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Paleontological records indicate the occurrence of open woodlands in a dry inland climate at the present-day Arctic coast in western Beringia during the Last Interglacial

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ABSTRACT

Permafrost records, accessible at outcrops along the coast of Oyogos Yar at the Dmitry Laptev Strait, NE-Siberia, provide unique insights into the environmental history of Western Beringia during the Last Interglacial. The remains of terrestrial and freshwater organisms, including plants, coleopterans, chironomids, cladocerans, ostracods and molluscs, have been preserved in the frozen deposits of a shallow paleo-lake and indicate a boreal climate at the present-day arctic mainland coast during the Last Interglacial. Terrestrial beetle and plant remains suggest the former existence of open forest-tundra with larch (*Larix dahurica*), tree alder (*Alnus incana*), birch and alder shrubs (*Duschekia fruticosa, Betula fruticosa, Betula divaricata, Betula nana*), interspersed with patches of steppe and meadows. Consequently, the tree line was shifted to at least 270 km north of its current position. Aquatic organisms, such as chironomids, cladocerans, ostracods, molluscs and hydrophytes, indicate the formation of a shallow lake as the result of thermokarst processes. Steppe plants and beetles suggest low net precipitation. Littoral pioneer plants and chironomids indicate intense lake level fluctuations due to high evaporation. Many of the organisms are thermophilous, indicating a mean air temperature of the warmest month that was greater than 13 °C, which is above the minimum requirements for tree growth. These temperatures are in contrast to the modern values of less than 4 °C in the study area. The terrestrial and freshwater organism remains were found at a coastal exposure that was only 3.5 m above sea level and in a position where they should have been under sea during the Last Interglacial when the global sea level was 6–10 m higher than the current levels. The results suggest that during the last warm stage, the site was inland, and its modern coastal situation is the result of tectonic subsidence.

1. Introduction

The high latitudes are expected to be particularly affected by global warming (ACIA, 2005; ACIS, 2008). Warming in the Arctic is amplified by positive feedback processes, such as decreasing albedo due to temporarily and spatially reduced sea ice and snow cover as well as greenhouse gases released from melting permafrost (Schuur et al., 2009; Screen and Simmonds, 2010). Another consequence might be the presumed northward shift of vegetation zones as is already indicated by expanding shrub vegetation (Stow et al., 2004; Tape et al., 2006), resulting in additional albedo changes that amplify arctic summer warming (Chapin et al., 2005). The biotic response to climate change is hardly predictable. Tree line advance, for example, is dependent on global temperature alterations, tree and shrub species characteristics and local environmental conditions (Danby and Hik, 2007). A suggested key factor is soil moisture. Global warming is possibly associated with increasing cloud cover and humidity in certain northern regions (Vavrus et al., 2009). Increased moisture may cause paludification, which in turn may decrease the

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ability of trees to regenerate on soggy soils. This may even result in a southerly retreat of the tree line (Crawford et al., 2003). Apart from precipitation, soil moisture in high latitudes is closely associated with frozen ground due to the damming effect and the high ice content of ice-bonded permafrost in continental areas in northern Yakutia and Alaska, regions that formed a common subcontinent – Beringia – during glacial sea level low stands. Soil moisture fluctuated in Beringia through time synchronously with the formation and thermal degradation of ice-bonded permafrost. During its formation under the extremely low ground temperatures of the last cold stage, permafrost extracted pore water from the active layer and accumulated it as ice. This ice comprises up to 80% of the sediment matrix, especially in the polygonal ice wedge systems that penetrate ice-bonded permafrost (Kaplina and Lozhkin, 1982). In the course of the subsequent Holocene warming, extensive thawing (thermokarst) of such ground ice released the formerly fixed water. The melting resulted in the shrinking of the permafrost matrix and the formation of numerous large-scale thermokarst depressions (alasses) separated by elevated mounds of remaining ice-bound permafrost (Yedoma). Alasses then formed wetlands and lakes fed by the permafrost melt water and precipitation. The casts of melting ice wedges were filled with alas sediments, mostly of lacustrine origin, forming pseudomorphs. Such pseudomorphs are a characteristic feature of sustained warming during the late Quaternary warm stages (Romanovskii, 1958; Péwé, 1973; Kaplina, 1987). Alasses and lakes currently constitute 90 to 95% of the landscape in the Yakutian tundra lowlands (Romanovskii et al., 2000).

The excessive thermokarst processes that proceeded during the Holocene caused a complete reorganisation of the hydrological system in the NE Siberian tundra. Warming and paludification resulted in the restructuring of the NE Siberian ecosystems and in the formation of novel biomes with a shift from xerophytic tundra-steppe via deciduous woodlands towards wetland tundra in the North and coniferous forests farther south (Binney et al., 2009; Edwards et al., 2005; Kienast et al., 2005). This ecosystem restructuring was accompanied by megafaunal extinctions, whose causes are still unclear (Gill et al., 2009). During earlier Pleistocene warm stages, the geographic ranges of megaherbivores, such as woolly mammoths, contracted periodically to refugia, which were small compared to their cold stage ranges but large enough to ensure the survival of megaherbivore populations. NE Siberia was a refuge for key elements of the cold-adapted mammoth faunal complex during the Pleistocene warm stages, and it served as a centre for their dispersal during cold stages (Sher, 1991, 1997; Kahlke 1999; Stuart et al., 2004; Campos et al., 2010). But, why did NE Siberia fail to provide habitats for the ice age fauna during the current interglacial in contrast to prior warm stages? As a precondition for large mammal survival, relatively constant environmental conditions can be assumed for their refugial areas throughout the glacial/interglacial cycles prior to the Holocene. Thermokarst processes, which were associated with Holocene ecosystem restructuring and megafaunal collapse in NE Siberia, also occurred during earlier Quaternary warm stages, as is observable in organic-rich deposits filling ice wedge pseudomorphs in the Yakutian coastal lowlands that are dated to the Last Interglacial (Table 1). Little is known about how arctic NE Siberian ecosystems responded to such warming and permafrost degradation events during earlier warm stages. Here we report on paleontological studies carried out on terrestrial and freshwater organism assemblages from the Last Interglacial (Kazantsevo, Eemian, Sangamonian, MIS 5e) that were preserved in frozen deposits within a shallow paleo-lake, outcropped at a permafrost cliff at Oyogos Yar on the mainland coast of the NE Siberian Dmitry Laptev Strait, Arctic Yakutia. To increase the range of reconstructible habitats and the reliability of interpretations, we included all available organism groups, including pollen, remains of plants, coleopterans, chironomids, cladocerans, ostracods and molluscs, as proxies for our paleoecological reconstruction. We discuss the implications on the environment, climate and coastline positions in this highly susceptible refuge for Pleistocene biocenoses during the Last Interglacial and contrast it with the Holocene to highlight the differences between these warm stages. These differences may have contributed to the megafaunal extinction.

2. Regional setting

The sampled exposure is situated in the coastal sector Oyogos Yar (72.68°N; 143.53°E) of the Yana-Indigirka lowlands between Cape Svyatoy Nos and the Merkushina Strelka Peninsula on the shore of Dmitry Laptev Strait in NE Siberia (Fig. 1). The Dmitry Laptev Strait connects the Laptev and East Siberian Seas, which are the widest and shallowest shelf seas in the world. Due to this special bathymetry, the NE Siberian coastline has oscillated several hundred kilometres during the Quaternary glacio-eustatic sea level fluctuations. The deposition site was situated inland during cold stages when the shelves became part of the Beringian subcontinent and was highly influenced by continental climate. Due to the continental climate and the resulting low net precipitation during the cold stages, Yakutia was free of inland glaciations since at least the Middle Pleistocene (Svendsen et al., 2004). Instead, 400- to 600-m-thick permafrost developed in the coastal lowlands and exposed shelves, which then formed a common accumulation plain. The modern climate in Arctic Yakutia is influenced by maritime air masses due to the proximity to the adjacent shelf seas. These effects are observable in the July and January isotherms, which roughly follow the coastline but are scarcely affected by latitude (VMGO, 1980). The maritime influence brings more precipitation and clouds, resulting in less insolation and sensible heat during the growing season. Consequently, on the coast, the mean temperature of the warmest month (MTWA) is only about 4 °C, and the mean temperature of the coldest month (MTCO) is about −30 °C (Station Cape Svyatoy Nos, 72° 53′ N, 140°, 45′ E in Rivas-Martínez, 1996–2009). Away from the coast, the seasonal temperature gradient increases rapidly, bringing warmer summers and colder winters, as demonstrated by the MTWA of 14.4 °C and MTCO of −44.7 °C at the inland site of Yansk (68° 27′ N, 134° 47′ E; Rivas-Martínez, 1996–2009). The annual mean temperature roughly corresponds at both sites. Due to the cool summers and

Table 1
Last Interglacial fossiliferous thermokarst deposits in the Northern Yakutian tundra lowlands.

Name of the sequence	Location	References
Achchagyy sequence	Allaikha River near the confluence into the Indigirka River	(Lavrushin, 1963; Kaplina et al., 1980b; Kaplina, 1981)
Bolshoy Khomus Yuryakh	Bolshoy Khomus Yuryakh River, Indigirka Kolyma interfluves	(Sher, 1991; Lozhkin and Anderson, 1995)
Duvanny Yar	Lower course of Kolyma River	(Kaplina et al., 1978; Giterman et al., 1982; Sher, 1991)
Stanchikov Yar	Malyy Anyuy River about 25 km E of the Kolyma River	(Kaplina et al., 1980a)
Krest Yuryakh sequence	Both coasts of the Dmitry Laptev Strait	(Romanovskii, 1961; Lavrushin, 1963; Barkova, 1971; Ivanov, 1972; Andreev et al., 2004; Kienast et al., 2008b; Wetterich et al., 2009)

