beitrag zur Erforschung der Vegetations- und Umweltentwicklung unter den kontinentalen Klimabedingungen West Berinigias.

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10. Appendices

Appendix A.1.

Unit I represents the active layer, with a thickness varying between 1.4 and 0.85m, as measured at the end of June 2014 and is composed of fine sand. One ^{14}C AMS age of 295 years BP from a sample directly above the permafrost table, the border to Unit II, indicates the modern origin of Unit I deposits.

Unit II consists of 30–40m thick Yedoma Ice Complex (YIC) deposits, composed of silty and, primarily, sandy sediments with a layered cryostructure and enclosed by up to 6m wide syngenetic ice wedges. The mean grain size of Unit II is fine-grained sand. The YIC deposits contain evenly distributed organic material, mainly plant detritus and vertical plant roots. Occasionally, layers and chunks with higher organic content were found, e.g. a fossilized ground squirrel nest with thick bedding of grasses, including numerous identifiable plant remains. Based on droppings preserved in the nest, it was attributed to an arctic ground squirrel (*Urocitellus parryii*, confirmed by L. Maul, Senckenberg Weimar, personal information). This ground squirrel nest was sampled in detail. Additionally, 28 samples from Unit II deposits were used for the palaeontological study. Seven AMS radiocarbon ages are available for Unit II (Table 1). An age of 33±0.5 ^{14}C ka BP was obtained from material 2.05m below the ground surface (bgs) in section A. Plant material sampled from the ground squirrel nest at 4.6m bgs in section A provided a ^{14}C AMS date of 26±0.22 ka BP. In section C, dating of organic material at 12.5 and 14.5m bgs resulted in non-finite ages of > 48 and > 51 ka ^{14}C BP, whereas plant material from 18.5m bgs was dated to 49±2 ^{14}C ka BP. According to the dating results and the stratigraphical interpretation, the YIC of Unit II was deposited over a long period during the last cold stage, e.g. MIS 2, 3, and 4.

Unit III is an organic layer rich in large macroscopic plant remains, including numerous branches and twigs of woody plants, situated directly below the YIC of Unit II. This horizon is detectable across the whole outcrop, mostly as a relatively thin layer about 1.5m thick, sharply delineated from the YIC and Unit IV. In places, the layer merges into accumulations of organic matter about 5m thick that are assumed to represent the fill of former trench-like depressions resembling modern gullies. Unit III was sampled in section B in the lower part of one such pocket-like accumulation below a coarse woody layer at a depth of about 43 to 44m bgs. The three samples consist largely of organic material, including numerous seeds, fruits, and plant debris in a distorted fine bedding alternating with silty fine sand beds. Radiocarbon dating of this material resulted in an non-finite age of > 44 ka BP. We assume that Unit III represents sediments from the last interglacial (MIS 5), owing to an OSL age of 142,800±25,300 a for underlying sediments from Unit IV and its position directly below last cold-stage deposits.

Unit IV is composed of horizontally layered frozen sand that is traceable without interruption over large distances along the headwall of the outcrop. This unit is about 25 m thick and in most places it reaches almost to the bottom of the exposure. In contrast to the YIC, Unit IV is not penetrated by wide ice wedges. Exposed exclusively at the headwall, Unit IV was not accessible for systematic sampling due to the danger of objects frequently falling from the > 60m high, intensely thawing and eroding, partly overhanging permafrost wall. Only one sample was collected in situ from a ridge of frozen deposits in 50m bgs for OSL dating as well as sedimentological and palaeontological analyses. According to the sedimentological characteristics of this material, Unit IV clearly differs from the overlying Units I–III in having the largest sand fraction (70 %) and the highest carbonate content 8.2 wt % within the sequence. OSL dating resulted in several non-finite minimum ages between 93.6 and 123.2 ka BP and a finite age of 142.8±25.3 ka (Table 2, Ashastina *et al*., 2017). Thus, unit IV probably accumulated during the late Middle Pleistocene and included the Saalian cold stage (MIS 6). This attribution is supported by data from the local Yana Geological Service, who sampled the upper part of Unit IV for detailed palynological analyses (L.Vdovina, personal communication).

Unit V represents the deepest part close to the bottom of the exposure. The main part of this unit is not exposed. The unit consists of ice-rich deposits with a layered cryostructure, embedded in syngenetic ice wedges similar to deposits of the YIC (Unit II) and is therefore assumed to be an older ice complex, probably formed during the Middle Pleistocene. Since exposed only directly at the headwall, Unit V was not accessible for sampling.

Table 1. Radiocarbon dating of the selected samples from the Batagay permafrost exposure.

Lab. No.	Sample name	Depth [m b.s.l.]	Radiocarbon ages [yr BP]	Calibrated ages 2 σ 95.4% [cal yr BP]	Description
Poz-78149	19.6/A/4/1.15	1.15	295±30	459 - 347	Plant remains
Poz-79751	19.6/A/5/2.05	2.05	33 400 ± 500		Plant remains
Poz-77152	20.6/A/1/460-472	4.6	26 180 ± 220	28 965 – 27 878	*Plantago sp., Artemisia sp.*, ground squirrel droppings
Poz-79756	22.6/C/2/8.5	8.5	12 660 ± 50		Plant remains
Poz-79753	22.6/C/6/12.5	12.5	>48 000		Plant remains
Poz-79754	22.6/C/9/14.5	14.5	>51 000		Plant remains
Poz-79755	29.6/E/2/18.5	18.5	46 000 ± 2 000		*Papaver sp.*
Poz-78150	29.6/C/10/24.5	24.5	110.31 ± 0.37 pMC	1991AD - 2005AD	*Alnus sp., Vaccinium vitis-idea*
Poz-66024	21.6/B/3/2	44	>44 000		Plant remains

Table 2. OSL and IRSL measurement data and respective dating results for the luminescence samples from Unit IV of the Batagay permafrost exposure Dose rate is the effective dose rate calculated based on results from gamma spectrometry and cosmic dose rate and corrected for mineral density, sediment density, grain sizes, and water content. Water is the in situ water content and saturation water content. N is the number of aliquots. PD is the palaeo-dose based on central age model, CAM, according to Galbraith *et al.* (1999). OD is the overdispersion. Age is the calculated ages according to CAM using the in situ water content. The > sign indicates that minimum age signals were close to saturation and hence tend to underestimate luminescence ages.

