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Late Pliocene and early Pleistocene environments of the north-eastern Russian Arctic inferred from the Lake El'gygytgyn pollen record

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Abstract

The 318 m thick lacustrine sediment record in Lake El'gygytgyn, northeastern Russian Arctic cored by the international El'gygytgyn Drilling Project provides unique opportunities allowing the time-continuous reconstruction of the regional paleoenvironmental history for the past 3.6 Myr. Pollen studies of the lower 216 m of the lacustrine sediments show their value as an excellent archive of vegetation and climate changes during the Late Pliocene and Early Pleistocene. About 3.50–3.35 Myr BP the vegetation at Lake El'gygytgyn, in nowadays tundra area, was dominated by spruce-larch-fir-hemlock forests. After ca. 3.4 Myr BP dark coniferous taxa gradually disappeared. A very pronounced environmental changes took place at ca. 3.305–3.275 Myr BP, corresponding with the Marine Isotope Stage (MIS) M2, when treeless tundra- and steppe-like habitats became dominant in the regional vegetation. Climate conditions were similar to those of Late Pleistocene cold intervals. Numerous coprophilous fungi spores identified in the pollen samples suggest the presence of grazing animals around the lake. Following the MIS M2 event, larch-pine forests with some spruce mostly dominated in the area until ca. 2.6 Myr BP, interrupted by colder and drier intervals ca. 3.04–3.02, 2.93–2.91, and 2.725–2.695 Myr BP. At the beginning of the Pleistocene, ca. 2.6 Myr BP, noticeable climatic deterioration occurred. Forested habitats changed to predominantly treeless and shrubby environments, which reflect a relatively cold and dry climate. Revealed peaks in green algae colonies (*Botryococcus*) around 2.53, 2.45, 2.320–2.305 and 2.175–2.150 Myr BP suggest a spread of shallow water environments. Few intervals (i.e. 2.55–2.53, ca. 2.37, and 2.35–2.32 Myr BP) with a higher presence of coniferous taxa (mostly pine and larch) document some relatively short-term climate ameliorations.

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1 Introduction

The Arctic is known to play a crucial, but not yet completely understood, role within the global climate system (ACIA, 2005). During the last decades the high Arctic latitudes have experienced significant warming, more dramatic than in other parts of the globe (e.g. Sundqvist et al., 2010 and references therein). Numerical observations show that Arctic temperatures have been increased by about 2 °C since 1961 (IPCC, 2007), and possible scenarios of future climate change and its regional and global consequences remain a major scientific challenge. Reliable climate projections for the Arctic, however, are hampered by the complexity of the underlying natural variability and feedback mechanisms (e.g. Christensen et al., 2007). An important prerequisite for the validation and improvement of the climate simulation scenarios is a better understanding of the long-term climate history of the Arctic.

The longest ice sheet records provide important information on the climate history, including former greenhouse gas concentrations, but in the Arctic they only cover the last glacial-interglacial climatic cycle and are restricted to the Greenland Ice Cap (e.g. NGRIP Members, 2004). Sedimentary archives from the Arctic Ocean can have a much longer time range, but their palaeoenvironmental significance often is hampered by slow, partly discontinuous formation and poor age control (e.g. Nowaczyk et al., 2001; Moran et al., 2006). In the terrestrial Arctic, continuous palaeoenvironmental archives are widely restricted to the Holocene and, in a few cases, to the last glacial/interglacial cycles, due to repeated glaciations that led to disturbance of many of the older sediments (e.g. Andreev et al., 2004, 2009, 2011; Lozhkin et al., 2007; Lozhkin and Anderson, 2011 and references therein). Where older sediments occur, they usually are fragmented and have a rather poor age control (e.g. Matthews and Telka, 1997; Ballantyne et al., 2010; Rybczynski et al., 2013).

The first widely continuous Pliocene/Pleistocene record from the entire terrestrial Arctic has recently become available from Lake El'gygytgyn, which was formed following a meteorite impact 3.58 ± 0.04 Myr ago (Layer, 2000) approximately 100 km to

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the north of the Arctic Circle in the northeastern Russian Arctic (67°30′ N, 172°05′ E, Fig. 1). Within the scope of the El'gygytgyn Drilling Project of the International Continental Scientific Drilling Program (ICDP), three holes were drilled in the center of the lake (Fig. 2) between March and May 2009, penetrating about 318 m of lake sediments and further about 200 m into impact rocks below (Melles et al., 2011, 2012).

Initial results from the upper part of the lake sediment succession, down to 2.8 Myr BP, have provided a complete record of glacial/interglacial changes in the Arctic (Melles et al., 2012). According to this study glacial settings with temperatures at least 4 °C lower than today, allowing perennial lake-ice coverage, first commenced at Lake El'gygytgyn at the Pliocene/Pleistocene boundary about 2.6 Myr ago. They gradually increase in frequency from ~ 2.3 to ~ 1.8 Myr, eventually occurring with all glacials and several stadials reflected globally in stacked marine isotope records (e.g., Lisiecky and Raymo, 2005). More variable climate parameters were reconstructed for the Quaternary interglacials. Whilst July temperature and annual precipitation around Lake El'gygytgyn during MIS 1 and MIS 5e were only slightly elevated compared to the modern values, they were about 4–5 °C and 300 mm higher than modern during MIS 11.3 and MIS 31 (Melles et al., 2012). The letter values according to GCM climate simulations could not readily be explained by interglacial greenhouse gas concentrations and orbital parameters alone; they rather are traced back to feedback mechanisms potentially involving ice sheet disintegrations in Antarctic (Melles et al., 2012).

A first compilation of data obtained from the lower part of the Lake El'gygytgyn sediment record, from ~ 3.6 to ~ 2.2 Myr ago, was provided by Brigham-Grette et al. (2013). In this study multiproxy evidence suggests extreme warmth and polar amplification during the middle Pliocene, ~ 3.6 and ~ 3.4 Myr ago, when temperatures were ~ 8 °C higher but pCO2 with ~ 400 ppm at a comparable level with today. Another important finding of Brigham-Grette et al. (2013) was that the Pliocene–Pleistocene transition at Lake El'gygytgyn was characterized by stepped cooling events and warmer than present Arctic summers until ~ 2.2 Myr ago, clearly postdating the onset of Northern Hemisphere glaciation.

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Building on the initial studies of Melles et al. (2012) and Brigham-Grette et al. (2013), this paper provides a more complete record and a more detailed discussion of climatical and environmentally driven vegetation change in the northeastern Russian Arctic between ∼ 3.6 and ∼ 2.15 Myr ago. Lake El'gygytgyn trapped pollen from a several thousand square-kilometer source area, thus providing reliable insights into regional and over-regional millennial-scale vegetation and climate changes. General geographical information concerning the geology, modern climate and vegetation cover of the study area has been described in Andreev et al. (2012) as well as other papers in this special issue and therefore is not repeated in the current paper.

2 Data and methods

The pollen record presented in this study includes a total of 750 pollen spectra from the lower part of ICDP core 5011-1 from Lake El'gygytgyn, below 101.9 m (Fig. 3a–d). Details concerning the preparation method, identification of pollen, spores and non-pollen-palynomorphs, percentage calculation, and drawing of diagram are described in Andreev et al. (2012).

To reconstruct relationships between the studied samples and their pollen taxa composition we have used non-metric Multidimensional Scaling (nMDS), an ordination method which is proved to be a robust technique for data sets with a high beta diversity and high number of zeros (Minchin, 1987). The samples were included in the analysis only if sum of counted terrestrial pollen and fern spores exceeded 150 grains; the pollen taxa were included if they occur in at least 5 samples with 0.5 %. To avoid that too many temperate trees were excluded by this threshold, the rare temperate tree taxa were summed up and included in the analyses. Bray–Curtis coefficient was used to calculate the dissimilarity matrix. A two-dimensional model was run. To avoid overcrowding only the pollen zone names (placed at the respective samples) were plotted. All analyses were carried out in R (R Development Core Team, 2011) using vegan package (Oksanen et al., 2013).

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Pollen-inferred vegetation reconstruction, performed using the quantitative method of biome reconstruction (also known as "biomization" approach), helps in objective interpretation of pollen data and facilitates data-model comparison (Prentice et al., 1996). In this approach pollen taxa are assigned to plant functional types (PFTs) and to principal vegetation types (biomes) on the basis of the modern ecology, bioclimatic tolerance and spatial distribution of pollen-producing plants. The method was tested using extensive surface pollen datasets and regionally adapted biome-taxon matrixes from northern Eurasia (Tarasov et al., 1998) and Beringia (Edwards et al., 2000), and further applied to the mid-Holocene, last Glacial (Edwards et al., 2000; Tarasov et al., 2000) and Last Interglacial pollen spectra (Tarasov et al., 2005).

In the Lake El'gygytgyn project the biome reconstruction approach has been applied to the modern and fossil pollen datasets. For details of the method, assignment of the pollen taxa to biomes and calculation of the biome affinity scores see Tarasov et al. (2013). In the current paper, quantitative biome reconstruction results obtained for the lower part of the 5011-1 core dated to ca. 3.58–2.15 Myr BP (Brigham-Grette et al., 2013; Tarasov et al., 2013) are presented for comparison with the conventional qualitative interpretation of the pollen data.

3 Results

3.1 Results of pollen analysis

A total of 750 samples have been investigated from the lower part (318–101.9 m) of the core composite from ICDP site 5011-1. A total of 135 different pollen, spore, and non-pollen-palynomorph types have been found in the studied samples (Fig. 3a–d). Almost no palynomorphs or very few were found below 300.74 m. Only in sediments accumulated between ca. 3.584 and 3.580 Myr BP pollen concentration in is slightly higher than in underlying and overlying layers. This layer contain few pollen grains of *Alnus*, *Betula*, *Larix*, *Myrica*, *Pinus*, Cyperaceae, Poaceae, Ericales; single grains of *Picea*,

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Tilia, *Salix*, *Artemisia*, Chenopodiaceae, Caryophyllaceae. The remains of *Botryococcus* and *Pediastrum* green algae colonies are also characteristic for this interval.

The pollen assemblages from 300.74 to 101.9 m) can be subdivided into 53 main pollen zones (PZ) based on visual inspection.

Single or few pollen grains of *Picea*, *Pinus* s/g *Haploxylon*, *Larix*, *Abies*, *Tsuga*, *Betula*, *Alnus*, Poaceae, Cyperaceae, Ericales, Lamiaceae and *Sphagnum* spores were found in PZ-1 (ca. 3.575–3.550 Myr BP). Pollen concentration gradually increases upwards reaching up to 9090 pollen grains/g in PZ-2 (ca. 3.55–3.48 Myr BP). The spectra are dominated by *Pinus* s/g *Haploxylon*, *Picea*, *Larix/Pseudotsuga*, *Alnus fruticosa* pollen and *Sphagnum* spores. Percentages of tree pollen (especially *Picea* and *Larix*) are the highest within the studied interval. Rather high contents of *Abies* pollen and permanent presence of pollen of some relatively thermophilic taxa, like *Tsuga*, *Carpinus*, *Corylus*, *Quercus*, *Pterocarya*, and *Carya* are also characteristic for PZ-2. Percentages of tree pollen, especially the more thermophilic ones like *Picea*, *Tsuga* and *Abies* decreased in the lower part of PZ-3 (ca. 3.48–3.45 Myr BP), while amounts of Poaceae and Cyperaceae pollen significantly increase. Higher presence spores of *Sphagnum*, *Lycopodium*, Polypodiaceae, *Sporormiella*, and *Sordaria* is also notable. PZ-4 (ca. 3.45–3.42 Myr BP) is characterized by a further decrease in *Picea* and *Abies* pollen percentages and higher contents of *Sphagnum*, *Sordaria* and *Sporormiella* spores.