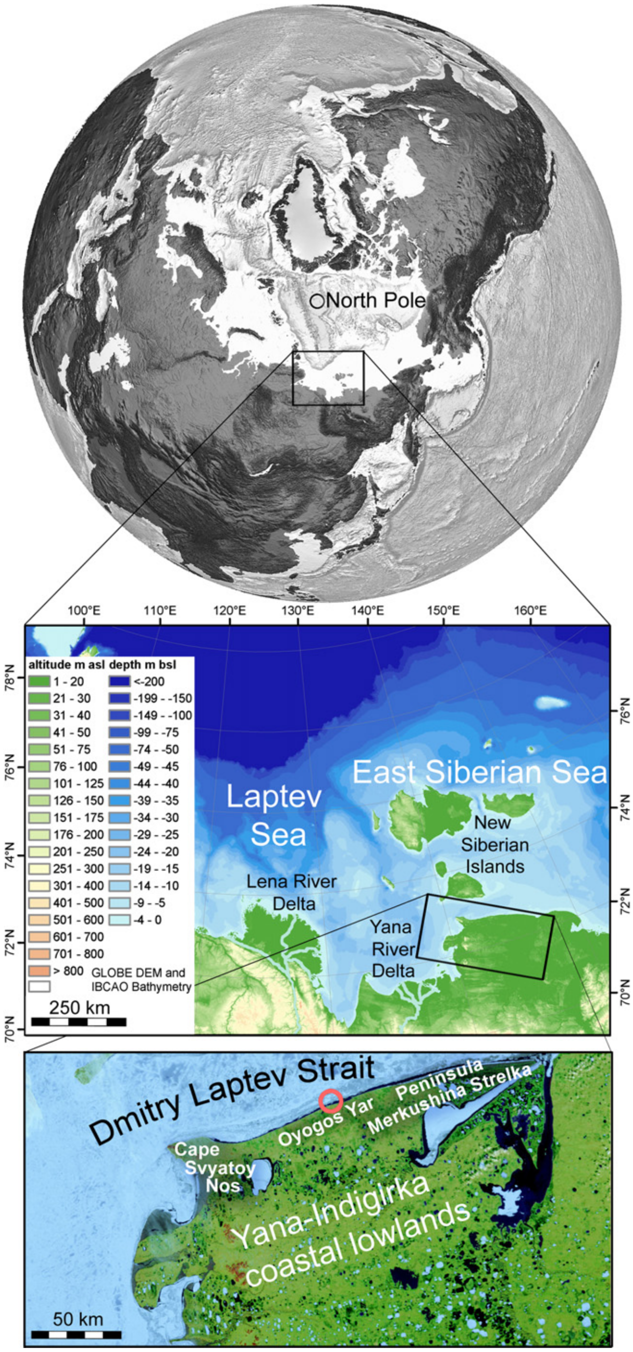

Fig. 1. Location, topography and regional context of the coastal sector Oyogos Yar in NE-Siberia. The bathymetrical map illustrates the extreme shallowness and width of the shelf seas adjacent to the studied coast (center). Numerous thermokarst lakes, visible in the satellite photo as black and, when still ice-covered, blue spots, indicate the magnitude of permafrost degradation in the coastal lowlands (lower part). Red circle, location of the studied exposure. Upper part adapted from the NGDC, NOAA Satellite and Information Service, available at http://www.ngdc.noaa.gov/mgg/global/; lower part, detail from satellite image (true- and false-colour images: MODIS from June 28, 2002) available at Visible Earth, http://veimages.gsfc.nasa.gov//3211/Russia.A2002179.0320.721.250m.jpg.

consequentially low evaporation, moist conditions are prevalent at Oyogos Yar. The active layer is mostly affected by excessive moisture, depending on the topography. Such topographic differences in soil moisture are well reflected by vegetation patterns in Oyogos Yar's coastal tundra (Kienast et al., 2008a). Accordingly, drainage is the most important local ecological factor in this area. The best drained sites, thermokarst mounds on top of Yedoma ridges, are the most diverse in terms of plant species (Kienast et al., 2008a; Tsuyuzaki et al., 2010). In spite of these small scale differences, the species diversity in the proximity of the study site is very low. Oyogos Yar is part of the East Siberian province of the southern arctic tundra, which is dominated by *Alopecurus alpinus*, *Salix polaris* and *Carex ensifolia* ssp. *arctisibirica* (Aleksandrova, 1980). Boreal or subarctic shrubs (*Duschekia fruticosa* or *Betula nana*), which can be found in more southern tundra subzones, are completely absent at this location. The only woody plants that currently occur are prostrate dwarf shrubs, such as *S. polaris* and *Dryas punctata* at favoured sites (Kienast et al., 2008a). According to the Circumpolar Arctic Vegetation Map (CAVM-Team, 2003), the study area is covered with sedge/grass, moss wetland vegetation (W1) that is typical of colder areas of the Arctic.

3. Material and methods

3.1. Studied deposits

The coastal exposures at Oyogos Yar and Bolshoy Lyakhovsky Island are the first sites in Yakutia in which the Last Interglacial thermokarst deposits, filling large ice wedge casts, were described (Romanovskii, 1961). Frozen sediments of various ages and accumulation types are exposed in steep bluffs by thermal erosion and wave action (Fig. 2; Andreev et al., 2004, 2009; Wetterich et al., 2009). Considered the longest and most comprehensive permafrost archive in the Arctic, at least two glacial-interglacial cycles from the Middle Pleistocene to the Holocene including Eemian deposits of lacustrine origin have been recorded (Fig. 3; Kayalainen and Kulakov, 1966; Ivanov, 1972; Konishchev and Koleshnikov, 1981; Andreev et al., 2004, 2009). These interglacial lake and marsh deposits, overlain by several decametres of thick Weichselian Ice Complex deposits, were analysed at Oyogos Yar and named the Krest Yuryakh Suite by Ivanov (1972). Krest Yuryakh sequences have recently been restudied at exposures along the southern coast of Bolshoy Lyakhovsky Island, where infrared stimulated luminescence (IRSL) dating revealed minimum ages of 99 ± 15 and 102 ± 16 kyr (Andreev et al., 2004; Kienast et al., 2008b; Wetterich et al., 2009). The general stratigraphic situation of the Quaternary sediment sequences is similar on both coasts of the Dmitry Laptev Strait (Romanovskii, 1961; Wetterich et al., 2009). Accordingly, four stratigraphic units have been identified here (Fig. 3). As specified in Table 2, these include: (1) pre-Eemian taberal sediments that occur below the Eemian lake bottom deposits. Taberal sediments develop below a lake when a layer of unfrozen ground (talik) refreezes after the lake above disappeared. (2) Lacustrine deposits from the Last Interglacial are preserved in ice wedge casts and are superimposed by terrestrial sediments from the Last Interglacial (3), which accumulated under subaerial conditions after the siltation of the lake. The whole interglacial sequence is covered by (4) Weichselian Ice Complex sediments (Schirrmeister et al., 2008c, in press). Interglacial deposits along the Oyogos Yar coast were sampled during a preliminary survey of the joint Russian-German expedition LENA 2002 in August, 2002. The purpose of the reconnaissance was to find fossiliferous late Quaternary sediment sequences that were accessible at coastal exposures for detailed future studies. The field work, carried out during a stay of only a few hours, included a tachymetrical survey of the coastal line and the collection of ground ice and permafrost deposits (Schirrmeister et al., 2003). The sediments for the present study were sampled from inside an ice wedge cast (Fig. 3). They were very rich in well-preserved organic remains. According to stratigraphy (directly below accelerator mass spectrometry (AMS)-dated last cold stage deposits) and enclosed organism remains (clearly warm stage spectra and including Late

Fig. 2. The Krest Yuryakh Suite at Oyogos Yar – Eemian lacustrine deposits superimposed by Weichselian ice complex.

Pleistocene mammals), the material was deposited during the Eemian interglacial. The diversity of freshwater organisms, such as molluscs, ostracods, cladocerans, chironomids and hydrophytes, indicate that the material was deposited in a shallow freshwater lake. Terrestrial organism remains, such as upland insects and plants, were also preserved. These were probably introduced into the lake by wind and melt water influx. The storage of these lake sediments in an ice wedge pseudomorph demonstrates the existence of ice wedges below the bottom of the lake during the time of deposition. The thawing of ice wedges and the sinking of the

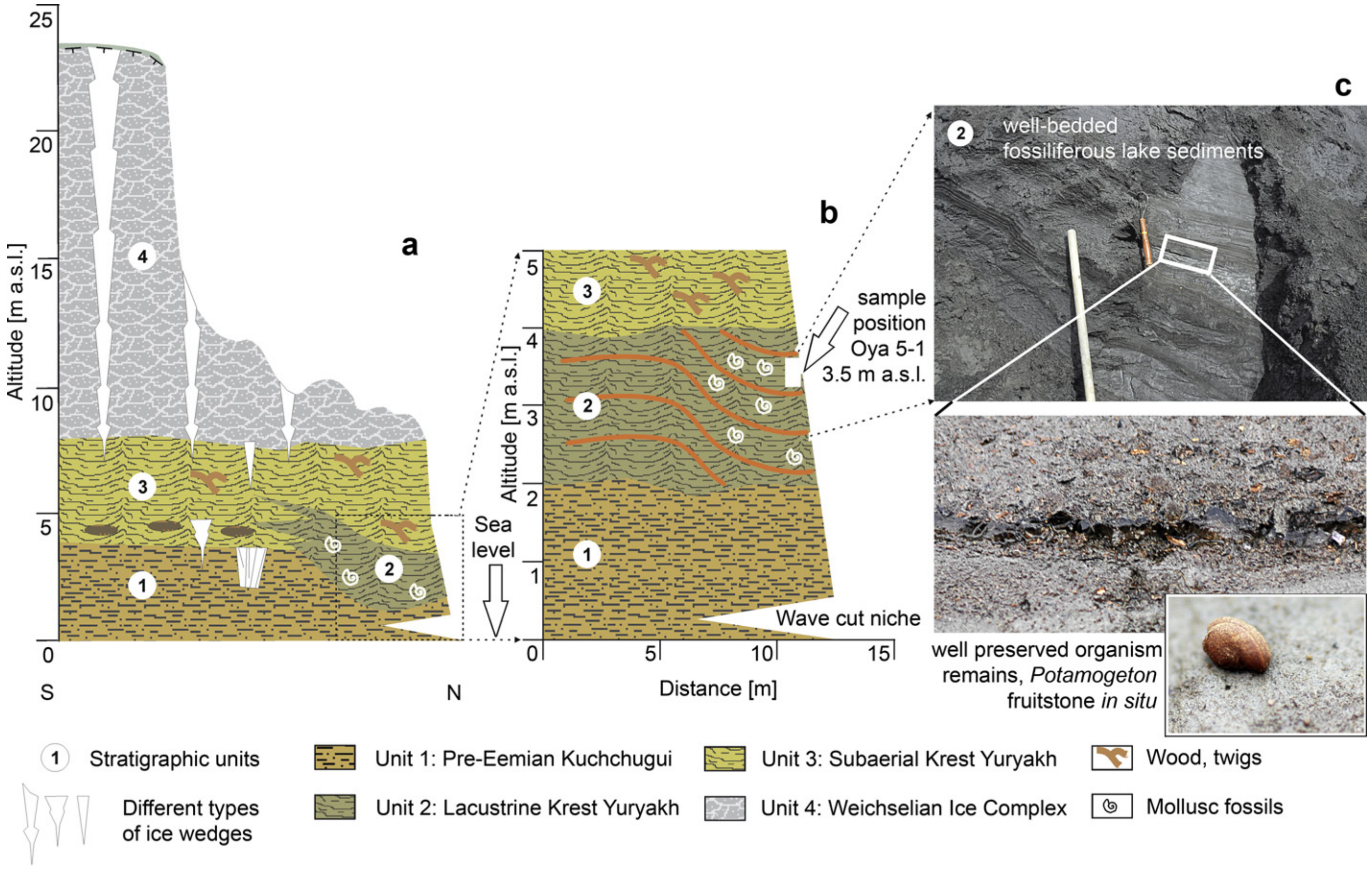

Fig. 3. Stratigraphic scheme of the Oyogos Yar ice wedge cast exposure: (a) General stratigraphic structure of the studied exposure. (b) Sample location of Last Interglacial lake sediments preserved in an ice wedge cast, bedding structures within the cast are redrawn by orange lines. (c) Photograph of well-bedded lake deposits (silty sand laminae alternate with plant detritus layers) and close up of frozen fossiliferous deposits.