Sample name	Depth [m]	Water [%]	Dose rate [Gy ka�1]	Grain size [µm]	N	PD (CAM) [Gy]	OD [%]	Age [ka]
QUARTZ								
2.7/B/1/47	47	30.1/49.6	1.3	90–160	26	123.8±6.2	26.5	> 93.6
			1.4	63–100	19	129.0±6.1	17.1	> 95.2
2.7/B/2/47	47	34.3/51.6	1.3	90–160	11	127.1±5.1	6.6	> 100.2
			1.3	63–100	11	185.3±26.1	42.9	142.8±25.3[a]
2.7/A/2/50	50	25.1/37.4	1.4	63–100	12	174.4±14.4	23.7	> 123.2
FELDSPAR								
2.7/B/2/47	47	34.3/51.6		63–100	25	274.2±3.32	3.9	210.0±23.0[b]

[a] The CAM age using the saturation water content yields 160.9_27.7 ka.

[b] The age using the saturation water content yields 236.6_24.0 ka.

Appendix A.2. Table 1. List of identified pollen with counts from the Batagay permafrost exposure.

Plant taxa	Dephts, m bgs																	
	0.2	**4.7**	**5.5**	**8.5**	**9.5**	**12.5**	**16.5**	**18.5**	**20**	**20.5**	**22**	**32**	**32.5**	**40**	**41**	**42**	**44**	**44**	**50**
Trees and shrubs																			
Abies													1						
Alnus subg. Alnobetula								1			3	18		1					
Betula						3		4		2	16	136	9	5			1		
Larix											2								
Picea						1						1	13						
Pinaceae spp.									2		1	2	3	2					
Pinus sg Diploxylon			1			1		2			4	2	1	4		2			
Salix				1		3	2	12	2		1	1	3						
Tsuga						1													
Herbs and semi shrubs																			
Amaranthaceae											3	2							
Artemisia		93	1		1	1		8	3	3	64	16	39	13	1	1		1	
Asteraceae		35	2	2		1	2	3		2	13	2	1	1	1			2	
Brassicaceae		1						4	2		2		3		1				
Caprifoliaceae subf. Valerianoideae													3						
Caryophyllaceae		165	12	1		2	2	101	1	3	59	15	20	9	1		1		
Cyperaceae		12	2	3	1	10	4	13	6	1	39	19	15	8	3	7			
Epilobium												6	6	1				1	
Ericales											1	51	173	24					
Polygonaceae														1					
Liliaceae												1	1						
Poaceae		13	1			2		5	1		7	2	1	2		1			
Ranunculaceae		1						17			7	2	3	3				1	
Rosaceae							1	1			2		2						

Appendix A.2. Table 1. List of identified pollen with counts from the Batagay permafrost exposure.

Plant taxa	**Dephts, m bgs**																		
	0.2	**4.7**	**5.5**	**8.5**	**9.5**	**12.5**	**16.5**	**18.5**	**20**	**20.5**	**22**	**32**	**32.5**	**40**	**41**	**42**	**44**	**44**	**50**
Saxifraga											6			1					
Thalictrum											5		1						
Pollen sum		**320**	**19**	**7**	**2**	**25**	**11**	**171**	**17**	**11**	**235**	**276**	**298**	**75**	**7**	**11**	**2**	**5**	**0**
Pollen concentracions (grains/gram)	N/A	**9019**	N/A	N/A	N/A	N/A	N/A	**2394**	N/A	N/A	**6459**	**7447**	**11057**	N/A	N/A	N/A	N/A	N/A	N/A
Spores																			
Huperzia											1		1						
Lycopodium			5	1	1						2	1	2	1					
Polypodiophyta		1	3	1		3	1	3	7	2	8	1	1	1					
Selaginella rupestris	1		56	42		3	10		31	2	17	1	9	1					
Sporae redep.			1								3								
Non-pollen palynomorphs																			
Arcella																		3	
Stomata of *Pinus*													2					1	
Sordaria									11		4	5						1	
Glomus			34						22					3					130
Gelasinospora											1	1							
Mycrothyrium																		3	
Podospora												1							
Valsaria									4		3								
Zygnema											1								
Sphagnum				1		1		1					1						
Total sum		**321**	**118**	**52**	**3**	**32**	**22**	**175**	**92**	**15**	**275**	**286**	**314**	**81**	**7**	**11**	**2**	**13**	**130**

Appendix A.3.

Figure 1. Pollen and spore diagram (%) illustrating four representative samples from Batagay outcrop (18.5, 22, 32, 32.5 m bgs).