Percentages of *Picea* and *Abies* increase again in PZ-5 (ca. 3.42–3.38 Myr BP), while amounts of Poaceae, and Cyperaceae pollen, as well as *Sphagnum*, *Sporormiella*, and *Sordaria* spores are significantly decreased. In PZ-6 (ca. 3.380–3.352 Myr BP) percentages of *Picea* and *Abies* decrease, while amounts of *Betula* sect. *Nanae*, *Artemisia*, Poaceae and Cyperaceae pollen significantly increase. Spores of *Selaginella rupestris* also become an important component of the pollen assemblages in this zone. PZ-7 (ca. 3.352–3.310 Myr BP) is distinguishable by disappearance of *Artemisia* pollen from the pollen assemblages and a further gradual decrease in coniferous pollen percentages.

PZ-8 (ca. 3.310–3.283 Myr BP) is remarkable by a distinct decrease in coniferous pollen percentages, while amounts of Poaceae, Cyperaceae, *Artemisia*,

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Caryophyllaceae, and other herb pollen, *Selaginella rupestris* and coprophilous fungi spores distinctly increase. Pollen concentration is rather low. PZ-9 (ca. 3.283–3.250 Myr BP) is characterized by higher contents of *Pinus* s/g *Haploxylon* and *Larix* pollen, while amounts of *Artemisia* and Caryophyllaceae pollen, *Selaginella rupestris* and coprophilous fungi spores drop significantly.

In PZ-10 (ca. 3.250–3.202 Myr BP) pollen concentrations are distinctly higher (up to 15 400 grains/g). This zone is characterized by a further increase in *Pinus* s/g *Haploxylon*, *Picea* and *Larix* pollen contents. Contents of *Artemisia*, Ericales, Caryophyllaceae pollen as well as *Selaginella rupestris* spores slightly increase as well. The zone is also notable for higher presence of *Botryococcus* green algae colonies.

Pollen concentration is even higher (up to 315 500 grains/g) in PZ-11 (ca. 3.202–3.060 Myr BP). As in PZ-10 the pollen assemblages in PZ-11 are characterized by high contents of *Pinus* s/g *Haploxylon*, *Picea* and *Larix* pollen. In addition, transparent cysts (Fig. 4) of unclear origin occur in high abundance. These cysts dominate many of the pollen assemblages upwards of the core. PZ-12 (ca. 3.060–3.025 Myr BP) shows an increase in pollen percentages of shrub taxa (*Alnus*, *Betula*), Poaceae and Cyperaceae pollen, *Selaginella rupestris* and Polypodiaceae spores, while the amounts of coniferous pollen decrease.

PZ-13 (ca. 3.025–2.988 Myr BP) is characterized by rather high contents of *Pinus* s/g *Haploxylon*, Poaceae, and Cyperaceae pollen, and *Selaginella rupestris* spores, while *Alnus* and *Betula* ones significantly decrease. PZ-14 (ca. 2.988–2.924 Myr BP) is remarkable by the disappearance of *Selaginella* spores, significant decrease in Poaceae and Cyperaceae pollen percentages and relatively high *Picea* ones. This zone can be subdivided in 2 subzones, with PZ-14b (ca. 2.957–2.924 Myr BP) being distinguishable from PZ-14a (ca. 2.988–2.957 Myr BP) by higher contents of *Alnus*, *Betula* and Ericales. PZ-15 (ca. 2.924–2.910 Myr BP) is characterized by low contents of coniferous pollen and a further increase in *Alnus*, *Betula*, and Cyperaceae pollen. In PZ-16 (ca. 2.91–2.80 Myr BP) coniferous pollen contents further increase simultaneous with the higher pollen concentration which reaches 34 300 grains/g.

PZ-17 (ca. 2.80–2.75 Myr BP) shows a significant decrease in *Betula*, Poaceae, Cyperaceae, and Ericales pollen contents. Pollen concentration reaches up to 127 130 grains/g. PZ-18 (ca. 2.75–2.74 Myr BP) is remarkable by a significant decrease in coniferous and *Alnus* pollen, while percentages of Poaceae, Cyperaceae, *Artemisia*, and Caryophyllaceae pollen and *Selaginella* spores remarkable increase. Pollen concentration in this zone is very low. PZ-19 (ca. 2.740–2.735 Myr BP) is characterized by an increase in coniferous and *Alnus* pollen, while herb percentages are greatly reduced. Pollen concentration is very high reaching 136 530 grains/g.

In PZ-20 (ca. 2.735–2.712 Myr BP) amounts of *Pinus* s/g *Haploxylon* pollen gradually decrease, while contents of Cyperaceae, Ericales and *Artemisia* pollen and *Selaginella* spores increase. Pollen concentration is much lower (up to 5070 grains/g) than in the previous zones. In PZ-21 (ca. 2.712–2.695 Myr BP) *Picea* and *Pinus* pollen are almost absent. This zone is also characterized by an increase in *Betula* and *Alnus* pollen contents and a high presence of *Botryococcus* green algae colonies. PZ-22 (ca. 2.695–2.680 Myr BP) differs from the pollen zones below and above by particularly high contents of *Pinus* and *Artemisia* pollen.

Pinus pollen disappear from the spectra again in PZ-23 (ca. 2.680–2.665 Myr BP). This zone is also notable for particularly high contents of *Gelasinospora*, *Glomus*, and coprophilous fungi spores. PZ-24 (ca. 2.665–2.646 Myr BP) pollen assemblages are characterized by a significant increase in *Pinus, Picea,* and *Larix* contents. Pollen concentration is very high (up to 98 850 grains/g). PZ-25 (ca. 2.645–2.625 Myr BP) is notable by the disappearance of coniferous pollen, while *Artemisia* pollen contents increase at the beginning of the zone and *Betula* at its upper part. In PZ-26 (ca. 2.625–2.595 Myr BP) *Pinus*, *Larix,* and Ericales pollen contents are significantly higher. This zone can be subdivided in 2 subzones. PZ-26a (ca. 2.625–2.612 Myr BP) is distinguishable by higher contents of coniferous pollen, while percentages of Poaceae and *Artemisia* pollen spores increased in PZ-26b (ca. 2.612–2.595 Myr BP).

In PZ-27 (ca. 2.595–2.588 Myr BP) coniferous pollen is almost absent. This zone is also characterized by low content of *Alnus* pollen, while percentages of *Betula*

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and Cyperaceae remarkably increase. Pollen concentration is very low (up to 4750 grains/g). PZ-28 (ca. 2.588–2.578 Myr BP) pollen assemblages differ from PZ-27 by peaks in *Larix* and *Alnus* pollen. In addition, the pollen concentration is much higher (up to 142 650 grains/g). In PZ-29 (ca. 2.578–2.556 Myr BP) is noticeable by a significant increase in Poaceae, Cyperaceae, Ericales, *Artemisia*, Caryophyllaceae, Ranunculaceae, Brassicaceae and Asteraceae pollen and *Selaginella* spores percentages. *Pinus* pollen contents are slightly increased as well.

In PZ-30 (ca. 2.560–2.552 Myr BP) *Pinus* disappear from the pollen spectra again. *Larix* pollen, in contrast show a distinct peak, while *Alnus*, Poaceae, Cyperaceae, and other herbs decrease their contents. In PZ-31 (ca. 2.552–2.533 Myr BP) *Pinus* pollen contents are significantly increased again. This zone is also notable for high contents of *Larix* pollen and *Lycopodium* spores. In PZ-32 (ca. 2.533–2.515 Myr BP) coniferous pollen disappear again. Large amounts of *Artemisia* pollen and remains of *Botryococcus* algae are also notable for this zone. PZ-33 (ca. 2.515–2.492 Myr BP) is characterized by peaks in contents of *Larix* and *Betula* pollen and *Sphagnum* spores. PZ-34 (ca. 2.492–2.479 Myr BP) is notable for a peak in *Artemisia* pollen and high contents of Poaceae.

PZ-35 (ca. 2.479–2.465 Myr BP) pollen assemblages show particularly high contents of *Selaginella*, Polypodiaceae, *Encalypta*, and *Gelasinospora* spores. The pollen concentration is rather low (up to 42 315 grains/g). PZ-36 (ca. 2.465–2.449 Myr BP) is characterized by higher contents of *Larix*, *Alnus,* and *Betula* pollen. In PZ-37 (ca. 2.449–2.428 Myr BP), in contrast *Larix* pollen is almost absent. This zone is also notable for high contents of Poaceae and *Artemisia* pollen, *Selaginella* spores and remains of *Botryococcus* colonies in its low part. In PZ-38 (ca. 2.428–2.400 Myr BP), pollen concentration is much higher (up to 112 300 grains/g). Characteristic for this zone area are also higher percentages of *Larix*, *Alnus,* and *Betula* pollen. In PZ-39 (ca. 2.400–2.383 Myr BP) *Larix* pollen contents decrease, while *Pinus* pollen appear and contents of *Sphagnum* spores increased.

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PZ-40 (ca. 2.383–2.373 Myr BP) is notable by peaks in *Pinus*, *Picea*, and *Alnus* pollen and high pollen concentration (up to 114 450 grains/g). In PZ-41 (ca. 2.373–2.368 Myr BP) *Pinus* pollen contents are much lower). In addition this pollen zone is characterized by peaks in *Artemisia* and Poaceae pollen as well as *Selaginella* spores. Coniferous pollen almost disappears from the pollen spectra after ca. 2.36 Myr BP.

PZ-42 (ca. 2.354–2.343 Myr BP) is notable for an increase in *Pinus* and *Larix* pollen contents, peaks in *Betula* and *Alnus* pollen, and rather high pollen concentration (up to 32 500 grains/g). Relatively high amounts of *Botryococcus* remains are also characteristic of the zone. In PZ-43 (ca. 2.343–2.330 Myr BP) high presence of *Botryococcus* colonies is associated with very high percentages of *Pinus* and a small peak in *Picea.* In PZ-44 (ca. 2.330–2.305 Myr BP) *Pinus* pollen contents are much lower. This zone is possible to subdivide in 3 subzones. PZ-44b (ca. 2.328–2.319 Myr BP) shows higher contents of Ericales pollen, while PZ-44a and PZ-44c (ca. 2.319–2.305 Myr BP) are notable by *Botryococcus* peaks. PZ-44c additionally shows a remarkable peak in *Artemisia* pollen.

In PZ-45 (ca. 2.307–2.290 Myr BP) *Pinus* pollen is absent but show a small peak in PZ-46 (ca. 2.290–2.270 Myr BP), which is differ from PZ-45 by the higher presence of *Larix* and Ericales pollen and higher pollen concentration (up to 183 265 grains/g). PZ-47 (ca. 2.270–2.253 Myr BP) is particularly notable for high contents in *Betula* and *Alnus* pollen and *Botryococcus* remains. In PZ-48 (ca. 2.253–2.230 Myr BP), in contrast, *Alnus* pollen content distinctly decrease, while *Artemisia* pollen, *Sphagnum* spores, and *Pediastrum* distinctly increase.

In PZ-49 (ca. 2.230–2.213 Myr BP) contents of *Betula* and *Alnus* pollen and spores of *Selaginella rupestris* increase and pollen concentration is rather high (up to 194 165 grains/g). In PZ-50 (ca. 2.213–2.198 Myr BP) and PZ-52 (ca. 2.181–2.163 Myr BP) *Pinus* pollen has small peaks, while being almost absent in PZ-51 (ca. 2.198–2.180 Myr BP), which yields the highest presence of *Betula* and *Alnus* pollen. PZ-53 (ca. 2.163–2.150 Myr BP) is remarkable by peaks in Poaceae, *Artemisia* and *Thalictrum* pollen, *Selaginella rupestris* spores as well as remains of *Botryococcus*.