Table 2
Cryolithological and sedimentological characteristics of the four stratigraphical units, which constitute the Quaternary sediment sequences at the Dmitry Laptev Strait.

	Unit 1	Unit 2	Unit 3	Unit 4
Name of the unit	Kuchchugui Suite	Krest Yuryakh Suite, lacustrine facies	Krest Yuryakh Suite, terrestrial facies	Yedoma Suite (ice complex)
Color	Brownish-grey	Dark-grey or bluish-grey	Dark-grey brownish-grey	Grey-brown
Sediment character	Weakly bedded silty sand	Silty sand with dark plant detritus layers (2–3 mm thick) filling ice wedge casts, alternated bedded lamination follows a synclinal scatter	Fine-grained sand with scattered plant-rich layers	Sandy silt with peat inclusions
Cryo-structure	Massive, no lenses, nets or bands	Massive in the lower part; slant, lens-like or lattice-like in the upper part	Ice-banded and lens-like reticulated between ice bands	Ice bands, between lens-like reticulated segregated ice; syngenetic ice wedges up to 20 m long, 2–5 m wide in the lowermost part and 8–10 m wide on top
Organic content	Numerous vertical in-situ grass roots	Numerous mollusc shells (<5 to 20 mm in diameter), plant detritus layers	Shrub twigs and wood remains (10–30 mm in diameter)	Peat inclusions, twig fragments, grass roots, and fine distributed plant detritus

bedded lake deposits into the casts happened later, indicating subsequent thermokarst processes in connection with lake expansion and deepening.

3.2. Sample processing

The sample was taken from undisturbed frozen deposits. After freeze-drying in the lab, 500 g of dry sediment was dispersed in water, sieved through a 0.25-mm mesh screen and then air-dried. From this fraction, macrofossils of plants, insects, molluscs and ostracods were picked and identified to the lowest possible taxonomic level with stereomicroscopes. The treatment of sediment samples for chironomid analysis followed standard techniques that were described in Brooks and Birks (2000). Subsamples of wet sediments were deflocculated in 10% KOH and heated to 70 °C for up to 10 min. Boiling water was added, and the mixture was left to stand for up to another 20 min. Subsequently, the sediment was sieved through 212-μm and 90-μm meshes. In total, 50 chironomid larval head capsules were picked out of a grooved Bogorov sorting tray using fine forceps under a stereomicroscope at 25–40× magnification. Larval head capsules were mounted two at a time in Hydromatrix, ventral side up, under a 6-mm diameter cover slip, with ten coverslips per microscope slide.

The preparation and enumeration of cladoceran taxa was adapted following Korhola and Rautio (2001). Approximately one gram of the sediment was deflocculated in 100 ml of 10% KOH solution and heated at 80 °C for approximately 40 min while gently stirring with a glass rod. The sediment was then washed under running tap water on 32- and 125-μm sieves. The sieving residue was transferred into small vials with distilled water, and a few drops of ethanol were added to prevent fungal growth. Three drops of a safranin–glycerin solution were added to stain the cladoceran remains, which were counted using a stereomicroscope at 200–400× magnification. Based on the equations of Frey (1986), the most numerous fragments, i.e., head shield, carapace, postabdomen, postabdomenal claws and ephippia, of each species were used to convert the counts into total numbers of individuals.

A standard hydrofluoric acid (HF) technique was used for pollen preparation (Berglund and Ralska-Jasiewiczowa, 1986). Pollen and spores were identified using a microscope with 400× magnification. Two hundred pollen grains were counted. The relative frequencies of pollen taxa were calculated from the sum of the terrestrial pollen taxa. Spore percentages are based on the sum of pollen and spores. The percentages of non-pollen palynomorphs are based on the sum of pollen and non-pollen palynomorphs. Algae percentages are based on the sum of pollen and algae.

The identification of fossils was based on reference collections (IQW, 2009) and relevant species descriptions for plant macrofossils (Jessen, 1955; Kats et al., 1965; Berggren, 1969, 1981; Anderberg, 1994), fossil insects (Sher et al., 2006), ostracods (Alm, 1914; Pietrzeniuk, 1977; Meisch, 2000), molluscs (Piechocki, 1989; Glöer, 2002; Glöer and Meier-Brook, 2003; Killeen et al., 2004), chironomids (Wiederholm, 1983; Makarchenko and Makarchenko, 1999; Brooks et al., 2007) and cladocerans (Frey, 1959; Goulden and Frey, 1963; Smirnov 1974, 1996; Alonso, 1996; Flössner, 2000). According to their abundance in the studied sample, the chironomid and cladoceran taxa were divided into three groups: >10%, dominant taxa (D); 5–10%, subdominant (SD) and <5%, seldom (S). The diversity and evenness of the chironomid and cladoceran communities were estimated using the Shannon Index (*H*) (Rjabov et al., 1980) and the Pielou Index (*I*) (Pielou, 1966).

A quantitative reconstruction of the Eemian MTWA was performed using the best modern analogue (BMA) approach (Guiot, 1990), based on representative modern reference pollen climate datasets (Tarasov et al., 2005, 2007). The BMA calculations were performed using the Polygon 2.0 software (Nakagawa et al., 2002). Based on the plant macrofossil composition, the MTWA was reconstructed using the method of Iversen (1944). The MTWA tolerances of plant species that were identified in the fossil record were calculated by correlating their distribution in Yakutia, as mapped in the Flora of Siberia (Malyschev, 2000, 2006; Malyschev and Peschkova, 2001a, 2001b, 2003, 2004; Krasnoborov and Malyshev, 2003; Polozhij and Malyschev, 2004; Peschkova, 2006) with the mean monthly climate values from the database of Leemans and Cramer (1991). By overlapping the individual temperature ranges of coexisting plant species, we obtained a coexistence interval or mutual climatic range – a narrow temperature range in which all of the identified plant species are able to coexist. In addition, the MTWA and water depth (WD) were calculated using a modern chironomid-based regional Yakutian MTWA and WD data set and transfer functions (Nazarova et al., 2011). Quantitative transfer functions were developed with weighted averaging partial least squares (WA PLS) techniques. The software C2 version 1.5 (Juggins 2007) was used to perform the reconstructions.

4. The fossil records

4.1. Plants

The results of the analysis of several thousand identifiable plant macrofossils (condensed in Table 3) revealed the occurrence of 87 vascular plant taxa from 25 families during the Last Interglacial. Most of them (55) are extralimital, i.e., they are found only outside the study area presently. Only 32 of the identified plant species are characteristic of modern arctic tundra in the study area. In Table 3, all identified plant taxa are listed according to their synecological

Table 3
List of the identified vascular plant macrofossils and their classification into plant communities (syntaxa). Dotted lines illustrate transitional synecological preferences, i.e. taxa may occur in two adjacent, ecologically similar communities. Extralimital taxa are marked by crosses.

Plant communities (syntaxa)	Plant taxa	Number and kind of specimen	Extra-limital
dry variant	*Arctostaphylos uva-ursi* (L.) Spreng.	24 fruits fragments	X
	Moehringia laterifolia (L.) Fenzl	1 seed	X
	Stellaria longifolia Muehl. ex Willd.	1 seed	X
	Chamaenerion angustifolium (L.) Scop.	5 seeds	X
Forests & forest tundra (Betulo-Adenostyletea Br.-Bl. & R.Tx. 1943; Vaccinio-Piceetea Br.-Bl. 1939; Epilobietea angustifolii R.Tx. &Prsg.ex v. Rochow)	*Larix dahurica* Turcz.	22 (1 needle tip, 1 seed fragment, 20 fascicles)	X
	Pinaceae indet.	2 seed fragments	X
	Alnus incana (L.) Moench	3 nutlets,	X
	Duschekia fruticosa Rupr. Pouzar	1 nutlet	X
	Betula cf. *pendula* Roth	7 wingless nutlets	X
	Betula divaricata Ledeb.	6 scales	X
	Betula fruticosa Pall.	24 (1 leaf fragment, 19 scales, 4 nuts)	X
	Betula nana L. s.l.	117 (72 leaf fragments, 10 scales, 35 nuts)	X
	Betula sp. L.	36 scale fragments	X
	Betulaceae indet.	214 wingless nuts	X
wet variant, associated to bogs	cf. *Vaccinium vitis-idaea* L.	1 seed	X
	Andromeda polifolia L.	1 seed, 6 leaf fragments	X
	Chamaedaphne calyculata Moench	1 seed	X
	Ranunculus lapponicus L.	18 nutlet fragments	X
Wetland & riparian vegetation (Oxycocco-Sphagnetea Br.-Bl. & R.Tx. 1943; Scheuchzerio caricetea nigrae (Nordh. 1936) R.Tx. 1937)	*Chrysosplenium* sp. L.	1 seed	
	Saxifraga hieracifolia Waldst. et Kit.	1 seed	
	Carex lugens H.T. Holm	1 utricle	X
	Carex stans Drej.	3 utricles	
	Carex sect. Phacocystis Dumort.	434 nutlets	
	Eriophorum scheuchzeri Hoppe	8 nutlets	
	Eriophorum brachyantherum Trautv. et C.A. Mey	11 nutlets	X
	Eriophorum russeolum Fries	3 nutlets	
	Eriophorum polystachion L.	2 nutlets	
	Caltha palustris L.	2 seeds	
	Carex redowskiana C.A. Mey	6 nutlets	X
	Comarum palustre L.	4 achenes	X
	Epilobium palustre L.	49 seeds	X
	Sparganium hyperboreum Laest.	9 achenes	X
Aquatic vegetation (Potamogetonetea pectinati R. Tx. & Prsg 1942)	*Hippuris vulgaris* L.	1 nutlet	X
	Myriophyllum spicatum L.	1 mericarp	X
	Batrachium sp. (DC.) S.F. Gray	20 nutlets	X
	Callitriche hermaphroditica L.	53 mericarps	X
	Potamogeton perfoliatus L.	116 fruitstones	X
	Potamogeton filiformis Pers.	21 fruitstones	X
	Potamogeton vaginatus Turcz.	6 fruitstones	X
	Potamogeton sp. L.	24 (20 fruitstone fragments, 3 seed fragments, 1 axis of infructescence)	X
	Ranunculus hyperboreus Rottb./ *gmelinii* DC.	1 nutlet	