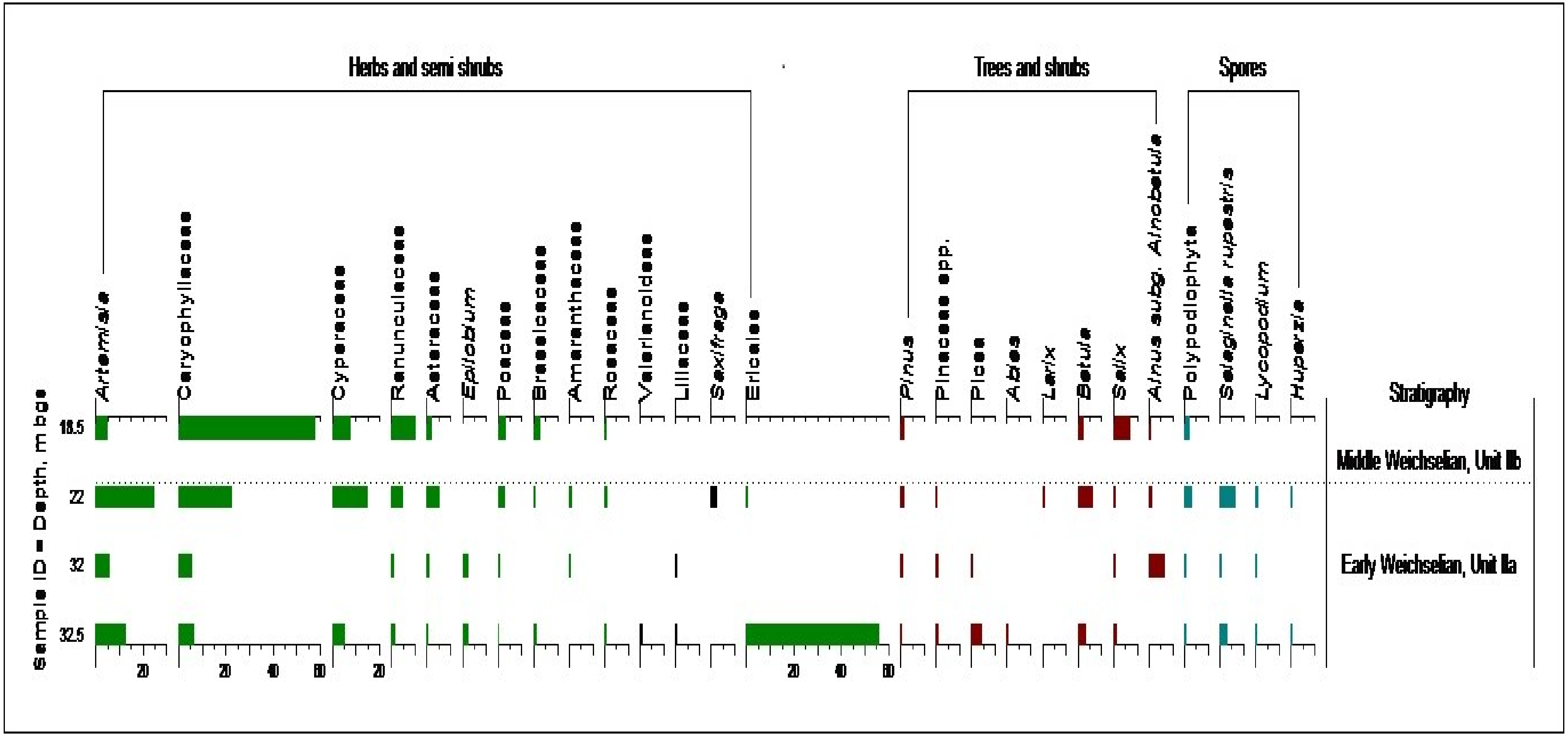
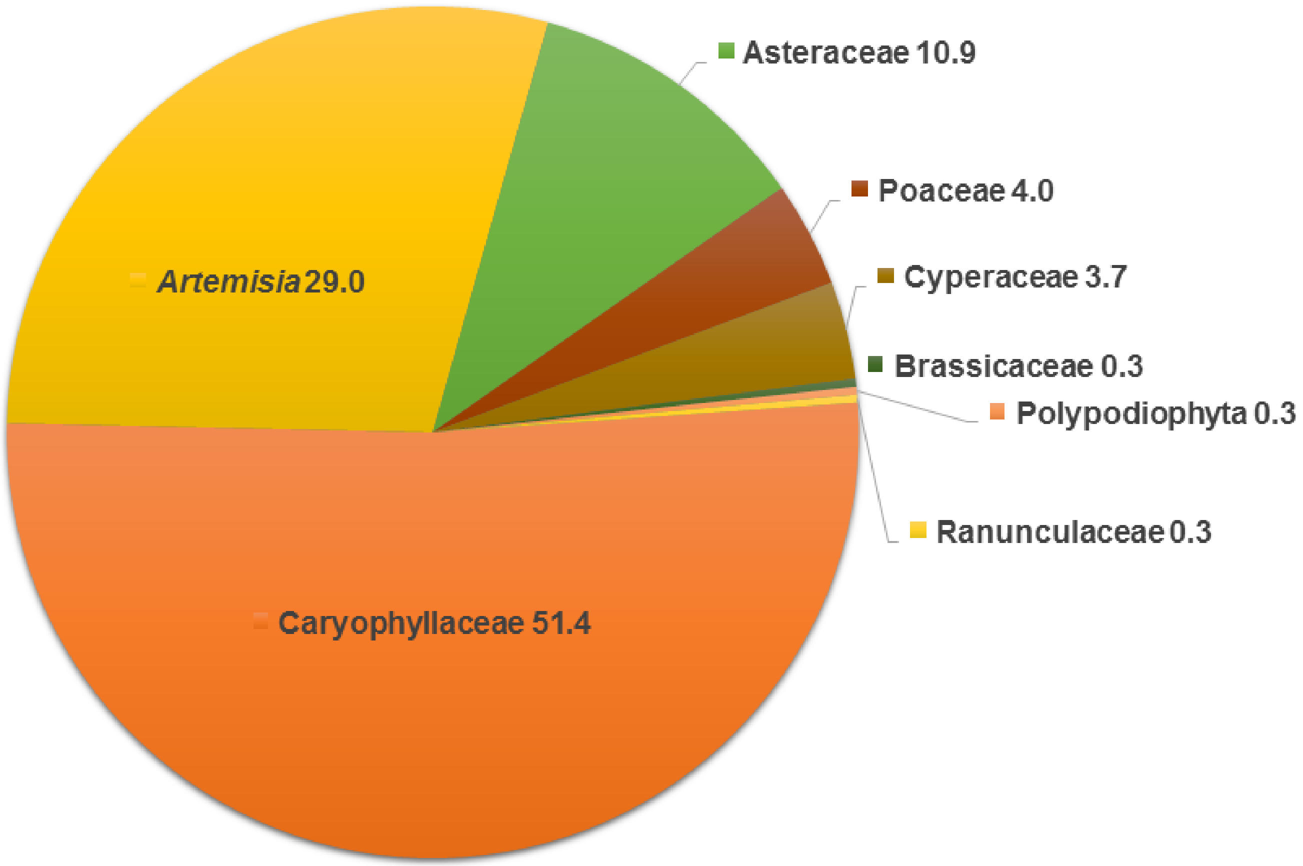