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3.2 Ordination of revealed pollen spectra

The two-dimensional nMDS produced a stress value of 18.5 % (stress type 1, weak ties). The nMDS plot (Fig. 5) mirrors the different pollen zones indicating major differences in the species assemblage through time. The first axis separates tree taxa (right side) from herbaceous taxa (left side) placing most shrubs in between. Taxa grouping on the lower right side of the plot (e.g. *Tsuga*, *Abies*, *Myrica* and temperate broad-leaved taxa) are associated with samples older than 3.355 Myr (PZs 2–7) and summarize elements of temperate and cool mixed or conifer forests. Typical taiga taxa such as *Larix*, *Pinus*, *Alnus* were placed on the upper central and upper right sight, however, related pollen zones originating from time slices throughout the pollen record younger than 3.2 Myr. Dry tundra and steppe elements (e.g. *Thalictrum*, *Artemisia*, Brassicaceae) and typical moist tundra elements and dwarf shrubs (Cyperaceae, Ericales, *Betula*, *Alnus*) are placed in the lower right part and the center of the plot, respectively. This indicates that the inferred pollen taxa relationships reflect their composition in modern vegetation types. The strong change between neighboring pollen zones occur. This is also obvious from the trends in the plots of the first and second axis through time (Fig. 5).

3.3 Biome reconstruction

Biome reconstruction results suggest that six main vegetation types dominated in the Lake El'gygytgyn area during the studied interval (Fig. 6). The types include not only boreal grass-shrub vegetation (i.e. tundra and cold steppe), cold deciduous forest and taiga growing in the eastern and north-eastern Siberia today, but also cool conifer forest and cool mixed forest biomes representing warmer climate regions of the southern Russian Far East. The reconstruction of the latter biomes is particularly noticeable for the lower part of the record (older than 3.37 Myr), although taiga and cold deciduous forest are also frequently reconstructed between 3.355 and 2.564 Myr. Tundra first appeared as the dominant vegetation type around 3.367 Myr ago. Two long intervals with

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dominated arctic tundra vegetation occurred around 3.367 and 3.305–3.273 Myr ago. The biome reconstruction shows a general trend in the vegetation evolution towards colder and drier environments. However, as suggested by the reconstructed fluctuations in the pollen taxa percentages and in the dominant biome scores, this process was not gradual. Biome reconstruction results are further used for the interpretation and discussion of the past environments together with other available records (for details see Tarasov et al., 2013).

4 Interpretation and discussion

4.1 Environmental conditions before 3.6 Myr BP

There are only a few data about environmental conditions before 3.6 Myr BP, obtained from a number of floodplain outcrops in the Enmyvaam River valley, south of the El'gygytgyn Lake basin (Belyi et al., 1994; Minyuk et al., 2006; Glushkova and Smirnov, 2007 and references therein). The sediments are paleomagnetically dated to Gauss chron (3.6–2.5 Myr BP) by Minyuk et al. (2006). They are overlain by the so-called, chaotic impact horizon, containing spherules, whose origin is connected to the El'gygytgyn impact event (Minyuk et al., 2006; Glushkova and Smirnov, 2007). Hence, it is very likely that studied sediments were accumulated shortly before the impact event, about 3.6 Myr BP.

The sediments contain numerous remains of trees (*Larix*, *Betula*, *Alnus*) and shrubs (*Pinus pumila*, *Alnus fruticosa*). Moreover, an extinct thermophilic shrub, *Aracispermum jonstrupii* (Myricaceae) has been found. Revealed pollen assemblages are dominated by *Pinus* s/g *Haploxylon*, *Picea*, *Abies*, *Betula,* and *Alnus* with rare pollen of more thermophilic taxa like *Tsuga*, *Myrica*, *Carpinus*, *Corylus*, *Quercus*, *Juglans, Ulmus*, *Ilex*, and *Acer* (Belyi et al., 1994; Minyuk et al., 2006). Thus, pollen and macrofossil data reflect that forests with pine, spruce, birch, alder, and some thermophilic trees were growing in the study area shortly before 3.6 Myr BP. Climate was much warmer than today: mean January temperatures are estimated to be −13–17 °C (at least 15° higher than modern) and mean July temperatures −14–17 °C (ca 8–10° higher than modern) (Glushkova and Smirnov, 2007).

Other early/Middle Pliocene pollen records from Chukotka and north-eastern Siberia (e.g. Fradkina, 1983, 1988; Fradkina et al., 2005a, b and references therein) also document that larch-spruce-birch-alder-hemlock forests were broadly distributed in north-eastern Siberia. The early-Middle Pliocene pollen and macrofossils records in eastern Beringia (central and northern Yukon, Alaska) show that mixed boreal forests with *Pinus*, *Abies*, *Larix, Pseudotsuga*, *Betula*, and *Alnus* also dominated the local vegetation of that region (Schweger et al., 2011 and references therein). The Middle Pliocene pollen record from Baikal Lake shows that mixed coniferous (*Pinus*, *Abies*, *Larix, Tsuga*) forests with some broadleaved taxa (*Quercus*, *Tilia*, *Corylus*, *Juglans*) were widely spread in southern Siberia (Demske et al., 2002).

4.2 Environmental conditions before ca. 3.575 Myr

Unfortunately, pollen, spores, and non-pollen-palynomorphs are almost completely absent in the studied lacustrine sediments accumulated before ca. 3.575 Myr BP. The absence of palynomorphs can be explained by two main reasons. First, plant communities as well as fertile soils that have existed in the study area before the impact event were likely destroyed in vast distances in and around the crater directly by the event and by following provoked fires. It is difficult to estimate the duration of natural vegetation recovery after such global natural catastrophe. But taking in consideration that not only the vegetation itself, but most probably also fertile soils were completely destroyed around the impact crater, the recovery processes might take many thousands years. Gradual increase of pollen content in PZ-I (ca. 3.575–3.55 Myr BP), where pollen concentration is extremely low, well coincides with such interpretation. However, the second and probably more important reason why we do not find many pollen grains below 299.54 m is the high sediment accumulation rate and weak pollen preservation in the lacustrine sediments during the initial phase of the lake formation. The rare

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pollen grains, which could be wind-transported from the further distance, were most likely mechanically and chemically destroyed because of active processes in the initial lake basin.

Thus, we are very limited in the information concerning the initial vegetation succession between the impact event and ca. 3.575 Myr BP. One exception is the short interval (ca. 3.5835 to 3.5800 Myr BP). Pollen presence is notable higher (although pollen concentration remains very low, < 300 grains/g) in the sediments dated to this interval. The revealed pollen assemblages reflect an initial stage of forestation. Forests with alder, birch, larch, possibly with few spruce and lime dominated in the area or in the close vicinity. The relatively numerous remains of *Botryococcus* and *Pediastrum* colonies reflect that green algae started to colonize the initial lake which was rather shallow during this interval.

4.3 Environmental conditions ca. 3.575–3.520 Myr

A few or single pollen grains of *Picea*, *Pinus* s/g *Haploxylon*, *Larix*, *Abies*, *Tsuga*, *Betula*, *Alnus*, *Populus*, *Salix*, Poaceae, Cyperaceae, Chenopodiaceae, Ericales, *Plantago*, *Artemisia*, *Saxifraga*, Fabaceae, Cichoriaceae, Rosaceae, Lamiaceae and spores of *Sphagnum*, Polypodiaceae, were found in the sediments dated ca. 3.575–3.550 Myr BP (PZ-1, Fig. 3a and b). These pollen data can be used for the paleoenvironmental interpretation only very carefully. Nevertheless, it is notable that the spectra from the bottom part of the zone contain more pollen of potential pioneer taxa from Chenopodiaceae, *Artemisia*, *Plantago*, *Saxifraga*, Cichoriaceae, and some others, while tree pollen types are more common in the upper part, which is also characterized by a higher pollen concentration. We may suggest that the revealed pollen spectra reflect the initial succession in the lake area: herb-dominated pioneer habitats where more common before ca. 3.55 Myr BP and gradually replaced by woody communities upwards.

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4.4 Environmental conditions ca. 3.55–3.48 Myr

Tree pollen percentages in the sediments formed 3.55–3.48 Myr ago (PZ-2, Fig. 3a) are relatively high. High contents of *Abies* pollen, the permanent presence of pollen of relatively thermophilic taxa, like *Tsuga*, and singe founds of pollen of broad-leaved taxa, like *Carpinus*, *Quercus*, *Corylus*, *Carya*, *Pterocarya*, are also characteristic (Fig. 3a and b). It is unlikely that broad-leaved taxa might have grown in the lake vicinity but, however, the presence of their long-transported pollen points to warm regional and over-regional climate conditions.

Contents of *Larix/Pseudotsuga* pollen type are the highest during the studied records and probably reflect the dominance of larch in the region. However, it is also possible that these pollen grains are at least partly produced by *Pseudotsuga* (Douglas fir). This suggestion is indirectly supported by very high pollen percentages of spruce and fir (up to 35 % and 8 % subsequently) as well as the presence of relatively thermophilic taxa pollen.

Pines were also numerous in the local vegetation. It is difficult to conclude whether pollen of *Pinus* s/g *Haploxylon* type was produced by tree pines (e.g., modern trees belonging to this subgenus and growing in Siberia and southern Far East are *P. sibirica* or *P. koraiensis*) or by shrub pine (e.g., broadly distributed today in the north-eastern and southern Siberia, Kamchatka, northern Japan *P. pumila*). Taking in consideration the high contents of *Picea* and *Abies*, we may assume that a high proportion of the *P.* s/g *Haploxylon* pollen was produced by tree pines. However, the relatively high content of *Alnus fruticosa* pollen show that shrub alder was common in the regional forests and most likely stone pine also has grown in the area, especially in higher elevations. Furthermore, rather high content of *Sphagnum* spores reflects broad distribution of open wetlands.

The published Pliocene pollen records from Chukotka and north-eastern Siberia (e.g. Fradkina, 1983, 1988; Giterman, 1985; Kyshtymov et al., 1988; Volobueva et al., 1990; Fradkina et al., 2005a, b and references therein) also document that forests with larch,

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spruce, birch, alder and hemlock were broadly distributed in the area at least until the end of Early Pliocene.

The relatively high-resolution Pliocene pollen record from Lake Baikal (Demske et al., 2002), which reflects rather favorable environmental conditions between 3.57 and 3.47 Myr BP is also in a good agreement with our data.

Thus, our pollen data along with published environmental records show that climate conditions in the study area at about 3.52–3.48 Myr BP were the warmest during the studied time intervals. Permafrost still was absent in the area, but there are first evidences for seasonally frozen sediments (Sher et al., 1979). In line with the qualitative interpretations of the regional botanical records, the biome reconstruction (Fig. 6) also indicates boreal forests in the region and suggests the predominance of boreal trees and shrubs and taiga-like vegetation during the colder intervals, whilst participation of cool temperate trees and shrubs in the vegetation was more pronounced during the warmer intervals leading to reconstruction of cool conifer forest.