Table 3. (*Continued*)

Plant communities (syntaxa)		Plant taxa	Number and kind of specimen	Extra-limital
	(halophytic) pioneers of lake littoral (Bidentetea tripartitae R.Tx. et al. ap. R.Tx. 1950)	*Ranunculus hyperboreus* Rottb.*/ gmelinii* DC.	1 nutlet	
		Tephroseris palustris (L.) Reichenb.	2 achenes	
		Chenopodium sp. L.	1 seed	X
		Chenopodium cf. *glaucum* L.	1 seed	X
		Spergularia salina J. et C. Presl.	1 seed	X
		Eleocharis palustris (L.) Roem. et Schult.	10 nutlets	X
(Floodplain) meadows (Juncetea maritimi Br.-Bl. 1931; Molinio-Arrhenateretea R.Tx. 1937)		*Puccinellia* sp. Parl.	201 caryopsis	X
		Alopecurus cf. *pratensis* L.	3 caryopsis	X
		Deschampsia sp. Beauv.	1 caryopsis	
		Arctagrostis latifolia (R.Br.) Griseb.	42 caryopsis	
		Rumex arcticus Trautv.	2 nutlets	X
		Equisetum arvense L.	5 sheaths	X
		Calamagrostis sp. Adans.	6 caryopsis	
	Steppes (Koelerio-Corynephoretea Klika ap. Klika & Nowak 1941, Festuco-Brometea Br.-Bl. & R.Tx. 1943)	*Poa* sp. L.	18 caryopsis	
		Festuca sp. L.	3 caryopsis	
		Rumex acetosella L. *s.l.*	3 nutlets	X
		Allium cf. *schoenoprasum* L.	1 seed	X
		Carex duriuscula C.A. Mey	63 nutlets	X
		Eritrichium sericeum	1 nutlet	X
		Carex cf. *spaniocarpa* Steud.	9 nutlets	X
		Alyssum cf. *obovatum* (C.A. Mey) Turcz.	1 seed fragment	X
		Asteraceae cf. *Achillea* L. */ Ptarmica* Hill	1 achene	X
Kobresia-mats (Carici rupestris- Kobresietea bellardii Ohba 1974)		*Potentilla stipularis* L.	550 nutlets	X
		Artemisia sp. L.	5 (3 flowers, 2 achenes)	
		Potentilla nivea L.	21 nutlets	
		Ranunculus affinis R.Br.	46 nutlets	X
		Rhododendron sp. L.	1 seed	X
		Kobresia myosuroides (Vill.)Viori	5 nutlets	X
		*Dryas octopetala s.l. (*Juz.) Hult.	150 leaf fragments	
	Arctic (and alpine) pioneer vegetation (Thaspitea rotundifolii Br.-Bl. 1948)	*Gastrolychnis involucrata* A.&D. Löve	3 seeds	X
		Saxifraga cf. *oppositifolia* L.	1 seed	X
		Stellaria longipes Goldie s.l.	1 seed	
		Cerastium beeringianum Cham. et Schlecht.	52 seeds	
		Draba sp. L.	352 seeds & fragments	
		Papaver Sect. Scapiflora Rchb.	6 seeds	
		Cf. *Minuartia rubella* (Wahlenb.) Hiern	1 seed	
		Chamaenerion latifolium (L.) Th. Fries	1 seed fragment	X
		Cf. *Descurainia sophioides* O.E. Schulz	1 seed	X
Snow bed vegetation (Salicitea herbaceae Br.-Bl. 1947)		*Luzula confusa* Lindeb.	3 seeds	
		Luzula wahlenbergii Rupr.	1seed	
		Ranunculus nivalis L.	2 nutlets	
		Juncus biglumis L.	5 seeds	
		Salix sp. L.	40 buds	
	Without indication	*Asteraceae indet.*	1 achene fragment	
		Poaceae indet.	3 caryopsis fragments	
		Carex indet. tricarpellata	5 nutlets	

preferences. To make reconstructed plant communities comparable with modern ones, we described (Table 3) the paleo-vegetation using higher syntaxa, according to the International Code of Phytosociological Nomenclature (Weber et al., 2000). When describing reconstructed habitats and vegetation, we referred to descriptions in the Circumpolar Arctic Vegetation Map (CAVM-Team, 2003). The largest group consists of forest or forest-tundra plants, including larch, alder and birch trees. Alder (*Alnus incana*) fruits with their characteristic corky wings are very distinctive (Fig. 4). *A. incana* is considered here *sensu lato* (s.l.) and includes the NE Siberian variety *A. incana* var. *hirsuta*. The fruits of Betulaceae were among the most numerous plant remains in the studied sample. Their preservation was relatively poor. In particular, the fragile membranous wings were generally eroded. Therefore, the identification of Betulaceae fruits was based on the size and shape of the wingless nutlets, which are indistinguishable between the species *Betula fruticosa, Betula divaricata, Betula pendula, Betula platyphylla* and *Duschekia fruticosa* (Fig. 4). Moreover, because birches, both trees and shrubs as well as dwarf birches tend to hybridise in subarctic environments (Dierßen, 1996; Krasnoborov and Malyshev, 2003), intermediate carpological properties might occur. Only the characteristic almost circular nutlets of *B. nana* s.l. could be identified with adequate certainty. On the basis of fruit scales, it was possible to establish the presence of *B. fruticosa*, *B. divaricata* and, with some uncertainty, *B. pendula*. Plants typical of the undergrowth of boreal forests (e.g., Ericaceae species, such as *Arctostaphylos uva-ursi, Vaccinium vitis-idaea, Andromeda polifolia* and *Chamaedaphne calyculata)* and forest herbs (e.g., *Stellaria longifolia* and *Moehringia laterifolia*) support the reconstruction of woodlands (Fig. 4). Other important groups include wetland, riparian and aquatic plants (Fig. 5), reflecting the thermokarst origin of the studied sediments and their lacustrine depositional environment. As already established from the Eemian macroflora of the nearby Bolshoy Lyakhovsky Island (Kienast et al., 2008b), floral elements that are characteristic of steppes, meadows and fluctuating lake shores also occur, indicating dry conditions during the Last Interglacial (Fig. 6). The pollen spectrum is dominated by the pollen of Poaceae (27%), *Betula* sect. *Nanae* (18%), *Betula* sect. *Albae* (5.4%), Cyperaceae (12%), *Artemisia* (10%), *D. fruticosa* (9%), *Larix* (5%) and spores of *Equisetum* (18%) and some fungi, such as *Podospora*, *Sporormiella*, *Sordaria* (24%) and *Glomus* (11%). The spectrum resembles the palynological assemblages of pollen zone IIIa in the Krest Yuryakh sequence on Oyogos Yar, described in Wetterich et al. (2009). Therefore, the studied deposits probably accumulated during the same time interval: the Last Interglacial thermal optimum. The palynological spectrum confirms the macrofossil analysis of an open woodland environment with larch, shrub birch and alder, alternating with grasslands.

4.2. *Insects*

4.2.1. *Coleopterans*

The extraction of 121 insect remains, representing a minimum of 68 individuals from only 500 g of sediment is remarkable because a sample of several tens of kg is usually required to yield enough material for fossil insect studies. The fossils are well preserved (Fig. 7), and identification to the species level was possible in most cases. The fossil species spectrum (Table 4) is composed of many insects typical of northeast Siberian assemblages (Kiselev, 1981; Sher et al., 2006; Kiselev and Nazarov, 2009). It consists of 34 species from 11 beetle (Coleoptera) families. We also found remains representing other insect orders: three species of true bugs (Heteroptera) and single remains of ants (Hymenoptera), flies (Diptera), caddisflies (Trichoptera), leafhoppers (Homoptera) and alderflies (Megaloptera). Caddisfly and alderfly larvae are aquatic, which is consistent with the lake origin of the deposits. The studied assemblage is dominated by insects associated with moist tundra (25%), dry tundra (19%), aquatic (13%) and riparian (13%) habitats, as well as insects associated with meadow-steppe (6%), cold steppe (4%), forests (3%) and dry, warm habitats and shrubs (1% each).

4.2.2. *Chironomids*

From a total of 50 chironomid (Insecta, Diptera) head capsules, 16 taxa were identified. Eight of these taxa belong to the subfamily Orthocladiinae and eight to the subfamily Chironominae (five Chironomini, three Tanytarsini). The investigated chironomid community is diverse (Shannon index: 2.40) with a stable and evenly distributed structure (Pielou index: 0.86). The dominant taxa, *Limnophyes, Smittia foliacea*-type and the acidophilic *Psectrocladius sordidellus*-type (Fig. 8) as well as the majority of rarer taxa are indicators of temperate shallow lakes or littoral conditions that are associated with macrophytes (Brodersen et al., 2001). *Limnophyes* and the subdominant taxa, *Metriocnemus eurynotus*-type and *Parametriocnemus/Paraphaenocladius* are also frequently associated with macrophytes (Cranston et al., 1983; Brodin, 1986). Furthermore, these taxa are typically indicative of lake level fluctuations (Massaferro and Brooks, 2002). *Smittia foliacea*-type could be indicative of erosional processes or unstable lake level conditions (Cranston et al., 1983). The subdominant taxa *Chironomus anthracinus*-type and *Cricotopus laricomalis*-type are among the most frequently occurring taxa in present-day Yakutian lakes and can be found in a broad range of ecological conditions (Nazarova et al., 2005, 2008). *Tanytarsus pallidicornis*-type 1 is characteristic of relatively warm and productive lakes (Brodin, 1986). In contrast, *Tanytarsus lugens*-type and *Parakiefferiella triquetra*-type are cold stenotherms, occurring in oligotrophic cold subarctic lakes (Walker and Mathewes, 1989; Brodin, 1986). *Brillia* and *Endochironomus albipennis*-type often are associated with submerged wood and dead leaves (Fig. 9; Cranston et al., 1983). Some species of the group *E. albipennis*-type are leaf or stem miners (Pinder and Reiss, 1983).

4.3. *Crustaceans*

4.3.1. *Cladocerans*

In total, 153 individual cladocerans (Crustacea, order Cladocera) were identified. The investigated cladoceran community is relatively diverse (Shannon index: 1.89) with a stable and evenly distributed structure (Pielou index: 0.86). Fossil remains of nine cladoceran taxa were identified (Table 5), most of which belong to the family Chydoridae (seven species). The dominant cladocerans were small-bodied species (Table 5) *Chydorus sphaericus* (37%), *Alona rectangula/guttata* (29%) and *Bosmina* spp. (29%). *C. sphaericus* is usually found clinging to filamentous algae but may be planktonic during cyanobacteria blooms in eutrophic water. Its dominance may thus indicate rising primary productivity of a lake (Sarmaja-Korjonen, 2002). This dominant species tolerates broad ranges of water temperature and pH (Smirnov, 1974). Two-thirds of the cladoceran individuals, mainly represented by *C. sphaericus* and *A. rectangula/guttata*, are littoral species. These species occur on plants or in detritus-rich silty sediments in the macrophyte zone of lake margins. One-third is planktonic (*Bosmina* spp. and *Daphnia pulex* agg).