Figure 2. Pollen and spore diagram (%) illustrating palynological assemblage found in the ground squirrel nest (4.6 m bgs, 26,180±0,22 ^{14}C a BP).



Appendix A.4.

Table 1. List of identified Batagay macrofossils. Index letters identify the counted part of the plant: b – bract; c - cone/catkin; ca – capsule; cl – calyx; cr – caryopsis; cs - cone scale; cy – cypsela; f – flower; fl – floret; I – infloresсense; k – knob; l – leave; m – megaspore; mk – mericarp; n – needle; nt – nutlet; py – pyrene; s – seed; sm - sterm; sp – spiklet; v - valve of silique. Split into several depth intervals (1.1–8.5m; 9.5–18.5m; 19.5–37.5m; 38.5–50.0m). Note that species list is different for depth intervals.

	Depth, m bgs							
Plant taxa	**1.1**	**2.0**	**3.0**	**3.5**	**4.6**	**5.5**	**6.5**	**8.5**
Agropyron cristatum					3^{fl}			
Alyssum obovatum					2^{l},150^{s}			
Artemisia sp.		1^{cy}			46^{f}, 1011^{a}, 15^{fl}			1^{cy}
Betula Subgenus *Betula*								6^{Nt}
Carex duriuscula						1^{Nt}		
Chenopodium sp.			1^{s}	15^{s}				
Comastoma tenellum								
Empetrum nigrum s.l.	2^{l}				1^{l}			
Equisetum scirpoides			1^{sm}					2^{sm}
Eremogone capillaris					10^{ca}, 356^{s}			
Erigeron acris								
Eritrichium villosum					1^{s}, 10^{mk}, 45^{l}			
Festuca sp.					55^{sp}			
Juncus sp.								
Koeleria sp.					3^{fl}			
Larix gmelinii	2^{N}		1^{N}		3^{N}	5^{N}	2^{N}	
Ledum palustre								
Lepidium densiflorum								
Minuartia arctica			1^{s}					
Myosotis asiatica					1^{s}, 1^{f}, 1^{sc}			
Papaver Sect. Scapiflora				4^{s}	12^{s}	3^{s}		
Phlox sibirica					2^{sc}			
Plantago canescens					284^{s}, 800^{sc}			
Poa sp.				13^{s}	48^{fl}			
Potentilla arenosa					1^{Nt}			
Potentilla tollii								
Puccinellia sp.			1^{cr}					
Ranunculus pedatifidus subsp. *affinis*					9^{s}			
Rumex maritimus						1^{s}		
Saxifraga cf. *oppositifolia*		1^{s}						
Selaginella sibirica/rupestris	3^{m}	2^{m}						
Silene repens		1^{s}						
Silene samojedorum		2^{s}			620^{s}, 1^{cl}	1^{s}		
Smelovskia sp. (sensu Al-Shehbaz 2006)				1^{s}				
Stellaria sp.					167^{s}, 2^{cl}			
Tephroseris integrifolia					31^{s}			
Vaccinium vitis-idaea								6^{l}

Table 1 (Continued). List of identified Batagay macrofossils. Index letters identify the counted part of the plant: b – bract; c - cone/catkin; ca – capsule; cl – calyx; cr – caryopsis; cs - cone scale; cy – cypsela; f – flower; fl – floret; I – inflorescense; k – knob; l – leave; m – megaspore; mk – mericarp; n – needle; nt – nutlet; py – pyrene; s – seed; sm - sterm; sp – spiklet; v - valve of silique.

	Depth, m bgs								
Plant taxa	**9.5**	**10.5**	**11.5**	**12.5**	**13.5**	**14.5**	**16.5**	**17.5**	**18.5**
Agropyron cristatum									
Alnus alnobetula subsp. *fruticosa*									
Alyssum obovatum						2^{s}			1^{s}
Artemisia sp.						1^{cy}			
Betula Subgenus *Betula*									
Carex duriuscula									2^{Nt}
Carex sp. *tricarpellata*								1^{Nt}	
Chenopodium prostratum									
Chenopodium suecicum									
Chenopodium sp.									
Comastoma tenellum									
Corispermum crassifolium									
Corydalis sibirica									
Descurainia sophioides									
Draba sp.									
Empetrum nigrum s.l.									
Equisetum scirpoides		1^{sm}					1^{sm}		
Eremogone capillaris						5^{s}			
Erigeron acris									
Eritrichium villosum									
Fabaceae tribe *Galegeae* (cf. *Oxytropis* sp.)	1^{s}								
Festuca sp.						4^{fl}			
Frankia alni									
Hordeum jubatum									
Juncus sp.					3^{s}				
Koeleria sp.									
Larix gmelinii		1^{N}	1^{N}						
Ledum palustre				1^{l}					
Myosotis asiatica									
Papaver Sect. Scapiflora		7^{s}	1^{s}	7^{s}	6^{s}			1^{s}	250^{s}
Poa sp.					2^{fl}	10^{fl}			
Potentilla arenosa									1^{Nt}
Potentilla tollii					1^{Nt}				
Puccinellia sp.									
Puccinellia tenuiflora					2^{cr}				
Selaginella sibirica/rupestris		2^{m}			4^{m}		1^{m}		
Silene repens									
Silene samojedorum				1^{s}					127^{s}
Vaccinium vitis-idaea		1^{l}		1^{l}					2^{l}