4.5 Environmental conditions ca. 3.48–3.45 Myr BP

A significant decrease in tree pollen percentages especially the more thermophilic ones like *Picea*, *Tsuga* and *Abies* at about 3.48 Myr BP (PZ-3, Fig. 3a) points to harsher environmental conditions than during the previous interval. Open habitats (increased Poaceae and Cyperaceae pollen percentages) became more common in the vegetation. Significant amounts of coprophilous fungi spores (primarily *Sporormiella*, *Sordaria* and *Podospora*) indirectly point to the presence of numerous large herbivores in the lake vicinity (Baker et al., 2013), thus confirming common open habitats. However, the rather high percentages of *Larix/Pseudotsuga* and *Pinus* pollen reflect that pine-larch-*Pseudotsuga* (?) forests were broadly distributed in the area. A further decrease in *Picea* and *Abies* pollen percentages at about 3.45 Myr BP (PZ-4, Fig. 3a), while contents of *Sphagnum*, *Sordaria* and *Sporormiella* spores increased reflect a further deforestation.

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Thus, we may assume that, although coniferous (mostly pine, larch and spruce) forests dominated the regional vegetation, open and partly treeless grassland habitats were also common in the landscape during the interval, which coincides well with the MIS MG8. Climate conditions became cooler and probably wetter (increase in *Sphagnum* spore contents) than during the previous interval, but dryer episodes also regularly occurred. The revealed environmental changes might be associated with climate fluctuations documented in the Kutuyakh Suite sediments broadly distributed in north-eastern Russia (including Chukotka), which are paleomagnetically dated between 3.4 and 1.8 Myr (Laukhin et al., 1999; Fradkina et al., 2005a, b). Larch-birch-spruce forest for the early Kutuyakh, tundra vegetation for the Middle Kutuyakh, and open larch-birch forests-tundra vegetation during the late Kutuyakh were reconstructed for north-eastern Siberia based on pollen assemblages (Giterman, 1985; Fradkina et al., 2005a, b). Environmental records from northern Yakutia also demonstrate a gradual vegetation change towards tundra and the expansion of larch-birch forests during the Kutuyakh interval (Grinenko et al., 1998).

The unconsolidated fluvial-lacustrine deposits that accumulated in the Enmyvaam River valley above the chaotic impact horizon yield pollen spectra, which suggest mosaic vegetation with open grasslands and coniferous forests with birch and alder trees (Glushkova and Smirnov, 2007). Birch and alder shrubs alternating with wetlands along rivers during the interval also attributed to the Kutuyakh (Belyi at al., 1994). However, the previously published regional paleobotanical records are very fragmented, poorly dated, and thus, cannot be directly compared with our record. On the contrary, the lacustrine pollen data from Lake Baikal (Demske et al., 2002), which reflect drier and colder episodes around 3.47 and 3.43 Myr BP are well comparable with the environmental fluctuations inferred from the Lake El'gygytgyn record.

The biome reconstruction (Fig. 6) demonstrates greater variations in the vegetation communities. As in the earlier part of the record, cool conifer and taiga forests are often reconstructed. However, colder phases are marked by the predominance of cold deciduous forest. The cool mixed forest reconstruction (twice in the middle part of this

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interval) suggests the presence of cool temperate broad-leaved taxa somewhere close to the lake, and thus indicates warmest climate of the whole record.

4.6 Environmental conditions ca. 3.42–3.39 Myr BP

The pollen spectra, which accumulated in the period 3.42–3.39 Myr BP (PZ-5, Fig. 3a and b) reflect a further increased presence of spruce and especially fir in the area, thus pointing to relatively warm climate conditions. The remains of fir twig (identified by V. R. Filin, Moscow State University) found in the sediments dated about 3.4 Myr BP directly confirm the presence of fir in the lake vicinity. Dark coniferous forest with spruce, pine, and fir dominate the regional vegetation. Higher presence of *Myrica* pollen and pollen of long-distance-transported broad-leaved taxa (*Carpinus*, *Corylus*, *Juglans*, *Tilia*) also confirm warmer climate. Another important peculiarity of the PZ-5 pollen assemblages is the permanent presence (sometimes up to 3 %) of *Gelasinospora* spores. *Gelasinospora* species are mainly fimicolous, but also carbonicolous and lignicolous. Their spores reach the highest frequencies in the highly decomposed buried peats, which contain burned woody remains and charcoals (van Geel, 2001). Therefore, rather high content of their spores may point to a higher frequency of fire events.

According to records from the Canadian Arctic, which were dated to 3.4 Myr BP, forest likely extended to the coast of Arctic Ocean (Schweger et al., 2011). The reconstructed mean annual temperatures were $+19\,^{\circ}$C warmer than today and summer growing temperatures were in the range of $+14\,^{\circ}$C (Ballantyne et al., 2010). These estimations are close to the climate reconstructions for PZ-5 based on our pollen record (Brigham-Grette et al., 2013).

4.7 Environmental conditions ca. 3.39–3.31 Myr BP

Significant decreases in *Picea* and *Abies* pollen percentages and increases in dwarf birch, and especially herbs (mainly Poaceae, Cyperaceae and *Artemisia*) after 3.38 Myr BP (PZ-6, Fig. 3a) reflect significantly colder and drier climate conditions.

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This interval coincides well with MIS MG4. *Selaginella rupestris* (indicator of dry environments) spores became an important component of the pollen assemblages as well. The revealed spectra indicate that pine-larch forests dominated the vegetation, but open, herb-dominated habitats also were common around the lake.

After 3.352 Myr BP (PZ-7, Fig. 3a, b) a further disappearance of tree pollen from the spectra accompanied by increase in herbs and spores reflect that environmental conditions became worse. The increase of *Selaginella rupestris* contents document very dry climate conditions. The disappearance of *Artemisia* indicates that steppe-like habitats with *Artemisia* were less common than before. Decreased spruce and dwarf birch pollen contents, along with increased contents of coprophilous fungi spores, suggest the presence of treeless habitats in the area. Significant amounts of coprophilous fungi spores (primarily *Sporormiella*, *Sordaria* and *Podospora*) in the sediments indirectly point to the presence of grazing animals in the lake vicinity and also confirm that open habitats were common in the study area.

The biome reconstruction (Fig. 6) shows the first appearance of tundra as a vegetation type in the study region, thus confirming notable climate deterioration. However, boreal vegetation continuously dominated the landscape.

The revealed pollen assemblages can be compared with pollen spectra in till sediments of the northeastern Chukotka Peninsula. These spectra reflect a significant cooling occurred about 3.5–3.2 Myr ago during the so-called Zhuravlinean Glaciation, the first local glaciation, when mountain glaciers extended into the lowlands (Laukhin et al., 1999; Fradkina et al., 2005b). However, the age control on these sediments is very poor. Pollen-based climate reconstructions using the so-called information-statistical method (Klimanov, 1984) suggest mean July temperatures of ca. 14–18 °C, January ones – of about −25–18 °C, and annual precipitation in the range of 425 to 500 mm (Laukhin et al., 1999). These estimations rather well correlate with climate reconstructions based on our pollen record (Brigham-Grette et al., 2013).

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4.8 Environmental conditions ca. 3.310–3.283 Myr BP

Low pollen percentages of coniferous in PZ-8 (Fig. 3a, b) and increased percentages of Poaceae, Cyperaceae, *Artemisia*, Caryophyllaceae, Brassicaceae, Ranunculaceae, Rosaceae and other herb pollen, as well as *Selaginella rupestris* and coprophilous fungi spores reflect that mostly treeless tundra- and steppe-like vegetation dominated during this interval which is synchronous with MIS M2. Although very pronounced changes in the pollen assemblages point to dry and cold climate conditions similar to those during the Late Pleistocene, relatively high pollen contents of alder, birch, pine, and larch show that tree and shrubby vegetation also survived in the area, probably in more protected localities. High contents of *Sphagnum* spores indicate the existence of wetlands in the lake vicinity.

Large amounts of coprophilous fungi spores indirectly imply a permanent presence of numerous grazing herds (bison, mammoth, horse) around the lake, thus confirming that open habitats became broadly distributed in the study area. Interestingly this episode corresponds to the so-called Mammoth paleomagnetic subchron.

The climate M2 interval at Lake El'gygytgyn well coincides with colder and drier climate conditions revealed from the Baikal record (Demske et al., 2002). Generally, the revealed pollen assemblages reflect a mosaic character of the vegetation. The M2 interval might also be linked to the final (coldest) stage of the Zhuravlinean Glaciation recorded in eastern Chukotka that is supposed to have occurred 3.5–3.2 Myr ago (Laukhin et al., 1999; Fradkina et al., 2005b).

The existing terrestrial and marine records also provide consistent evidences for an intensification of continental glaciations in the Northern Hemisphere during the Middle Pliocene (e.g. Matthiessen et al., 2009 and references therein). Therefore, we suggest dry and cold environments reconstructed from PZ-8 pollen assemblages are simultaneous with the coldest stage(s) of the Zhuravlinean Glaciation traced in eastern Chukotka. Environmental records from eastern Beringia also indicate more open forest conditions and the existence of permafrost (ice wedge casts) at about 3 Myr (Schweger

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et al., 2011 and references therein). In the biome reconstruction (Fig. 5) this interval is marked by a continuous dominance of tundra and absence of forest biomes.

4.9 Environmental conditions ca. 3.283–3.200 Myr BP

A distinct increase of coniferous pollen percentages (mostly *Pinus* s/g *Haploxylon*) at about 3.283 Myr BP (PZ-9, Fig. 3a) reflects the dominance of pine stands in the region. The pollen spectra also contain *Larix* and *Picea* reflecting that pine-larch-spruce forests dominated the area between ca. 3.283 and 3.250 Myr BP. The pollen assemblages of PZ-10 (ca. 3.250–3.202 Myr BP) contain rather large amounts of alder, grass and other herb pollen such as *Artemisia*, Ericales, Caryophyllaceae, Chenopodiaceae pollen as well as *Selaginella rupestris* and coprophilous fungi spores. Thus, open herb-dominated habitats were more common again in the landscape than during the previous interval, pointing to the drier climate conditions. Our data well coincide with colder and drier climate conditions revealed from the Baikal record around 3.26 Myr ago (Demske et al., 2002).

Rather high amounts of coprophilous fungi spores (mostly *Sordaria*) in the Lake El'gygytgyn record indirectly show that grazing animal were still numerous, although in a reduced abundance. Small peaks of *Botryococcus* green algae colonies suggesting to a lower lake level are also notable until ca 3.2 Myr BP. This boundary well coincides with the upper boundary of the paleomagnetic Mammoth subchron (Brigham-Grette et al., 2013; Nowaczyk et al., 2013).

Large amounts of *Alnus fruticosa* pollen in PZ-10 show that shrub alder was the most common shrub in the local forests. We may also imply that pollen of *Pinus* s/g *Haploxylon* was at least partly produced by shrub pine (*P. pumila*), which may cover higher elevations as nowadays in south-eastern Siberia. However, a better subdivision of pine pollen produced by trees and by shrubs it is not possible.

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4.10 Environmental conditions ca. 3.20–3.06 Myr BP

After ca. 3.20 Myr BP (PZ-11, Fig. 3a) spruce again became a more important component in the local forests reflecting further climate amelioration. A significant decrease of Poaceae and Cyperaceae pollen and *Sphagnum* spores contents, as well as the disappearance of coprophilous fungi spores from the pollen assemblages reflect that open habitats decreased in the vegetation. A higher presence of *Myrica* pollen and pollen of long-distance-transported broad-leaved taxa such as *Carpinus*, *Corylus*, *Juglans*, and *Tilia* (Fig. 3b) also points to warmer climate conditions during the interval. Climate reconstructions based on our pollen record show that temperature of the warmest month might have reached 16–17 °C (Brigham-Grette et al., 2013).