4.3.2. *Ostracods*

Ostracods (Crustacea, Class Ostracoda) form bi-valved low-Mg calcite carapaces. From several thousand freshwater ostracod valves, a representative subsample of 1192 valves from adult specimens were picked, counted and identified. The ostracod shells are well preserved as indicated by high numbers of fragile juvenile

Fig. 4. Macrofossils of forest and forest tundra plants found in Krest Yuryakh deposits at Oyogos Yar. 1 – *Alnus incana* s.l., fossil nutlet with characteristic corky wings, both sides; 2 – for comparison: *Alnus incana ssp. tenuifolia*, modern nutlet; 3 – *Duschekia fruticosa*, fossil nutlet; 4 – *Betula fruticosa*, catkin scale, two sides; 5 – *Betula divaricata*, both sides of a catkin scale; 6 – *Betula divaricata*, another catkin scale; 7 – *Betula nana*, catkin scale, both sides; 8 – *Larix dahurica*, fossil needle tip, two sides; 9 – *Larix dahurica*, fossil fascicle (short shoot); 10 – *Larix dahurica*, modern fascicle; 11 – *Larix dahurica*, seed fragment; 12 – *Andromeda polifolia*, upper and lower side of a leaf fragment, 13 – *Andromeda polifolia*, two sides of a fossil seed; 14 – *Chamaedaphne calyculata*, fossil seed, both sides; 15 – *Moehringia laterifolia*, two sides of a seed; 16 – *Chamaenerion angustifolium*, two different seeds; 17 – *Stellaria longifolia*, seed, both sides; 18–23: *Arctostaphylos uva-ursi*, 18 – part of a modern infructescence showing characteristically short peduncles; 19 – fossil berry with preserved very short peduncle, 20 – fossil berry with attachment scar; 21 – modern berry with attachment scar; 22 – modern berry with style scar; 23 – fossil berry with style scar. Scale for *Arctostaphylos uva-ursi* (on a gray background) 5 mm.

Fig. 5. Macrofossils of aquatic, littoral and wetland plants. 1 – *Potamogeton perfoliatus*, fruitstone, lateral view of both sides, 1b – bottom view highlighting stalk, warts at the base and keeled lid; 2 – *Potamogeton vaginatus*, lateral view of each side, 2b – top view showing shoulder (distance between lid and beak), which is shorter than at the related *P. pectinatus*; 3 – *P. filiformis*, fruitstone with opened lid and enclosed seed remain from both sides, 3b – top view showing shoulder and rounded lid; 4 – *P. filiformis*, fruitstone with preserved exocarp; 5 – *Callitriche hermaphroditica*, two different mericarps; 6 – *Myriophyllum spicatum*, mericarp, lateral; 6b – ventral; 7 – *Hippuris vulgaris*, two sides of the fruit; 8 – *Sparganium minimum*, fruit from two sides; 9 – *Batrachium sp.*, nutlet, both sides; 10 – *Ranunculus gmelinii vel R. hyperboreus*, nutlet; 11 – *Eleocharis palustris*, both sides of a nutlet; 12 – *Carex lugens*, fossil utricle; 13 – *C. lugens*, modern utricle; 14 – *C. redowskiana*, modern utricle; 15 – *C. redowskiana*, fossil utricle; 16 – *C. redowskiana*, other side of the utricle with enclosed nutlet and thick utricle wall; 17 – *C. redowskiana*, modern utricle broken to illustrate thick wall; 18 – *Chenopodium cf. glaucum*, seed, both sides; 19 – *Spergularia salina*, fossil and recent seed; 20 – *Epilobium palustre*, seed, both sides; 21 – *Ranunculus lapponicus*, two sides of a nutlet with partly preserved spongy parenchyma at the apex.

Fig. 6. Macrofossils of meadow, steppe and arctic upland plants. 1 — *Puccinellia* sp., caryopsis from two sides; 2 — *Alopecurus pratensis*, lateral view of fossil caryopsis with preserved remnant of palea; 3 — *A. pratensis*, modern caryopsis; 4 — *Arctagrostis latifolia*, fossil fruit, 5 — *A. latifolia*, modern caryopsis; 6 — *Equisetum arvense*, fossil sheath; 7 — *Rumex arcticus*, nutlet with partly preserved perianth, three sides; 8 — *Allium schoenoprasum*, seed, two sides; 9 & 10 — *Artemisia sp.* two different fossil flowers, each from two sides; 11 & 12 — *Carex duriuscula*, two different fossil nutlets; 13 & 14 — *C. duriuscula* two different modern nutlets for comparison; 15 — *Carex supina ssp. spaniocarpa*, modern tricarpellate nutlet; 15 — *Carex supina* s.l., fossil nutlet; 17 & 18 — *Rumex acetosella*, two different nutlets; 19 — *Eritrichum sericeum*, fossil nutlet; 20 — *Potentilla stipularis*, both sides of a nutlet; 21 — *P. nivea*, nutlet, two sides; 22 — *Rhododendron sp.*, seed from two sides; 23 — *Ranunculus affinis*, nutlet from both sides; 24 — *R. nivalis*, nutlet, both-sided; 25 — *Stellaria longipes*, two sides of a seed; 26 — modern seed of *Gastrolychnis involucrata*; 27 — *G. involucrata*, two sides of a fossil seed; 28 & 29 — *Dryas octopetala* s.l., leaf fragments from two sides; 30 — *Chamaenerion latifolium*, fossil seed fragment from two sides (note size in comparison to *Ch. angustifolium* in Fig. 4, Nr. 18).

Fig. 7. Insect remains from Krest Yuryakh deposits of Oyogos Yar. 1 & 2 — *Curtonotus alpinus*, pronotum and elytron; 3 & 4 — *Bembidion (Notaphus) varium*, pronotum and elytron; 5 — *Harpalus amputates*, pronotum; 6 — *Pterostichus* (*Cryobius*) *ventricosus*, pronotum; 7 — *Agabus cf. moestus*, pronotum; 8 — *Colymbetes cf. dolabratus*, head; 9 & 10 — *Cholevinus sp.*, pronotum and elytron; 11–13 — *Cholevinus sibiricus*, pronotum, elytron and head; 14 — *Cyrtoplastus irregularis*, elytron; 15 — *Colon sp*., elytron; 16 to 18 — *Eucnecosum tenue*, head, pronotum and elytron; 19 to 21 — *Lathrobium cf. longulum*, head, pronotum and connected elytra; 22 to 24 — *Tachinus brevipennis* head, pronotum and elytron; 25 — *Stenus* sp., head; 26 & 27 — *Helophorus sibiricus*, head and elytron; 28 & 29 — *H. splendidus*, head and elytron; 30 — *Morychus viridis*, elytron; 31 — *Simplocaria elongata*, elytron; 32 — *Hippodamia arctica*, pronotum; 33 — *Caenocara bovistae*, elytron; 34 — *Gonioctena affinis*, base of elytron; 35 & 36 — *Hydrothassa hannoverana*, head and elytron; 37 — *Pelenomus cf. velaris* head; 38 — *Phyllobius kolymensis* head; 39 — *Hypera ornata*, elytron; 40 — *Saldula pallipes*, pronotum; 41 — *Salda cf. littoralis*, pronotum; 42 & 43 — *Sciocoris microphthalmus*, head and pronotum; 44 & 45 — *Leptothorax acervorum*, head and abdomen; 46 — *Trichoptera* larvae, mandible; 47 — *Diptera* indet., pseudopupia; 48 — *Tipulidae* larvae, head; 49 — *Sialidae* larvae head.

Table 4
List of the identified fossil insects and their habitats illustrated by an Eco-Code: aq – aquatic, ri – riparian, mt – moist tundra, dt – dry tundra, ms – meadow-steppe, ss – cold steppe, fo – forests, ks – dry, warm habitats, sh – shrubs, oth – others (no certain habitat inferable), MNI – number of individuals.

Taxon	Eco-Code	Capita	Prono-tum	Elytra sin	Elytra dex	Elytra sin+dex	Other	MNI	SUM of fossils
Phylum Arthropoda									
Class Insecta									
Order Coleoptera									
Family Carabidae									
Bembidion (Notaphus) varium (Ol.)	ri	0	1	0	1	0	0	1	2
Pterostichus (Cryobius) ventricosus Esch.	mt	0	4	0	1	0	0	4	5
P. (Tundraphilus) sublaevis Sahlb.	dt	0	0	0	2	0	0	2	2
Curtonotus alpinus Payk.	dt	0	8	1	3	0	0	8	14
C. bokori Csiki	dt	0	1	0	0	0	0	1	1
Harpalus amputatus (Say)	ms	0	1	0	0	0	0	1	1
Family Dytiscidae									
Agabus cf.moestus (Curt.)	aq	0	1	0	0	0	2	2	3
Colymbetes cf. dolabratus (Payk.)	aq	1	0	0	0	0	0	1	1
Family Hydrophilidae									
Helophorus splendidus Sahlb.	aq	2	0	1	1	0	0	2	4
H. sibiricus Motsch.	aq	2	0	0	1	0	0	2	3
H. obscurellus Popp.	aq	0	0	0	2	0	0	2	2
Family Leiodidae									
Cholevinus sibiricus (Jean.)	mt	1	2	4	4	0	0	5	11
Cholevinus sp.	oth	0	1	0	2	0	0	2	3
Cyrtoplastus irregularis Rtt.	oth	0	0	1	0	0	0	1	1
Anisotoma sp.	oth	0	0	0	2	0	0	2	2
Colon sp.	oth	0	0	0	1	0	0	1	1
Family Staphylinidae									
Eucnecosum tenue (LeC.)	oth	1	1	1	2	0	0	2	5
Tachinus brevipennis Sahlb.	mt	4	6	4	2	0	0	6	22
T. arcticus Motsch.	mt	0	1	0	0	0	1	1	
Stenus sp.	ri	1	0	0	0	0	0	1	1
Lathrobium cf. longulum Grav.	oth	1	1	0	0	1	0	1	3
cf. Gymnusa sp.	ri	1	0	0	0	0	0	1	1
Family Scarabaeidae									
Aphodius sp.	ks	0	0	0	0	0	2	1	2
Family Byrrhidae									
Simplocaria elongata J. Sahl	dt	0	0	1	0	0	0	1	1
Morychus viridis Kuzm. and Kor.	ss	1	2	3	3	0	0	3	9
Family Melyridae									
Troglocollops cf. arcticus L. Medv.	ms	1	0	0	0	0	0	1	1
Family Coccinellidae									
Hippodamia arctica Schneid.	ri	0	1	0	0	0	0	1	1
Family Chrysomelidae									
Chrysolina sp.	mt?	1	0	0	0	0	1	1	2
Hydrothassa hannoverana F.	ri	2	1	0	1	0	0	2	4
Gonioctena affinis Gyll.	sh	0	0	1	0	0	0	1	1
Family Curculionidae									
Phyllobius kolymensis Kor. and Egorov	ms	1	0	0	0	0	0	1	1
Coniocleonus sp.	ms	0	1	0	0	0	0	1	1
Hypera ornata Cap.	dt	1	1	0	1	0	0	1	3
Pelenomus cf. velaris Gyll.	ri	1	0	0	0	0	0	1	1
Order Heteroptera									
Family Saldidae									
Salda cf. littoralis L.	ri	0	1	0	0	0	0	1	1
Saldula pallipes (F.)	ri	0	1	0	0	0	0	1	1
Family Pentatomidae									
Sciocoris microphthalmus Flor.	fo	1	1	0	0	0	0	1	2
Order Hymenoptera									
Family Formicidae									
Leptothorax acervorum Fabr.	fo	1	0	0	0	0	1	1	2
Order Trichoptera									
Trichoptera gen. indet. (larvae)	aq	4	4	0	0	0	5		
Order Diptera									
Diptera gen. indet (pseudopupia)	oth						4		
Tipulidae larvae	aq	2							