Table 1 (Continued). List of identified Batagay macrofossils. Index letters identify the counted part of the plant: b – bract; c - cone/catkin; ca – capsule; cl – calyx; cr – caryopsis; cs - cone scale; cy – cypsela; f – flower; fl – floret; I – inflorescense; k – knob; l – leave; m – megaspore; mk – mericarp; n – needle; nt – nutlet; py – pyrene; s – seed; sm - sterm; sp – spiklet; v - valve of silique.

	Depth, m bgs								
Plant taxa	**19.5**	**25.5**	**32.5**	**33.5**	**34.5**	**35.5**	**36.5**	**36.7**	**37.5**
Alnus alnobetula subsp. *fruticosa*									3^{cs}
Artemisia sp.								1^{cy}	
Betula Subgenus *Betula*						1^{Nt}			
Carex duriuscula	8^{Nt}								
Carex sp. *tricarpellata*									1^{Nt}
Descurainia sophioides							11^{s}	12^{s}	5^{s}
Draba sp.							2^{s}	8^{s}	
Empetrum nigrum s.l.			1^{l}						
Equisetum scirpoides	3^{sm}								
Eremogone capillaris									
Erigeron acris									
Eritrichium villosum									
Fabaceae tribe *Galegeae* (cf. *Oxytropis* sp.)		1^{s}							
Festuca sp.									
Frankia alni									
Hordeum jubatum									
Juncus sp.			1^{s}	1^{s}					
Koeleria sp.									
Larix gmelinii			8^{s}, 2^{N}	1^{N}	1^{N}				
Ledum palustre									
Lepidium densiflorum							1^{v}		
Minuartia arctica									
Minuartia rubella			1^{s}						
Papaver Sect. Scapiflora	1^{s}						60^{s}		
Phlox sibirica								2^{l}	
Plantago canescens									
Poa sp.						15^{fl}	2^{fl}	5^{fl}	8^{fl}
Potentilla arenosa								4^{Nt}	
Potentilla tollii						8^{Nt}		9^{Nt}	
Puccinellia sp.									
Puccinellia tenuiflora							1^{cr}		
Saxifraga sp.			1^{s}						
Selaginella sibirica/rupestris									5^{m}
Silene repens						4^{s}	4^{s}		
Silene samojedorum									
Smelovskia sp. (sensu Al-Shehbaz 2006)							10^{s}		
Urtica dioica			1^{s}						
Vaccinium vitis-idaea				1^{l}	3^{l}				

Table 1 (Continued). List of identified Batagay macrofossils. Index letters identify the counted part of the plant: b – bract; c - cone/catkin; ca – capsule; cl – calyx; cr – caryopsis; cs - cone scale; cy – cypsela; f – flower; fl – floret; I – inflorescense; k – knob; l – leave; m – megaspore; mk – mericarp; n – needle; nt – nutlet; py – pyrene; s – seed; sm - sterm; sp – spiklet; v - valve of silique.

	Depth, m bgs							
Plant taxa	**38.5**	**40.5**	**41.5**	**42.5**	**43.0**	**43.5**	**44.0**	**50.0**
Alnus alnobetula subsp. *fruticosa*					35^{c}, 84^{cs}	9^{sc}	153^{sc}, 55^{c}	
Alyssum obovatum								6^{s}
Artemisia sp.							4^{cy}	4^{cy}
Betula Subgenus *Betula*					8^{c}, 500^{Nt}	47^{Nt}	150^{Nt}	
Betula sp.					12^{b}, 566^{Nt}	5^{b}	8^{b}, 7^{l}, 526^{Nt}, 1^{c}	
Carex duriuscula	5^{Nt}			1^{Nt}	1^{Nt}		1^{Nt}	
Carex sp. *tricarpellata*					3^{Nt}			
Chenopodium prostratum					3^{s}			2^{s}
Chenopodium suecicum					4^{s}		2^{s}	
Chenopodium sp.					1^{s}			
Comastoma tenellum							2^{s}	
Corispermum crassifolium							1^{s}	
Corydalis sibirica					1^{s}			
Descurainia sophioides								1^{s}
Draba sp.							1^{s}	4^{s}
Equisetum scirpoides					3^{sm}	8^{sm}	9^{sm}	
Eremogone capillaris								
Erigeron acris							1^{cy}	
Eritrichium villosum								4^{s}, 19^{b}
Fabaceae tribe *Galegeae* (cf. *Oxytropis* sp.)			1^{s}					3^{s}
Festuca sp.				2^{fl}			1^{fl}	19^{fl}
Frankia alni						12	3	
Hordeum jubatum					1^{fl}			
Juncus sp.							1^{s}	
Koeleria sp.								20^{fl}
Larix gmelinii		1^{N}	1^{N}		141^{s}, 3^{N}, 41^{k}, 5^{cs}	12^{s}, 200^{N}	55^{s}, 1000^{N}	7^{N}
Ledum palustre					1^{l}			1^{l}
Minuartia verna							1^{s}	
Moehringia laterifolia					7^{s}		3^{s}	
Papaver Sect. Scapiflora			1^{s}		200^{s}		2^{s}	24^{s}
Phlox sibirica		3^{l}						
Poa sp.	1^{fl}	1^{fl}		2^{fl}	1^{fl}	1^{fl}	7^{fl}	142^{fl}
Potentilla arenosa		1^{Nt}			24^{Nt}			2^{Nt}
Potentilla tollii	2^{Nt}		41^{Nt}	6^{Nt}	14^{Nt}		11^{Nt}	4^{Nt}
Puccinellia sp.							1^{cr}	2^{cr}
Rosa acicularis					6^{Nt}	1^{Nt}	1^{Nt}	
Rubus idaea					107^{py}, 1^{f}	4^{py}	106^{py}	
Salix sp.						4^{l}		
Silene repens					2^{s}			
Silene samojedorum					1^{s}			
Sonchus arvensis					4^{cy}		1^{cy}	
Stellaria jacutica					1^{s}			
Thymus serpyllum							1^{s}	
Urtica dioica					400^{s}	1^{s}	47^{s}	