Generally, the interval 3.20–3.06 Myr, which coincides well with the PRISM interval (Dowsett et al., 2010) was not as warm or wet as it was between 3.58 and 3.40 Myr (PZs 1–5). However, it is also notable that the reconstructed temperatures of the warmest month during the 3.20–3.06 Myr interval are ca. 1.5 °C warmer as in multi-model simulations of the Pliocene Model Intercomparison Project (Haywood et al., 2013).

PZ-11 interval at least partly may coincide with the top of the Pliocene Beaufort Formation at Meighen Island in the Canadian Arctic, which was dated to 3.2 Myr. This formation contains two- and five needle pines with beetle assemblages suggesting minimum and maximum season temperatures +10 to +15 °C warmer than today (Elias and Matthews, 2002; Schweger et al., 2011). Boreal forests at this time stretched from 60 to 80° N and included pine taxa, which are absent in the modern Alaska and Yukon forests (Matthews and Telka, 1997).

In the Lake El'gygytgyn sediments deposited since ca. 3.087 Myr BP numerous small (ca. 12–15 µm in diameter) globose and transparent macrofossils, often with an S-shaped furrow occur (Fig. 4). This type has been described as the so-called *Coccus nivalis* from the alpine lacustrine and peaty sediments by Klaus (1977). There, concentration of these cysts reaches more than 300 000 cm^3 in the Weichselian sediments, but their numbers drastically decreased in the early Holocene deposits (Klaus, 1977;

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Schultze, 1984). The cysts in Lake El'gygytgyn are also similar to type 128B of van Geel (2001 and references therein), but spines are missing by our specimens.

Most likely the cysts are hypnozygote spores of algae from *Chlamydomonas* genus, which commonly produce thick-walled cysts under environmental unsuitable conditions (e.g. van den Hoek et al., 1995). Such hypnozygote spores might be produced by the so-called snow-algae from *Chlamydomonas* or *Chloromonas* genera (T. Leya, Fraunhofer IBMT and R. Below, University of Cologne, personal communication, 2013).

The snow-algae are common in snow and ice fields in arctic and alpine regions around the world (e.g., Kol, 1968; Müller et al., 1998; Gorton and Vogelmann, 2003; Remias et al., 2010 and references therein). Many *Chlamydomonas* species are also numerous under aquatic conditions. Their cells and resting hypnozygotes are often responsible for the blood-red color seen on surfaces of snow fields and at the bottoms of desiccated rock pools and bird baths. They are known to produce and rapidly accumulate their cysts under unfavorable environmental conditions. Müller et al. (1998) reported that small (ca. 10 µm), round cysts were the most common type in snow surface samples from Svalbard. Moreover, such cysts are very common in modern pollen samples collected from surface ice and snow fields in the coastal areas of West Siberia (Vasil'chuk and Vasil'chuk, 2009, 2010) or at the North Pole (Ukraintseva et al., 2009). Unfortunately, the identification of such small, round cells in the pollen slides is problematic and they are often reported in the pollen records as spores of green mosses (the so-called Bryales). Such "Bryales" are very often reported in palynological assemblages of Quaternary deposits in Russian literature being interpreted as green moss spores however, their real origin remains uncertain.

Thus, we regard it as rather likely that the numerous cysts found in the El'gygytgyn lacustrine sediments were produced by snow algae. Snow algae are known to be well adapted to a rather narrow temperature range around 0 °C with optimum growth conditions below 10 °C (Müller et al., 1998). The presence of numerous hypnozygotes in the El'gygytgyn sediments younger than ca. 3.087 Myr BP (upwards 163.5 m core depth), therefore may indirectly reflect a longer persistence of large snow fields in the study

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area during the cyst-dominated intervals. Air temperatures are supposed to have varied between 0 and 10 °C during their growing season (spring).

At the end of PZ-11, at about 3.08 Myr BP during the paleomagnetic Kaena subchron (Nowaczyk et al., 2013), a significant increase of dwarf birch and herb pollen contents occurred simultaneous with a decrease in coniferous contents. This suggests a climate deterioration that may coincide with MIS G20. At the same time, a peak of herbs (especially *Artemisia*) is also documented in the pollen record from Lake Baikal (Demske et al., 2002).

4.11 Environmental conditions ca. 3.06–2.99 Myr BP

In the sediments deposited ca. 3.060 and 3.025 Myr ago (PZ-12, Fig. 3a) higher contents of shrub taxa (*Betula* sect. *Nanae*, *Alnus fruticosa*), Poaceae and Cyperaceae pollen, *Selaginella rupestris* and Polypodiaceae spores appear, while tree pollen percentages are significantly reduced, reflecting broader distribution of open treeless habitats in the study area. Such changes point to colder and drier climate conditions in the region. Similar climatic conditions are reflected in the Baikal pollen record by an increase in spores of *Selaginella rupestris* around 3.03 Myr ago (Demske et al., 2002).

Around 3.025 Myr contents of birch and alder shrub pollen significantly decrease in the spectra BP (PZ-13, Fig. 3a), while pine, spruce and larch ones increase. Hence, pollen spectra document that pine-larch forest with some spruce trees was the most common vegetation type between ca. 3.025 and 3.010 Myr BP. The subsequent climate amelioration is also reflected in the Baikal pollen record, which shows a distinct increase in *Tsuga* pollen at that interval (Demske et al., 2002).

Increased shrub and herb pollen contents as well as *Selaginella rupestris* spores show that open treeless habitats became common in the study area again after 3.01 Myr BP, coinciding with the onset of the MIS G20. Open treeless habitats, where grazing mammals were more common than before, are also suggested by higher contents of coprophilous fungi (*Sordaria*).

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4.12 Environmental conditions ca. 2.988–2.910 Myr BP

The interval ca. 2.988–2.924 Myr BP (PZ-14a, Fig. 3a) is remarkable by the disappearance of *Selaginella* and coprophilous fungi spores from the pollen assemblages, and significantly decreased Poaceae, Cyperaceae contents, while *Picea* shows relatively high contents. The increase of coniferous pollen percentages imply that forests with pines, larch, spruce, and probably some fir became dominant in the regional vegetation pointing to a significant amelioration of environmental conditions. Rather favorable climate conditions before ca 2.94 Myr ago are documented in the Baikal pollen record as well (Demske et al., 2002).

Low contents of coniferous pollen and a further increase in *Alnus*, *Betula*, Poaceae, Cyperaceae, and Ericales pollen after ca. 2.957 (PZ-14b, Fig. 3a) point to some climate deterioration. Between 2.924 Myr and 2.910 Myr BP (PZ-15; Fig. 3a) climate conditions became even worse, as reflected by the disappearance of coniferous taxa from the vegetation. The revealed deterioration of climate conditions well coincides with the onset of an intensified Northern Hemisphere glaciation during the Late Pliocene, which is dated between 3.0 and 2.9 Myr BP (Matthiessen et al., 2009 and references therein).

4.13 Environmental conditions ca. 2.91–2.80 Myr BP

After 2.91 Myr BP (PZ-16, Fig. 3a) further increases in coniferous, Cyperaceae and Ericales pollen percentages reflect that the climate conditions became wetter and warmer. The climate amelioration is also suggested by an increase in the long-distance transported pollen influx. Pine-larch forest with some spruce dominated the regional vegetation. In understory of the forest and around the lake alder, birch, hearth shrubs and grass-sedge communities were also common. Some increase in willow, Caryophyllaceae, sage, *Saxifraga* and other herb pollen percentages at 2.85–2.83 Myr BP, along with a decrease in pine percentages points to drier and colder climate during that period. This short-term climate deterioration may coincide with MIS G10 and a phase of

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reduced *Tsuga-Picea* moist forests that documented in the Baikal pollen record around 2.89–2.68 Myr (Demske et al., 2002).

4.14 Environmental conditions 2.800–2.735 Myr BP

Generally, environmental conditions between 2.800 and 2.735 Myr BP (PZ-17, Fig. 3c) were similar to those in the previous interval, but larch became more common in the forests, while birch and hearth shrubs were significantly decreased in the vegetation cover. Open grass-sedges-herb communities are also decreased. These changes point to a dominance of dense larch forests with shrub pine and alder around the lake. Climate conditions were slightly colder than before.

A remarkable decrease in coniferous and *Alnus* pollen percentages between 2.75 and 2.74 Myr BP (PZ-18, Fig. 3c), while percentages of Poaceae, Cyperaceae, *Artemisia*, and Caryophyllaceae pollen and *Selaginella* spores increased reflects an interval when steppe-like communities dominated around the lake and very dry climate conditions occurred. This climate deterioration can coincide with MIS G8.

A further increase in coniferous and *Alnus* pollen ca. 2.74 Myr BP (PZ-19, Fig. 3c) points to the disappearance of open, steppe-like vegetation from the lake area. Favorable climate conditions are also reflected by a very high pollen concentration during this time.

4.15 Environmental conditions 2.735–2.695 Myr BP

Coniferous gradually decrease from pollen assemblages accumulated after 2.735 Myr BP (PZ-20, Fig. 3c), while contents of birch, grass, Caryophyllaceae, and especially sage, increase. These changes show that forests disappeared from the vegetation, while open steppe- and tundra-like habitats became more common in the area. The implied climate deterioration towards much drier and colder conditions coincides with MIS G6. It may also coincide with build-up of regional ice caps in north-western

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Canada and an early Cordilleran ice sheet, which certainly took place between 3.00 and 2.58 Myr, but most likely started at 2.74 Myr (Duk-Rodkin et al., 2010).

Climatic deterioration culminated between 2.710 and 2.695 Myr BP, as reflected by the absence of pine and spruce pollen, while shrub alder and dwarf birch increased and contents of herb pollen remain high, (PZ-21, Fig. 3c). Such pollen assemblages reflect that open herb and dwarf shrub communities dominated the vegetation reflecting very cold and dry climate conditions. Significant climate deterioration after 2.71 Myr was also reconstructed from the pollen record of Lake Baikal, in particular by the almost complete disappearance of hemlock pollen (Demske et al., 2002). Rather numerous remains of *Botryococcus* green algae colonies in the sediments from Lake El'gygytgyn furthermore point to shallower environments in the lake.

4.16 Environmental conditions 2.695–2.665 Myr BP

Between 2.695 and 2.680 Myr BP (PZ-22; Fig. 3c) rather high presence of pine pollen reflects some amelioration of the climate conditions and a retreat of pine to the local vegetation. However, high contents of sage pollen suggest a rather dry climate. Larch forest with stone pine, shrubby alder and birch were alternated with open, steppe-like habitats.

Further disappearance of *Pinus* and *Larix* pollen from the spectra between 2.680 and 2.665 Myr BP (PZ-23, Fig. 3a), coinciding with the MIS G4, indicates a further deterioration of the climate. Open tundra and steppe-like herb communities dominated the local vegetation. Higher contents of *Gelasinospora*, *Glomus,* and coprophilous fungi spores point to presence of grazing animals around the lake during this interval and disturbed soils. Dry forest types also expanded in Baikal region after 2.68 Myr BP (Demske et al., 2002).

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4.17 Environmental conditions ca. 2.665–2.625 Myr BP

A drastic increase in *Pinus*, *Picea*, *Larix* and Ericales pollen contents between 2.665 and 2.646 Myr BP (PZ-24, Fig. 3c) reflects dominating larch-spruce-pine forest in the Lake El'gygytgyn region. The climate conditions became much warmer and wetter.