Table 4 (*continued*)

Taxon	Eco-Code	Capita	Prono-tum	Elytra sin	Elytra dex	Elytra sin+dex	Other	MNI	SUM of fossils
Order Homoptera									
Cicadellidae gen. indet	oth	3							
Order Megaloptera									
Sialidae larvae	aq	2							
Sum								68	121

specimens of all species and numerous findings of intact closed carapaces, pointing to *in situ* preservation. In total, the fossil ostracod assemblage comprises 11 species (Fig. 10). The most abundant species are *Candona candida* (34.2%), *Fabaeformiscandona rawsoni* (15.4%) and *Cytherissa lacustris* (26.0%). All other species occur at substantially lower percentages: *Fabaeformiscandona harmsworthi* 365 (5.6%), *Fabaeformiscandona levanderi* (1.1%), *Fabaeformiscandona pedata* (0.1%), *Fabaeformiscandona tricicatricosa* (5.2%), *Ilyocypris lacustris* (9.0%), *Cyclocypris ovum* (1.4%), *Cypria ophtalmica* (1.0%) and *Bradleystrandesia reticulata* (0.9%). In general, the modern occurrence of freshwater ostracods in Arctic Siberia is poorly studied. With the exception of two species (*C. lacustris* and *I. lacustris*), all the taxa recovered in the Eemian ice wedge cast (Table 6) are known from modern environments in northern and central Yakutia (Wetterich et al., 2008b, c). The close similarity of the Eemian ostracod assemblage to modern Yakutian records suggests an environmental setting that results from intense permafrost degradation (thermokarst). The shallow water margin zone of a thermokarst lake above thawing ice wedges and ice wedge casts, where lake sediments accumulate, is the most probable habitat for the fossil ostracod assemblage. The most abundant species *C. candida, F. rawsoni* and *C. lacustris* are tolerant to a wide range of physical and chemical conditions. They are able to tolerate significant variations in salinity and temperature. *C. ovum*, in contrast, is thermophilous and does not occur in North Yakutia today.

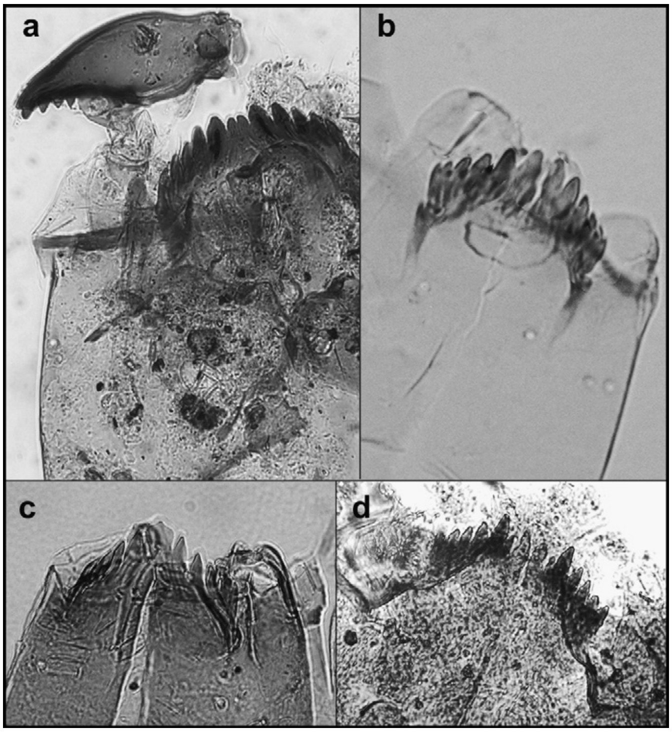

Fig. 8. Some chironomid taxa from Krest Yuryakh deposits of Oyogos Yar. (a) *Metriocnemus eurinotus*-type; (b) *Limnophies*; (c) *Smittia foliacea*-type; (d) *Microtendipes pedellus*-type.

4.4. Molluscs

The malacological record consists of two freshwater gastropods and five bivalve species. Only a few juvenile shell fragments of the gastropod genera *Radix* and *Gyraulus* were available (Fig. 11), so identification to the species level or precise ecological inferences were not possible. *Radix* is a ubiquitous taxon, occurring in various kinds of stagnant or floating freshwater systems and tolerating brackish water (Glöer, 2002). The occurrence of this common freshwater gastropod in Asia, documents a more northerly distribution of that genus during the Last Interglacial. The bivalve assemblage is dominated by 390 individuals representing various sphaeriid species. Five species of pea mussels were identified: *Pisidium casertanum*, *Pisidium subtruncatum* (frequent), *Pisidium* cf. *lilljeborgii*, *Pisidium obtusale* f. *lapponicum* (2 shells), and *Pisidium stewarti* (frequent) (Figs. 11 and 12). The most frequently represented *P. casertanum* and *P. subtruncatum* are eurytopic and occur in a wide range of aquatic habitats (Glöer and Meier-Brook, 2003). A faunal element of arctic and subarctic regions is documented by two shells of *P. obtusale* f. *lapponicum*. This pea mussel was also distributed in Central Europe during the colder phases of the Pleistocene (Kuiper, 1968; Piechocki, 1989). *P. lilljeborgii* (Kuiper, 1968), documented by one valve, is a stenoecious pea mussel that is restricted to oxygen-rich, oligotrophic, stagnant water bodies (Piechocki, 1989). This is the first time shells of *P. stewarti* have been found at such high latitudes. This species is only known from a few localities on the Tibetan plateau and the Siberian Irtysch region (Kuiper, 1962, 1968).

5. Habitats and biocenoses during the Last Interglacial

In view of the low species diversity in modern terrestrial and freshwater habitats of Oyogos Yar's lowland tundra, the variety of fossil organisms preserved in our study sample is surprisingly high, reflecting favourable living conditions and a broad range of available habitats during their lifetime. On the basis of their modern ecological preferences, we have reconstructed a complex of biocenoses, mainly consisting of forest-tundra alternating with steppes, meadows, wetlands and shallow lakes with large macrophyte belts and fluctuating shorelines. The most important reconstructed Last Interglacial biocenoses are discussed below.

5.1. Forest and forest-tundra

The Eemian presence of larch at Oyogos Yar was already inferred from pollen evidence from Krest Yuryakh deposits along the Dmitry

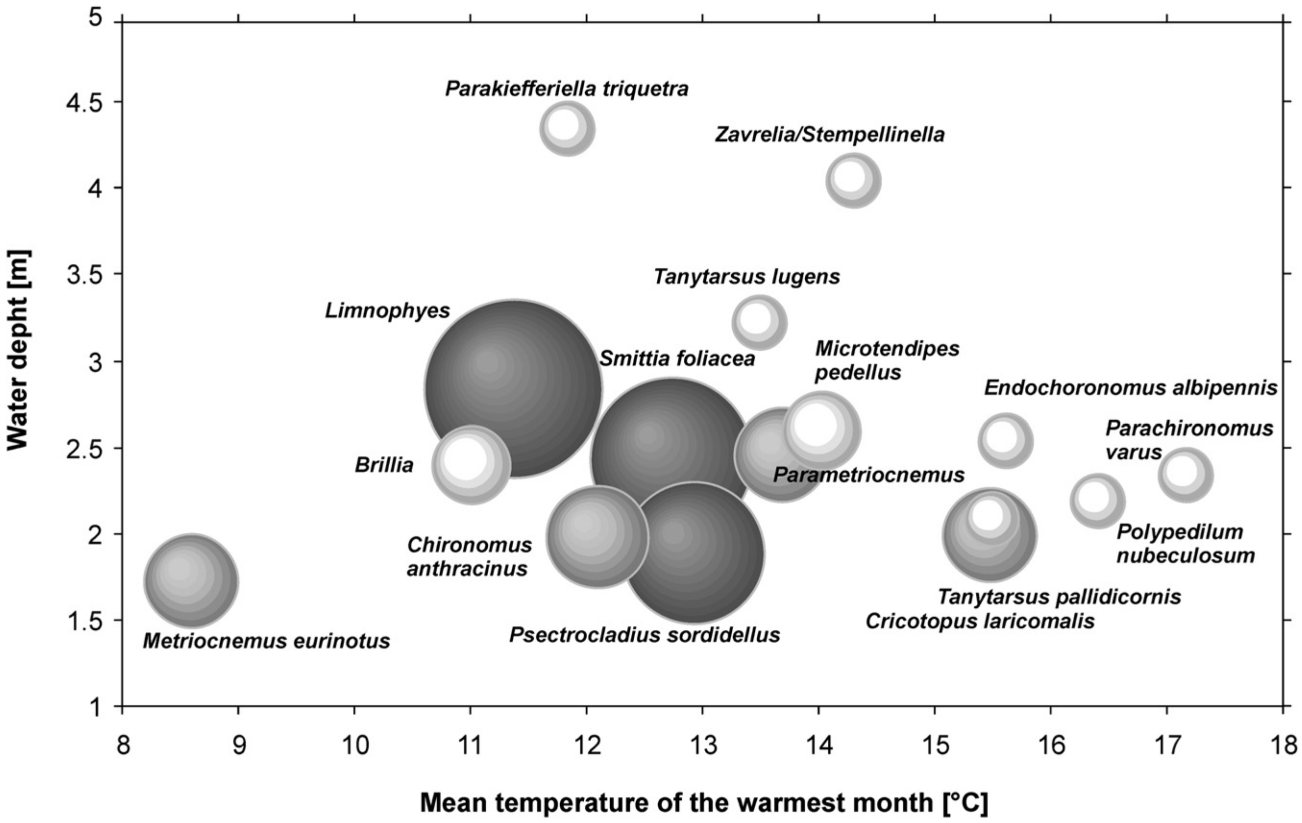

Fig. 9. Structure of chironomid community and ecological preferences of the chironomid taxa in relation to mean July air temperature and water depth according to Yakutian inference models (Nazarova et al., 2011). The size of the circles corresponds to the relative abundance of the taxa (%). In black are shown dominant taxa (D), in grey are shown subdominant taxa (SD), in white are seldom taxa (S).