Appendix A.5.

Table 1. A list of coleoptera species, identified from the Batagay samples.

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

species sample	EcoCode	20.6/A				21.6/B		22.6/C					29.6/C1/24.5	29.6/E		30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	30.6/N			2.7/A/2/50
		1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5		2/18.5	3/19.5				5/37.5	6/38.5	8/40.5	
Fam. Carabidae																						
Subfamily Scaritinae																						
Dyschiriodes melancholicus (Putz.)	pl	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subfamily Trechinae																						
Bembidion (Asioperyphus) umiatense Ldrt.	ri	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subfamily Harpalinae																						
Ttribe Harpalini																						
Dicheirotrichus mannerheimi Sahlb.	dt	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Harpalus amputatus amputatoides Mln.	ms	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. amputatus obtusus Gebl.	ms	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0
Harpalus sp.	ms	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Tribe Lebiini																						
Cymindis arctica Kryzh. et Em.	st	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	2	0	0
Cymindis vaporariorum L.?	dt	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

species sample	EcoCode	20.6/A				21.6/B		22.6/C					29.6/C1/24.5	29.6/E		30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	30.6/N			2.7/A/2/50
		1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5		2/18.5	3/19.5				5/37.5	6/38.5	8/40.5	
Tribe Pterostichini																						
Poecilus (Derus) nearcticus Lth.	dt	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pterostichus (Cryobius) brevicornis (Kby.)	mt	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	5	0	0	0	0
P. (Cryobius) pinguedineus Esch.	mt	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pterostichus (Cryobius) sp.	mt	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
P. (Lenapterus) vermiculosus Men.	mt	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. (Petrophilus) montanus (Motsch.)	dt	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pterostichus sp.	oth	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Carabidae gen. indet.	oth	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Dytiscidae																						
Subfamily Agabinae																						
Agabus sp.	aq	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Fam. Hydrophilidae																						
Subfamily Hydrophilinae																						
Hydrobius fuscipes F.	aq	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Leiodidae																						
Subfamily Leiodinae																						

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

species sample	EcoCode	20.6/A				21.6/B		22.6/C					29.6/C1/24.5	29.6/E		30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	30.6/N			2.7/A/2/50
		1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5		2/18.5	3/19.5				5/37.5	6/38.5	8/40.5	
Agathidium sp.	pl	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtoplastus irregularis Rtt.	pl	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leiodes sp.	pl	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subfamily Coloninae																						
Colon sp.	pl	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Subfamily Cholevinae																						
Cholevinus sibiricus (Jean.)	mt	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Leiodidae gen. indet.?	pl	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Staphylinidae																						
Subfamily Omaliinae																						
Tribe Anthophagini																						
Arpedium quadrum (Grav.)	pl	0	0	0	0	1	3	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0
Subfamily Tachyporinae																						
Tribe Tachiporini																						
Tachyporus sp.	pl	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subfamily Aleocharinae																						
Tribe Athetini																						
Atheta sp.	pl	0	0	0	0	7	11	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Tribe Gymnusini																						

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

species sample	EcoCode	20.6/A				21.6/B		22.6/C					29.6/C1/24.5	29.6/E		30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	30.6/N			2.7/A/2/50
		1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5		2/18.5	3/19.5				5/37.5	6/38.5	8/40.5	
Gymmusa sp.	pl	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aleocharinae gen. indet	pl	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	1	0	0
Subfamily Steninae																						
Stenus spp.	ri	0	0	0	0	4	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Subfamily Paederinae																						
Lathrobium cf. *longulum*	pl	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lathrobium sp.	pl	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staphylinidae gen. indet.	pl	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Fam. Silphidae																						
Subfamily Silphinae																						
Phosphuga atrata L.	fo	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thanatophilus sp.?	oth	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Scarabaeidae																						
Aphodius sp.	xe	0	2	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Scarabaeidae gen. indet.	oth	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Byrrhydae																						
Subfamily Byrrhinae																						
Morychus viridis Kuzm. et Kor.	ss	0	1	0	0	0	2	0	0	0	0	0	2	0	31	2	0	0	1	1	1	0
Simplocaria elongata J. Sahl	dt	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