The interval ca. 2.645–2.625 Myr BP (PZ-25, Fig. 3c) is notable by the wide disappearance of coniferous pollen from the spectra, pointing to significant climate deterioration. Open steppe-like herb communities dominated the local vegetation. The increase of *Gelasinospora* and coprophilous fungi spore contents reflects presence of numerous grazing animals around the lake. Higher presence of saga pollen at the beginning of the interval reflects a dry climate. Contents of *Betula* sect. *Nanae* and *Alnus fruticosa*, Cyperaceae pollen and *Sphagnum* spores show a significant increase after 2.635 Myr BP, which reflects that birch and alder shrubs were common in the region, thus hinting on much wetter climate conditions. This period of dry and wet climate may be correlated with onset of the most extensive Cordilleran ice sheet in north-western Canada, which dated to at 2.64 Myr BP (Hidy et al., 2013).

4.18 Environmental conditions ca. 2.625–2.595 Myr BP

Around 2.625 Myr BP (PZ-26, Fig. 3c) the pollen spectra reflect a retreat of pine and larch in the area, presumably as a consequence of some climate amelioration. This suggestion is confirmed by an increase in Ericales pollen. The climate conditions became much warmer and wetter than during the previous interval. However, rather high pollen contents of sage, Caryophyllaceae, Brassicaceae, and other herb and *Selaginella* spores, which appear after ca. 2.612 Myr BP, suggest drier environmental conditions between 2.612 and 2.595 Myr BP. Based on the pollen assemblages we may assume that the regional vegetation was characterized by larch forests with stone pine, shrubby alder and birch, alternating with open steppe- and tundra-like habitats.

The upper boundary of the interval well coincides with the paleomagnetic Gauss/Matuyama boundary (Melles et al., 2011, 2012; Nowaczyk et al., 2013). Thus,

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vegetation changes showing a transition from interglacial environmental conditions to glacial ones well reflect the Pliocene/Pleistocene (MIS 104/MIS 103) boundary. The biome reconstruction (Fig. 6) suggests a broad spectrum of vegetation communities representing arctic herb/shrub as well as boreal tree/shrub plant functional types. Tundra, cold deciduous forest and taiga are reconstructed, reflecting a larger variability in the regional climate.

4.19 Environmental conditions ca. 2.595–2.560 Myr BP

Between 2.595 and 2.588 Myr BP (PZ-27; Fig. 3c), during MIS 103, coniferous pollen is almost completely absent. *Alnus fruticosa* pollen contents and total pollen concentration significantly drop as well, while contents of *Betula* sect. *Nanae* and Cyperaceae increase. The spectra reflect that dwarf shrubs became dominant in the regional vegetation, as a consequence of serious climate deterioration at the onset of the Pleistocene. Climate conditions became cooler and significantly drier compared with the previous interval.

In the Baikal area, a remarkably reduction of forested areas, while steppe environments show a strong expansion took place after 2.61 Myr BP (Demske et al., 2002). In eastern Beringia pollen and macrofossils from also demonstrate that *Pinus* and *Picea* species disappeared or greatly reduced their participation in the local vegetation after ca 2.6 Myr, while grasses and other herbaceous taxa increased (Schweger et al., 2011 and references therein).

Between 2.588 and 2.578 Myr BP (PZ-28, Fig. 3c) increases of *Larix* and, especially *Alnus* pollen contents show that open larch forests with shrub alder, tundra- and steppe-like communities dominated in the region.

A slightly more favorable climate between 2.578 and 2.560 Myr BP (PZ-29, Fig. 3c) is suggested by slight increases in *Pinus* pollen contents. However, simultaneous significant increases in Poaceae, Cyperaceae, Ericales, *Artemisia*, Caryophyllaceae, Ranunculaceae, Brassicaceae, and Asteraceae pollen and *Selaginella* spore percentages

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document rather dry and cold climate conditions. Furthermore, relatively high contents of coprophilous fungi spores reflect presence of grazing animals around the lake.

The environmental changes between 2.595 and 2.560 Myr BP maybe also associated with the beginning of the second, so-called Okanaanean Glaciation that occurred in eastern Chukotka at the beginning of the Pleistocene around 2.5 Myr BP (e.g. Laukhin et al., 1999; Fradkina et al., 2005b). Pollen-based climate estimations yielded mean July temperatures in order of 14 °C, mean January temperatures ranging between −20 and −28 °C, and annual precipitation – between 400 and 450 mm (Laukhin et al., 1999). In difference to the Zhuravlinean Glaciation, which was centered towards the ocean shore, the Okanaanean Glaciation was developed further to the west (Laukhin et al., 1999). However, the age control of the till sediments attributed to the Okanaanean glaciation is rather poor.

4.20 Environmental conditions ca. 2.560–2.533 Myr BP

Ca. 2.56 Myr BP (PZ-30, Fig. 3c) *Pinus* disappear from the pollen spectra again. The interval up to 2.552 Myr BP is additionally characterized by a *Larix* pollen peak and lower contents of *Alnus*, Poaceae, Cyperaceae, and other herbs. Such pollen assemblages reflect that larch forest again became more wide-spread around the lake, thus pointing to a slightly more favorable (wetter and probably warmer) climate. This suggestion is also supported by a small increase in *Sphagnum* spores.

A peak in pine pollen and rather high larch contents between ca. 2.552 and 2.533 Myr BP (PZ-31, Fig. 3c) documents further climate amelioration which may coincide with MIS 101. Larch forests with stone pine, shrubby alder, and birch in understory dominated the vegetation. Large amounts of *Lycopodium* spores in the spectra show that they also were important elements in the local vegetation.

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4.21 Environmental conditions ca. 2.533–2.465 Myr BP

Coniferous is absent again between 2.533 and 2.515 Myr BP (PZ-32, Fig. 3c). This interval is also notable for high contents of *Artemisia*, *Thalictrum* and Poaceae pollen marking broadly distributed steppe-like habitats. Numerous remains of *Botryococcus* algae colonies reflect abundant shallow-water environments in the lake, thus suggesting very dry climate conditions.

The pollen assemblages that have accumulated between 2.515 and 2.492 Myr BP (PZ-33, Fig. 3c) reflect that larch forest with dwarf birch in understory dominated the area. High contents of *Sphagnum* spores may be traced back to a paludification and wetter soil conditions during this interval. Also the contemporaneous Baikal pollen record suggest that environmental conditions at about 2.5 Myr ago became relatively favorable, facilitating the growth of moisture-dependent fir and even broadleaved taxa in the area (Demske et al., 2002).

Between ca. 2.492 and 2.479 Myr (PZ-34, Fig. 3c) larch stands again played only a minor role in the vegetation. High contents of sage and grass pollen reflect that steppe habitats became more common around the lake. Contents of trees and shrubs further decreased in the pollen assemblages between 2.479 and 2.465 Myr BP (PZ-35, Fig. 3c). Very high contents of *Selaginella*, Polypodiaceae, *Encalypta*, and *Gelasinospora* spores in this interval also point to deterioration of the environmental conditions.

4.22 Environmental conditions ca. 2.465–2.400 Myr BP

Relatively high contents of *Larix*, *Alnus,* and *Betula* pollen in PZ-36 (Fig. 3c) reflect that larch forests with shrubby birch and alder in understory grew around the lake between 2.465 and 2.449 Myr BP. It is possible that shrubby habitats dominated at higher elevations. An increase in sage pollen contents and a remarkable peak in *Botryococcus* algae colony remains point to a short-term event of particularly dry climate, leading to increased and shallow-water conditions environment in Lake El'gygytgyn around

2.45 Myr BP. At the same time, coinciding with the beginning of MIS 96, dry forests and steppe communities reached broad distribution and maximum herb diversity in Baikal region (Demske et al., 2002).

Between 2.449 and 2.428 Myr BP (PZ-37, Fig. 3c) larch and shrub alder stands probably were completely absent in the lake area. Instead, as suggested by high contents of Poaceae and *Artemisia* pollen and *Selaginella* spores, open, steppe-like communities were broadly distributed. The retreat of larch forests with shrubby birch and alder in understory took place between 2.428 and 2.400 Myr BP (PZ-38, Fig. 3c) as reflected by much higher percentages of *Larix*, *Alnus,* and *Betula* pollen.

4.23 Environmental conditions ca. 2.400–2.373 Myr BP

A gradual increase in *Pinus* pollen percentages starting around 2.400 Myr BP (PZ-39, Fig. 3c) documents that stone pine stands have increasingly appeared in the lake vicinity or relatively close by, although larch forests with shrubby birch and alder in understory still dominated around the lake. This suggests that the climate became slightly warmer than before. A higher presence of *Sphagnum* spores in addition points to wetter conditions.

A drastic increase in pine pollen percentages and pollen concentration between about 2.383 and 2.373 Myr BP (PZ-40, Fig. 3c) indicates that dense stone pine communities dominated vegetation in the area during this period. However, shrub alder and birch stands were also common. The vegetation cover was probably very similar to the modern northern larch taiga in north-eastern Siberia, where numerous stone pine, birch, and alder shrubs make understory and dominate higher elevations. The relatively high presence of *Picea* pollen may reflect that spruce also grew in the crater or in its close vicinity. Consequently, climate conditions during PZ-40 became wetter and warmer than during PZ-39.

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4.24 Environmental conditions ca. 2.373–2.354 Myr BP

Starting ca. 2.373 Myr BP (PZ-41, Fig. 3c) percentages of *Pinus* pollen became much lower, reflecting a significant decrease in pine stands around the lake. Shrub alder also partly disappeared from the local plant communities. Simultaneous peaks in *Artemisia* and Poaceae show that open steppe habitats again became dominant in the region. Thus, climate conditions are supposed to be much drier than before.

Between ca. 2.365 and 2.354 Myr BP, coniferous and alders completely disappeared from the lake vicinity. Instead, open steppe communities dominated the vegetation. This implies climate conditions even drier and also significantly colder than before. This climate deterioration probably coincides with MIS 92.

4.25 Environmental conditions ca. 2.354–2.333 Myr BP

Increases in *Pinus* and *Larix* pollen contents and peaks in *Betula* and *Alnus* between 2.354 and 2.345 Myr BP (PZ-42, Fig. 3c) reflect that the vegetation cover became similar to the northern limit of modern northern larch taiga and/or tundra-forest zones in north-eastern Siberia where open larch stands are alternating with shrubby stone pine, alder and birch communities. Climate conditions were much wetter and warmer than during the previous period. However, relatively high amounts of *Botryococcus* remains found in the sediments reflect shallow environments in the lake during the interval. This can best be explained by flooding of rather plain parts of the crater due to a lake-level rise.

The amounts of *Botryococcus* colonies keep relatively high in the sediments deposited between ca. 2.345 and 2.333 Myr BP (PZ-43, Fig. 3c), suggesting the persistence of shallow-water environments in the lake. Very high percentages of *Pinus*, small peak in *Picea* and the presence of *Larix* pollen in the same interval show that the area was dominated by larch taiga with dense stone pine communities in understory. Shrub alder and birch stands were also broadly distributed around lake.

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4.26 Environmental conditions ca. 2.333–2.290 Myr BP

Successively decreasing *Pinus* pollen contents between 2.333 and 2.308 Myr BP (PZ-44 of the Fig. 3c) reflect a gradual disappearance of pine from the vegetation. However, larch forest with shrub alder, dwarf birch, and probably some stone pines dominated the area until ca 2.318 Myr BP (PZ-44a and b). The simultaneous increase in Ericales pollen contents shows that heath communities were especially broadly distributed around the lake during that time.

Environmental conditions obviously became drier between ca. 2.318 and 2.308 Myr BP (PZ-44c, Fig. 3c), as evidenced by increases in sage and grass pollen contents. Steppe coenoses were common in the area. The presence of numerous remains of *Botryococcus* algae colonies points to the existence of wide shallow-water environments in the lake.