Table 5
List of cladoceran species based on Smirnov (1974), Bellmann (1991), Hess (1993), Flössner (2000), Streble and Krauter (2002). Explanations: C – cosmopolite, E – ethiopian, H – holarctic, N – neotropical; L – littoral, B – benthic, Pl – planktonic, Ph – phytophilic.

Taxon	Frequency [%]	Distribution	Habitat	Temperature tolerance
Phylum Arthropoda				
Subphylum Crustacea				
Class Branchiopoda				
Order Cladocera				
Suborder Anomopoda				
Family Daphniidae				
Daphnia pulex agg. O.F. Müller	1.3		Pl	
Family Bosminidae				
Bosmina spp. Baird	28.8	C	Pl	
Family Chydoridae				
Alonella excisa (Fischer)	0.7	C	L, Ph	cold-water
Chydorus sphaericus (O.F. Müller)	37.3	C	L	eurythermic
Subfamily Aloninae Frey, 1967				
Alona quadrangularis (O.F. Müller)	0.7	H, E, N	L, Ph	
A. rectangula Sars	29.4	C	L, Ph	eurythermic
A. guttata Sars				
A. guttata tuberculata Kurz	0.7			
A. intermedia Sars	0.7	C	L, Ph	cold-water
Acroperus harpae (Baird)	0.7	H, E, N	L, Ph	cold-water

Laptev Strait (Barkova, 1971; Andreev et al., 2004; Wetterich et al., 2009). Our macrofossil record confirms that larch and alder were locally present at Oyogos Yar during the Last Interglacial. This is the northernmost local Pleistocene evidence of both tree species in Yakutia. Apart from larch, the macrofossil evidence of tree alder (*Alnus incana* s.l.) is remarkable for a region where it is now too cold even for shrub alder and dwarf birch to survive. It indicates that considerably warmer conditions existed during the growing season at the height of the Last Interglacial. Some of the boreal shrubs in our fossil record, such as *Betula fruticosa, Betula middendoffi* and *Duschekia fruticosa,* may grow today as trees several meters tall. It is evident that birches with a potential height of at least 6 m existed in the High Arctic Yakutian region during the Last Interglacial. Such shrubs also reached tree sizes in response to the rapid early Holocene warming (Edwards et al., 2005). Considering the abundance of birch remains and the evidence of larch and alder trees in the record, the existence of tree-sized birches can also be inferred for the Last Interglacial. In contrast to the modern larch-dominated taiga, the reconstructed interglacial woody vegetation was probably dominated by birches. Birches are dominant today in the transitional zone between the northern boreal and southern arctic zones. An open northern boreal forest or a southern subarctic forest-tundra, resembling the low shrub tundra S2 in the Circumpolar Arctic Vegetation Map (CAVM-Team, 2003), can be reconstructed. Several plant taxa from the Oyogos Yar Eemian record (*Arctostaphylus uva-ursi, Vaccinium vitis-idaea, Moehringia laterifolia, Stellaria longifolia* and *Chamaenerion angustifolium)* are characteristic of the undergrowth of modern boreal forests. Other boreal taxa (*Andromeda polifolia, Chamaedaphne calyculata* and *Ranunculus lapponicus*) occur in wet forest-tundra that is associated with acidic bogs. The plant-based forest-tundra reconstruction is strengthened by forest insects, such as the ant *Leptothorax acervorum* and the turtle bug *Sciocoris microphthalmus*, which typically do not occur north of tree line. *L. acervorum* is only sporadically found above the tree line in some mountain regions (Berman et al., 2007). A single nest of *L. acervorum* has also been recorded in the southern zone of lowland tundra (Chernov, 1972). Apart from these exceptions, this ant species is restricted to the boreal zone. The second forest indicator, *S. microphthalmus,* is a true forest species and has never been recorded in the tundra. In Siberia, *S. microphthalmus* is only known from central Yakutia (Vinokurov, 1979). Some of the recorded plant litter feeders, such as the beetles *Cyrtoplastus irregularis, Anisotoma* sp., *Colon* sp., *Eucnecosum tenue and Lathrobium longulum* as well as the borer beetle *Caenocara bovistae* are also mostly restricted to the forest zone. The chironomids *Brillia* and *E. albipennis*-type are associated with submerged wood and dead leaves (Cranston et al., 1983). Some species of the group *E. albipennis*-type are leaf or stem miners (Pinder and Reiss, 1983). The chironomid record indicates the presence of submerged coarse plant debris in the paleo-lake, most probably the remains of trees and shrubs.

5.2. Lacustrine, littoral and riparian habitats

Although modern tundra is largely covered with lakes and ponds, aquatic vascular plants are very rare in the Arctic today due to the short ice-free season and low water temperatures during the growing season. Correspondingly, the aquatic faunal spectrum is very poor. In contrast, during the Last Interglacial, rich freshwater communities existed at Oyogos Yar, as indicated by the diverse fossil record of aquatic plants and animals. Most of the identified chironomids (Fig. 9) and cladocerans (Table 5) indicate shallow water conditions and a pronounced macrophyte zone (Cranston et al., 1983; Brodin, 1986; Flössner, 2000). Consistently, eight macrophyte species, including three pondweeds, were identified from plant remains (Table 3, Fig. 5). Since they are restricted to the boreal zone today, these plants indicate a relatively long and warm growing season during the Last Interglacial. Extralimital aquatic faunal elements, such as the ostracod *Cyclocypris ovum* and the pea mussel *Pisidium stewarti*, also indicate summer conditions distinctly warmer than today. All identified aquatic plant species have a certain affinity to brackish waters and frequent disturbances – conditions that are characteristic of fluctuating lake levels and shorelines (Dierßen, 1996). The majority of preserved chironomids are also littoral taxa, i.e., they are indicative of unstable environmental conditions, such as subaerial exposure and fluctuations in insolation, water temperature and oxygen concentration. Thus, they reflect erosion processes due to fluctuating water levels (Cranston et al., 1983; Massaferro and Brooks, 2002). Plants occurring at the littoral zone of lakes, i.e., along the shoreline, are typically affected by seasonal flooding and drying. Taxa such as *Eleocharis palustris*, *Chenopodium* sp., *Spergularia salina* and *Puccinellia* sp. indicate shoreline fluctuations. Such fluctuations are probably the result of high evaporation and related seasonal lake shrinking. Because they are salt-tolerant, these plants also indicate salinification. The preservation of abundant and diverse calcareous ostracod and mollusc fossils, lacking any signs of dissolution, is

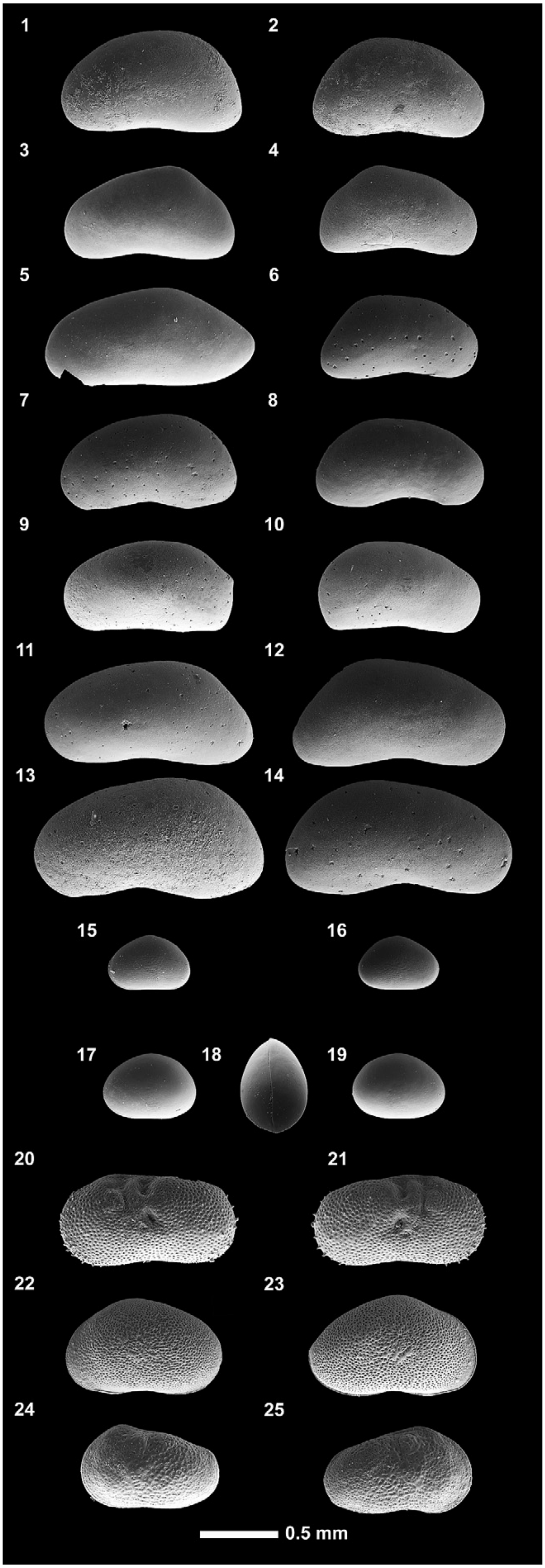

Fig. 10. SEM images of ostracod valves from Oyogos Yar's Last Interglacial sediments. (LV – left valve, RV – right valve). *Candona candida*: 1 – female LV, 2 – female RV; *Fabaeformiscandona harmsworthi*: 3 – female LV, 4 – female RV; *F. pedata*: 5 – female LV; *F. levanderi*: 6 – female RV, 7 – male LV, 8 – male RV; *F. rawsoni*: 9 – female LV, 10 – female RV; *F. tricicatricosa*: 11– female LV, 12 – female RV, – male LV, 14 – male RV; *Cypria exsculpta*: 15 – female LV, 16 – female RV; *Cyclocypris ovum*: 17 – female LV, 18 – female carapace in dorsal view, 19 – female RV; *Ilyocypris lacustris*: 20 – female LV, 21 – female RV; *Eucypris dulcifons*: 22 – female LV, 23 – female RV; *Cytherissa lacustris*: 24 – female LV, 25 – female RV.

Table 6
Taxonomic reference list of all identified ostracod species and their modern and fossil occurrences in Yakutia. The specification of sexes allows for conclusions on the occurrence of parthenogenesis.