	EcoCode	20.6/A				21.6/B		22.6/C					29.6/C1/24.5	29.6/E		30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	30.6/N			2.7/A/2/50
species sample		1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5		2/18.5	3/19.5				5/37.5	6/38.5	8/40.5	
Byrrhidae gen. indet.	oth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Fam. Heteroceridae																						
Heterocerus sp.	ri	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Bostrichidae																						
Stephanopachys substriatus Payk.	fo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Fam. Ptinidae																						
Subfamily Ptininae																						
Ptinus sp.	fo	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Fam. Melyridae																						
Troglocollops arcticus L.Medv.	ms	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Cryptophagidae																						
Subfamily Atomariinae																						
Atomaria kamtschatica Rup.	pl	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atomaria sp.	pl	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0
Subfamily Cryptophaginae																						
Cryptophagus acutangulus Gyll.	pl	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptophagus sp.	pl	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	2	
Caenoscelis ferruginea (Sahl.)	pl	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Fam. Laemopholoeidae																						

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

species sample	EcoCode	20.6/A				21.6/B		22.6/C					29.6/C1/24.5	29.6/E		30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	30.6/N			2.7/A/2/50
		1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5		2/18.5	3/19.5				5/37.5	6/38.5	8/40.5	
Leptophloeus angustulus (LeC.)	fo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Fam. Nitidulidae																						
Subfamily Meligethinae																						
Meligethes sp.	me	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Coccinellidae																						
Subfamily Coccinellinae																						
Tribe Scymnini																						
Scymnus sp.	ri	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephus bipunctatus (Kug.)	oth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tribe Coccinellini																						
Hippodamia arctica Schneid.	ri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Fam. Lathridiidae																						
Subfamily Corticariinae																						
Corticaria rubripes Man.	pl	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. ferruginea Marsh.	pl	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corticaria sp.	pl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Fam. Anthicidae																						
Anthicus ater Pz.	me	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Chrysomelidae																						

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

species sample	EcoCode	20.6/A				21.6/B		22.6/C					29.6/C1/24.5	29.6/E		30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	30.6/N			2.7/A/2/50
		1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5		2/18.5	3/19.5				5/37.5	6/38.5	8/40.5	
Subfamily Eumolpinae																						
Bromius obscurus (L)	me	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subfamily Chrysomelinae																						
Chrysolina arctica Medv.	ms	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. brunnicornis bermani Medv.	st	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Chrysolina sp.	oth	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Phaedon sp.?	me	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Subfamily Galerucinae																						
Tribe Alticini																						
Altica engstromi (Sahlb.)	me	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Brachyceridae																						
Subfamily Erirhininae																						
Fam. Curculionidae																						
Subfamily Bagoinae																						
Bagous sp.?	aq	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subfamily Entiminae																						
Tribe Otiorhynchini																						
Otiorhynchus cribrosicollis Boh.	ms	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tribe Phyllobini																						

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

species sample	EcoCode	20.6/A				21.6/B		22.6/C					29.6/C1/24.5	29.6/E		30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	30.6/N			2.7/A/2/50
		1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5		2/18.5	3/19.5				5/37.5	6/38.5	8/40.5	
Phyllobius kolymensis Kor. et Egorov ?	ms	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Phyllobius (Angarophyllobius) sp.	ms	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Phyllobius virideaeris Laich.	me	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tribe Polydrusini																						
Liophloeus tessulatus (Mull.)	me	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subfamily Hyperinae																						
Hypera diversipunctata (Schrank.)	dt	0	2	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Subfamily Lixinae																						
Tribe Cleonini																						
Coniocleonus sp.	ms	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Stephanocleonus eruditus Faust	st	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	4	0
S. incertus T.-M.	st	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
Stephanocleonus sp.	st	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Cleonini gen. indet.	ms	0	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0
Subfamily Mesoptilinae																						
Magdalis carbonaria L.?	fo	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subfamily Molytinae																						
Tribe Lepyrini																						

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

species sample	EcoCode	20.6/A				21.6/B		22.6/C					29.6/C1/24.5	29.6/E		30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	30.6/N			2.7/A/2/50
		1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5		2/18.5	3/19.5				5/37.5	6/38.5	8/40.5	
Lepyrus nordenskioeldi Faust	sh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Lepyrus sp.	sh	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subfamily Curculioninae																						
Tribe Elliscini																						
Dorytomus rufulus amplipennis Tourn.	sh	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tribe Rhamphini																						
Rhynchaenus sp.	sh	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Curculionidae gen. indet.	oth	0	0	0	1	2	4	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0
Ord. Hemiptera, subord. Auchenorryncha																						
Fam. Cicadellidae																						
Cicadellidae gen. indet.	me	0	0	0	0	0	1	0	0	0	0	3	1	0	0	0	0	0	2	1	2	1
Fam. Saldidae																						
Saldula sp.	aq	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Scutelleridae																						
Eurygaster sp.	ms	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Pentatomidae																						
Aelia sp.	ms	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fam. Tingidae																						

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

species sample	EcoCode	20.6/A				21.6/B		22.6/C					29.6/C1/24.5	29.6/E		30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	30.6/N			2.7/A/2/50
		1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5		2/18.5	3/19.5				5/37.5	6/38.5	8/40.5	
Tingidae gen. indet	oth	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ord. Hymenoptera																						
Fam. Formicidae																						
Leptothorax acervorum F.	fo	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Camponotus herculeanus L.	fo	0	0	0	0	62	10	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Hymenoptera gen. indet.	oth	2	0	0	1	8	5	0	0	0	0	0	4	0	0	0	0	2	0	0	0	0
Ord. Trichoptera																						
Trichoptera gen. indet. (larvae)	aq	0	2	0	4	0	0	2	1	4	6	4	0	0	0	0	0	0	0	0	0	0
Ord. Diptera																						
Fam. Tipulidae																						
Tipulidae gen. indet. (larvae)	oth	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Diptera gen. indet.	oth	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera gen. indet. (puparia)	oth	2	0	0	1	16	20	0	1	0	0	0	0	0	0	0	0	0	0	0	11	0
Order Ephemeroptera																						
Ephemeroptera gen. indet.	aq	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Class Arachnida																						
Ord. Oribatida																						
Oribatida gen. indet.	oth	0	0	0	0	16	39	0	1	1	0	8	25	2	18	0	3	9	5	0	1	0
Ord. Araneae																						