From ca. 2.308 to 2.290 Myr BP (PZ-45, Fig. 3c) pine was probably completely absent in the regional vegetation. However, a higher presence of larch, alder and birch in the spectra, along with decreases in herb pollen contents reflect that larch forest with shrub alder and dwarf birch in understory became broader distributed around the lake. Climate was wetter and warmer than during the previous time interval. A comparable, presumably coincident climate change is deduced from palynological data in north-western Canada and Alaska, which show that floristic elements required to form northern boreal forests and tundra ecosystems were first established in the region about 2.3 Myr (e.g., White et al., 1997 and references therein).

4.27 Environmental conditions ca. 2.29–2.23 Myr BP

Pinus pollen shows a small peak in the Lake El'gygytgyn sediments deposited between 2.290 and 2.268 Myr BP (PZ-46, Fig. 3c). PZ-46 also differs from PZ-45 by higher presence of *Larix* and Ericales. Such changes point to some climate amelioration. Larch forests with shrub alder, dwarf birch, and probably few stone pines dominated the vegetation around the lake.

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Stone pine completely disappeared again between ca. 2.268 and 2.253 Myr BP (PZ-47, Fig. 3c), while birch and alder increased at the beginning of this interval, but gradually decreased later on. Relatively high contents of *Botryococcus* remains in PZ-47 point to the existence of shallow-water environments in the lake.

The role of open steppe grass-sage and heath communities significantly increased between 2.253 and 2.243 Myr BP (lower part of PZ-48, Fig. 3c). This suggests that environmental conditions became drier and probably colder coincident with the beginning of MIS 86. Some increase in *Botryococcus* and a small peak of *Pediastrum* algae colony remains in the sediments point to shallow-water environments, likely as a result of lake level lowering. However, high contents of *Sphagnum* spores document that boggy habitats were also common around the lake.

Environmental conditions became worse between ca. 2.243 and 2.230 Myr BP, when larch, birch and especially alder shrub stands were further reduced. Peaks in *Artemisia* and Poaceae pollen contents suggest a broader distribution of steppe habitats under significantly drier climate conditions.

4.28 Environmental conditions ca. 2.230–2.198 Myr BP

Between ca. 2.230 and 2.214 Myr BP (PZ-49, Fig. 3c) increased *Betula* and *Alnus* pollen contents and the disappearance of *Artemisia* reflect that shrubby communities became again more common in the local vegetation. Climate conditions were probably wetter and warmer than during the PZ-48 interval, although an increase in *Selaginella rupestris* spores indicate that climate was still rather harsh.

A small peak of *Pinus* pollen between 2.214 and 2.198 Myr BP (PZ-50, Fig. 3c) reflects that stone pine might have grown in the region, thus pointing to some further climate amelioration. This suggestion is confirmed by peaks in *Alnus* and partly *Betula*, simultaneous with decreases in herb pollen contents. Climate conditions were probably slightly warmer than during the PZ-49 interval.

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4.29 Environmental conditions ca. 2.198–2.150 Myr BP

Pine disappeared again from the regional vegetation after 2.198 Myr BP (PZ-51, Fig. 3c) reflecting a further climate deterioration. Birch and alder shrubs dominated the area. Larch stands might have survived in more protected habitats such as river valleys.

Between 2.181 and 2.163 Myr BP (PZ-52, Fig. 3c) increased amounts of *Pinus* pollen reflect that stone pine might have migrated back into the region. Simultaneous decreases in herb pollen contents can indicate a reduction of open steppe- and tundra like communities, presumably reflecting wetter climate conditions.

The pollen assemblages dated between 2.163 and 2.150 Myr BP (PZ-53, Fig. 3c) suggest that shrubs (especially stone pine) were significantly reduced in the vegetation cover, while open steppe- and tundra like communities became broadly distributed. However, the presence of single larch pollen grains indicates that larch might still have survived in more protected habitats (e.g. river valleys). The inferred vegetation changes reflect a deterioration of the climate conditions. Further decreases in grass, sage, *Thalictrum*, and other herb pollen at the end of the interval point to an enhanced deforestation of the lake vicinities and very dry and cold climate conditions. Numerous remains of *Botryococcus* algae colonies found in the sediments points to extensive shallow-water environments in Lake El'gygytgyn.

5 Conclusions

The results of this study demonstrate that the Pliocene/Pleistocene pollen record of Lake El'gygytgyn is an excellent archive of vegetation and climate changes on the Chukchi Peninsula in the northeastern Siberian Arctic. The record well reflects main paleoenvironmental fluctuations in the region during the late Pliocene since ca. 3.56 Myr BP. Spruce-larch-fir-hemlock forests grew in the area about 3.50–3.35 Myr BP. Climate conditions in the study area were the warmest between 3.5–3.4 Myr BP. Most

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pronounced environmental changes (appearance of tundra and steppe like habitats) are revealed about ca. 3.305–3.28 Myr BP and around 2.71 and 2.60 Myr BP pointing to cold and dry conditions.

Open treeless vegetation dominated during the early Pleistocene: however, relatively warm intervals with larch forest and stone pine growing around the lake occurred about 2.550–2.535, 2.395–2.365, and 2.355–2.320 Myr ago.

Drastic peaks in green algae colonies (*Botryococcus*) around 2.55, 2.45, 2.320–2.305, and 2.175–2.150 Myr BP point to enhanced shallow-water conditions and a dry climate.

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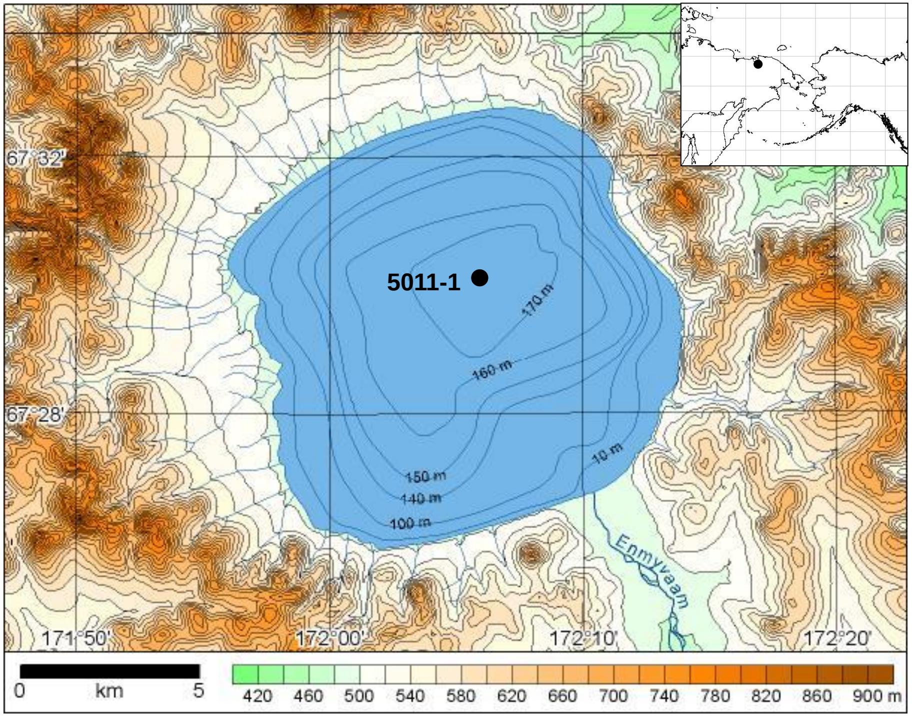

Fig. 1. Location of map Lake El'gygytgyn in north-eastern Russia (inserted map) with location of the core site.

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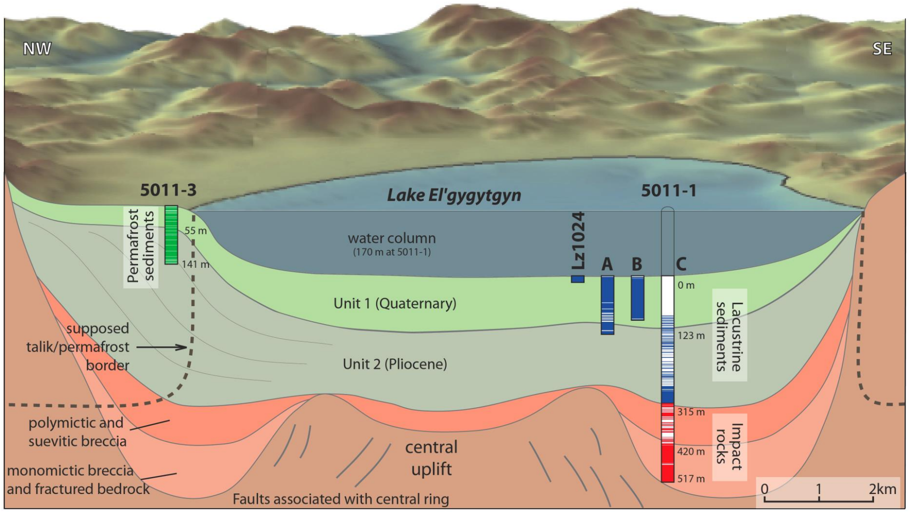

Fig. 2. Schematic cross-section of the El'gygytgyn basin stratigraphy showing the location of ICDP Sites 5011-1 and 5011-3 (after Melles et al., 2012).

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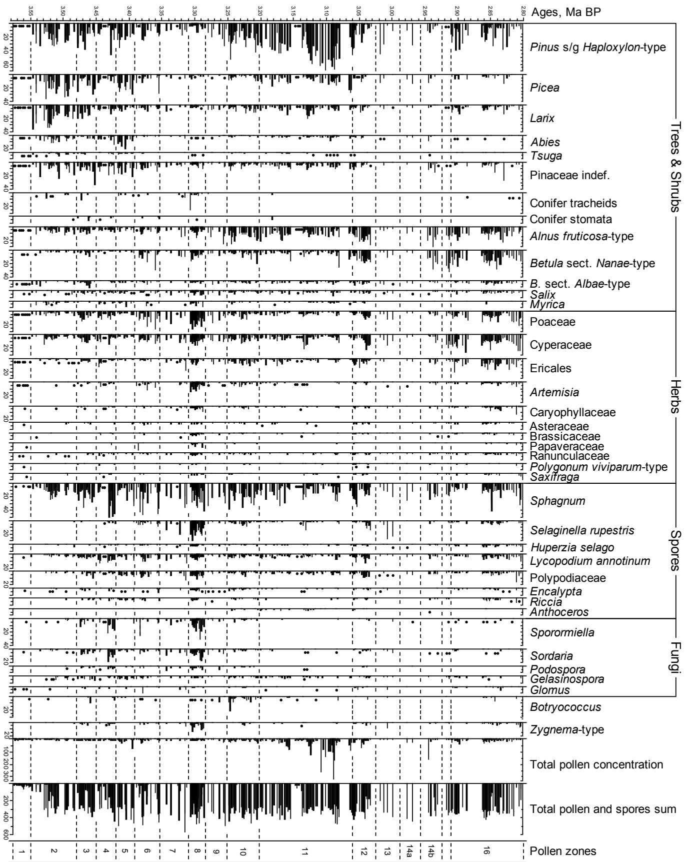

Fig. 3a. Percentage pollen, spore, and non-pollen-palynomorph diagram: the most common pollen and spores types between ca. 3.58 and 2.8 Myr BP.

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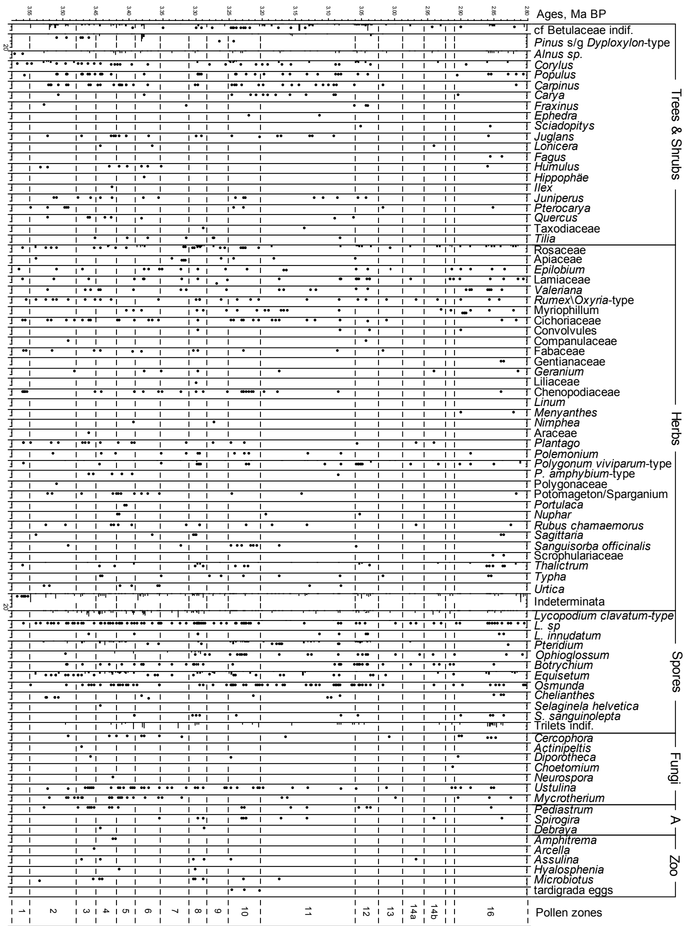

Fig. 3b. Percentage pollen, spore, and non-pollen-palynomorph diagram: the minor pollen and spores types between ca. 3.58 and 2.8 Myr BP.

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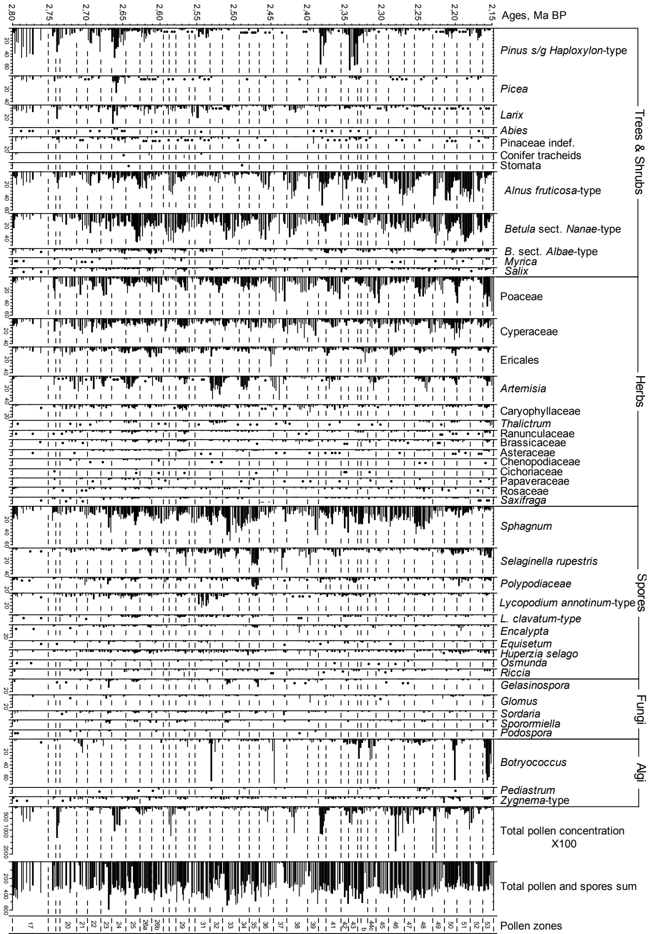

Fig. 3c. Percentage pollen, spore, and non-pollen-palynomorph diagram: the most common pollen and spores types between ca. 2.8 and 2.15 Myr BP.

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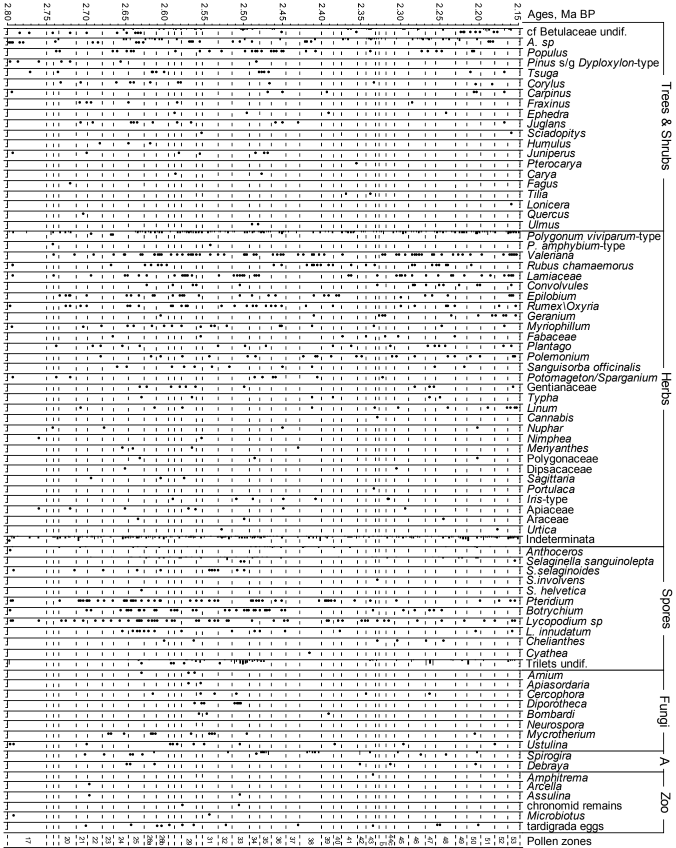

Fig. 3d. Percentage pollen, spore, and non-pollen-palynomorph diagram: the minor pollen and spores types between ca. 2.8 and 2.15 Myr BP.

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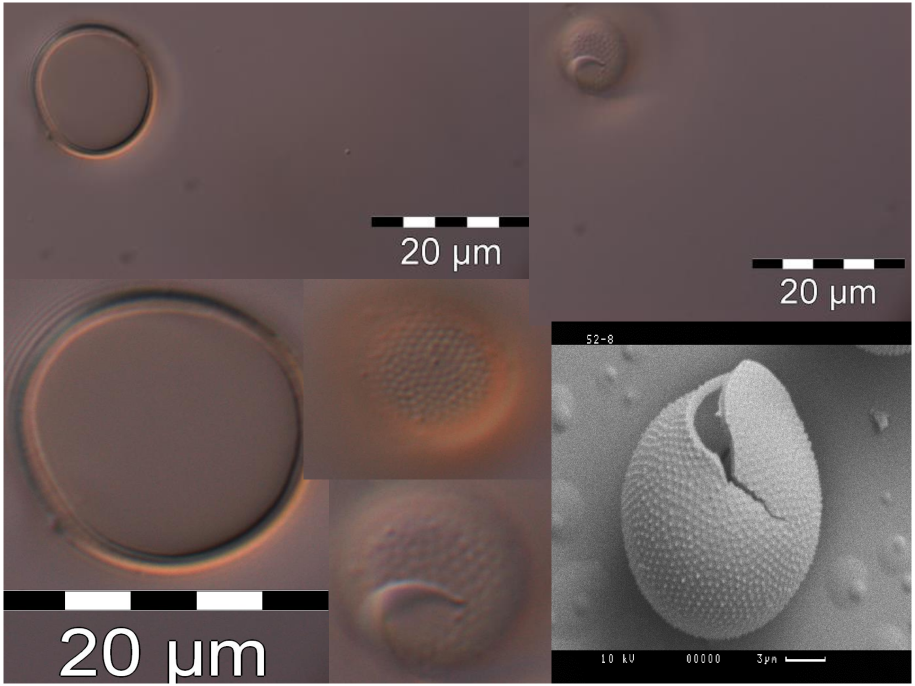

Fig. 4. Photos of cysts possibly produced by the so-called snow-algae (species from genera of *Chlamydomonas*, *Chloromonas Haematococcus (Sphaerella)*, *Chlamydomonas*, and *Chloromonas*). Photos by Thomas Leya from Fraunhofer IBMT, CryoCulture Collection of Cryophilic Algae and H. Cieszynski, University of Cologne.

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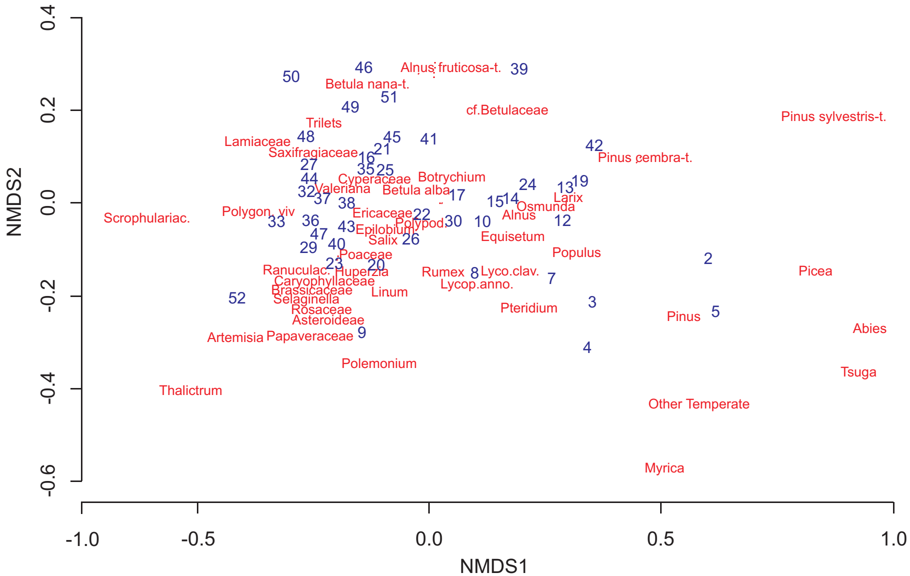

Fig. 5. Ordination of revealed pollen spectra. The two-dimensional nMDS plot mirrors the different pollen zones indicating major differences in the species assemblage through time.

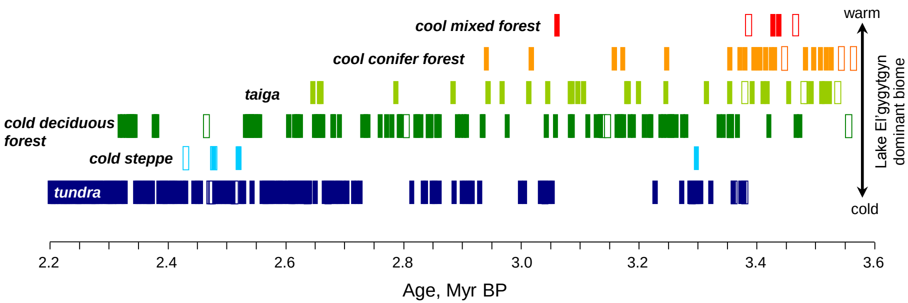

Fig. 6. Pollen-based biome reconstruction showing changes in the dominant vegetation type around Lake El'gygytgyn between ca. 3.58 and 2.15 Myr BP. Open squares indicate the biome reconstruction derived from the spectra with low pollen content (i.e. less than 100 terrestrial pollen grains, see Tarasov et al., 2013, for details).

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