Table 1 (Continued). Insect ecological groups: st - steppe, ms - meadow-steppe, ss - cry-steppe, dt - dry tundra, mt - wet tundra, me - meadow, sh -shrubs, pl - plant litter, fo - forest, ri - riparian, aq -aquatic, oth - others

		20.6/A				21.6/B		22.6/C						29.6/E					30.6/N			
species sample	EcoCode	1/4.6-4.72	2/5.5	4/7.5	5/8.5	1/43	3/44	2/8.5	2/9.5	4/10.5	6/12.5	8/13.5	29.6/C1/24.5	2/18.5	3/19.5	30.6/J/3/27.5	30.6/K/1/29.0	30.6/L/4/32.5	5/37.5	6/38.5	8/40.5	2.7/A/2/50
Araneae gen. indet.	oth	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	2	0
Arachnida gen. indet.	oth	0	0	0	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Class Branchiopoda, Ord. Cladocera																						
Daphnia sp.	aq	0	1	13	0	0	0	0	5	1	0	5	0	0	0	0	0	0	1	0	0	0
Phylum Annelida, Class Clitellata Ord. Haplotaxida, Fam. Lumbricidae																						
Lumbricidae cocoons	pl	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phylum Nematoda																						
Nematoda eggs?	pl	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sum		23	8	14	7	198	137	2	10	7	8	26	54	5	60	5	10	28	17	12	23	2

Appendix A.6.

Abbreviations of species names used in a DCA plot (Figure 5 in Chapter 3, figure 5.4 in Chapter 5)

Short	**Species in modern vegetation**	**Species in palaeo-vegetation**
AgroCri	*Agropyron cristatum*	*Agropyron cristatum*
AlysObo	*Alyssum obovatum*	*Alyssum obovatum*
ArteCom	*Artemisia commutata*	*Artemisia* sp.
ArteFri	*Artemisia frigida*	*Artemisia* sp.
BetuSpe	*Betula species*	*Betula species*
CareDur	*Carex duriuscula*	*Carex duriuscula*
ChenAlb	*Chenopodium album*	*Chenopodium sp.*
ChenSpe	*Chenopodium species*	*Chenopodium species*
EmpeNig	*Empetrum nigrum*	*Empetrum nigrum*
EquiSci	*Equisetum scirpoides*	*Equisetum scirpoides*
EremCap	*Eremogone capillaris*	*Eremogone capillaris*
ErigAce	*Erigeron acer*	*Erigeron acris*
ErigAcr	*Erigeron acris*	*Erigeron acris*
EritVil	*Eritrichium villosum*	*Eritrichium villosum*
FestLen	*Festuca lenensis*	*Festuca* sp.
KoelPyr	*Koeleria pyramidata*	*Koeleria* sp.
LariGme	*Larix gmelinii*	*Larix gmelinii*
LeduPal	*Ledum palustre*	*Ledum palustre*
LepiDen	*Lepidium densiflorum*	*Lepidium densiflorum*
MinuRub	*Minuartia rubella*	*Minuartia rubella*
MinuVer	*Minuartia verna*	*Minuartia verna*
MoehLat	*Moehringia lateriflora*	*Moehringia lateriflora*
MyosAsi	*Myosotis asiatica*	*Myosotis asiatica*
MyosSpe	*Myosotis species*	*Myosotis asiatica*
PapaAlp	*Papaver alpinum*	*Papaver Sect. Scapiflora*
PhloSib	*Phlox sibirica*	*Phlox sibirica*
PlanCan	*Plantago canescens*	*Plantago canescens*
PoaAtt	*Poa attenuata*	*Poa* sp.
PoaSib	*Poa sibirica*	*Poa* sp.
PoaSpe	*Poa species*	*Poa species*
PoteAre	*Potentilla arenosa*	*Potentilla arenosa*
PoteTol	*Potentilla tollii*	*Potentilla tollii*
PuccHau	*Puccinellia hauptiana*	*Puccinellia* sp.
RanuPed	*Ranunculus pedatifidus*	*Ranunculus pedatifidus* subsp. *affinis*
RosaAci	*Rosa acicularis*	*Rosa acicularis*
RubuIda	*Rubus idaeus*	*Rubus idaeus*
SelaSel	*Selaginella sellowii*	*Selaginella rupestris*
SileRep	*Silene repens*	*Silene repens*
SileSam	*Silene samojedorum*	*Silene samojedorum*
StelJac	*Stellaria jacutica*	*Stellaria jacutica*
TephInt	*Tephroseris integrifolia*	*Tephroseris integrifolia*
UrtiDio	*Urtica dioica*	*Urtica dioica*
VaccVit	*Vaccinium vitis-idaea*	*Vaccinium vitis-idaea*

11. Declaration of Honour

I, Kseniia Ashastina, hereby declare that I am the sole author of this dissertation entitled "Palaeo-environments at the Batagay site in West Beringia during the late Quaternary". I am familiar with the relevant course of examination for doctoral candidates (Promotionsordnung) and followed its instructions. All references, assistance received and data sources used in this dissertation have been appropriately acknowledged. Furthermore, I declare that this work has not been submitted elsewhere in any form as part of another dissertation procedure, no doctoral consultant (Promotionsberater) assisted during the process of writing this thesis and no third parties have received either direct or indirect monetary benefits from the work connected to the dissertation submitted.

Jena, 28.03.2018

Ашастина

(Kseniia Ashastina)