	Sex	Modern records in Central Yakutia[a, b]	Modern records in North Yakutia[c]	Eemian records in North Yakutia[d]
Phylum Arthropoda				
Subphylum Crustacea				
Class Ostracoda				
Order Podocopida				
Family Candonidae				
Candona candida O.F. Müller, 1776	♀♀	X	X	X
Fabaeformiscandona harmsworthi Scott, 1899	♀♀	–	X	X
Fabaeformiscandona levanderi Hirschmann, 1912	♀♀, ♂♂	–	–	X
Fabaeformiscandona pedata Alm, 1914	♀♀	–	X	–
Fabaeformiscandona rawsoni Tressler, 1957	♀♀	X	–	X
Fabaeformiscandona tricicatricosa Diebel & Pietrzeniuk, 1969	♀♀, ♂♂	–	X	X
Family Cytherideidae				
Cytherissa lacustris Sars, 1863	♀♀	–	–	X
Cypria ophtalmica Jurine, 1820	♀♀	–	X	–
Cyclocypris ovum Jurine, 1820	♀♀	X	–	–
Family Ilyocyprididae				
Ilyocypris lacustris Kaufmann, 1900	♀♀	–	–	X
Family Cyprididae				
Eucypris dulcifons Diebel and Pietrzeniuk, 1969		–	–	–

[a] Pietrzeniuk (1977).
[b] Wetterich et al. (2008a).
[c] Wetterich et al. (2008b).
[d] Wetterich et al. (2009).

another indicator of deposition in an alkaline aquatic environment, presumably as a result of solute enrichment due to high evaporation in a closed lake basin. Unstable lacustrine environments are also indicated by the ostracod record. The typical habitats of the most abundant ostracod species (*C. candida, F. rawsoni* and *C. lacustris*) are characterised by significant variations in salinity and temperature. Such environments are typical of regions with continental climate. An environmental setting mainly controlled by continentality is also indicated by the similarity of the Eemian ostracod assemblage to modern Yakutian records (Table 6, Wetterich et al., 2008b) and by the evidence of the mussel *Pisidium stewarti*. This species is only known from a few localities on the Tibetan Plateau and the Siberian Irtysch region (Kuiper, 1962, 1968). During the late Pleistocene, there are some documented invasions of this species in Europe in connection with the expansion of climatically continental periglacial conditions. The Oyogos Yar record now shows that this species has spread not only to the west (reaching Europe) but also to the north in Siberia during the late Pleistocene. The macrophytes *Potamogeton filiformis* and *Callitriche hermaphroditica* are characteristic of calcareous, oligotrophic shallow lakes (Dierßen, 1996). Also the cold stenotherm larvae of the midges *Tanytarsus lugens*-type and *Parakiefferiella triquetra*-type occur in oligotrophic subarctic lakes (Brodin, 1986; Walker and Mathewes, 1989). Likewise, the stenoecious pea mussel *Pisidium lilljeborgi* is restricted to oxygen-rich, oligotrophic and stagnant water bodies (Kuiper, 1968; Piechocki, 1989). In contrast, the aquatic plants *Myriophyllum spicatum* and, in particular, the abundant *Potamogeton perfoliatus*, as well as the chironomid *T. pallidicornis*-type and small-bodied cladocerans, such as the dominant *C. sphaericus*, are characteristic of eutrophic and productive lakes (Pejler, 1975; DeMott and Kerfoot, 1982; Brodin, 1986; Dierßen, 1996; Sarmaja-Korjonen, 2002). The lacustrine fossil assemblage might represent a pooled sample, which embodies an ecological succession due to the eutrophication during lake aging.

5.3. *Wet tundra*

Wetland habitats in tundra are associated with thermokarst processes. Although the plant remains were accumulated in thermokarst deposits, the fossil assemblage is not dominated by wetland taxa, either in specimen abundance or in taxonomic diversity. Only water sedges (*Carex* sect. *Phacocystis*) are represented by relatively high numbers, which might be associated with their floating fruit dispersal strategy. Among the insects, only 25% of all recorded individuals are wet tundra species (Table 4). Wet habitats were obviously spatially restricted during the Last Interglacial. As in other ecological groupings, the wetland vegetation was mainly composed of southern extralimitals, e.g., *Carex lugens, Carex redowskiana, Eriophorum brachyantherum, Comarum palustre* and *Epilobium palustre*. Their past presence in a region that today is high arctic tundra indicates substantially higher MTWA during the Last Interglacial. Besides the numerous extralimital plant species, pioneer plants typical of disturbed sites in the Arctic (e.g., *Draba* sp., *Cerastium beeringianum, Stellaria longipes s.l.* and *Papaver* sect. *Scapiflora*) and snow bed plants, such as *Ranunculus nivalis* and *Juncus biglumis*, were also constituents of the fossil flora.

5.4. *Meadows, steppes and Dryas–Kobresia-mats*

The record contains a high percentage of plant species characteristic of dry or, at least, well-drained habitats, including saline meadows, steppes and xerophilous arctic upland vegetation (*Dryas–Kobresia*-mats; Table 3, Fig. 6). These vegetation patterns are in contrast to the modern lowland tundra of the study site, where truly dry habitats are nonexistent (Aleksandrova, 1980; Kienast et al., 2008a). However, they are in accordance with the vegetation of cold stages, when the climate was considerably more continental than present (Kienast et al., 2005). Macroremains of extralimital steppe plants, such as *Alyssum obovatum, Allium schoenoprasum, Artemisia* sp., *Carex duriuscula, Carex supina s.l., Eritrichium sericeum* and *Rumex acetosella*, clearly show that despite widespread thermokarst processes, dry places persisted in Yakutia's coastal lowlands during the Last Interglacial. Moreover, the high percentage of *Artemisia* in the pollen spectrum of Oyogos Yar indicates that steppe habitats existed not just locally but were widespread. The remains of thermophilous (warmth demanding) meadow-steppe beetles, such as *Harpalus amputatus* and *Phyllobius kolymensis*, demonstrate the

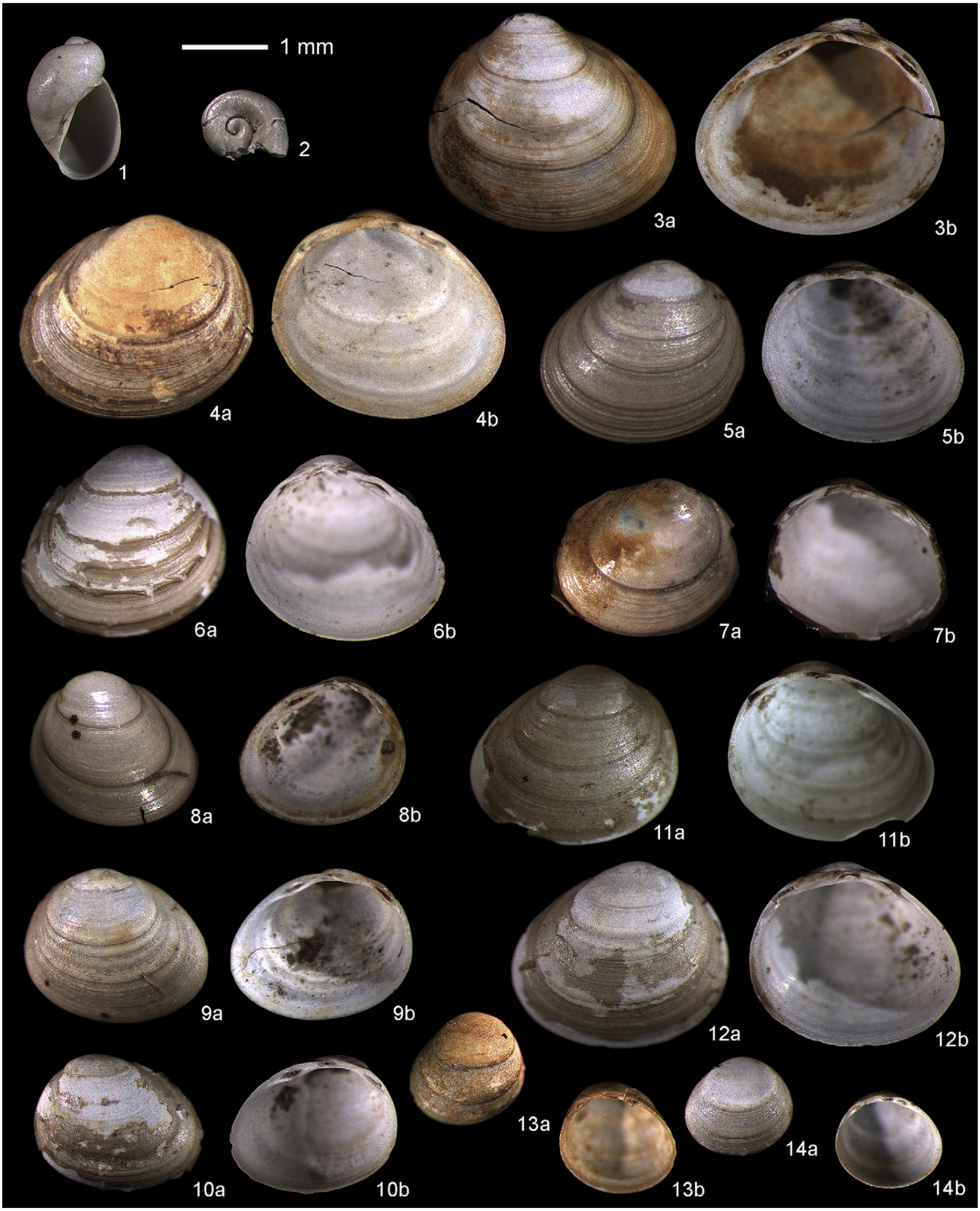

Fig. 11. Mollusc remains from Eemian deposits at Oyogos Yar. – Juvenile specimen of *Radix sp.;* 2 – Incomplete, juvenile specimen of *Gyraulus sp.*; 3 to 14 – Bivalve species from Oyogos Yar showing variability in shape of shells; 3a – *Pisidium casertanum*, lateral view of a right valve; 3b – internal view of same specimen; 4a, 5a – *Pisidium casertanum*, lateral view of left valves; 4b, 5b – corresponding internal view; 6a, 7a – *Pisidium stewarti,* lateral view of left valves, 6b, 7b – corresponding internal view; 8a – *Pisidium stewarti*, lateral view of a right valve; 8b – corresponding internal view; 9a, 10a – *Pisidium subtruncatum*, lateral view of right valves; 9b, 10b – corresponding internal view; 11a – *Pisidium subtruncatum*, lateral view of a left valve; 11b – corresponding internal view; 12a – *Pisidium lilljeborgii*, lateral view of a left valve; 12b – corresponding internal view; 13a, 14a – *Pisidium obtusale* f. *lapponicum*, lateral view of left valves; 13b, 14b – corresponding internal view.

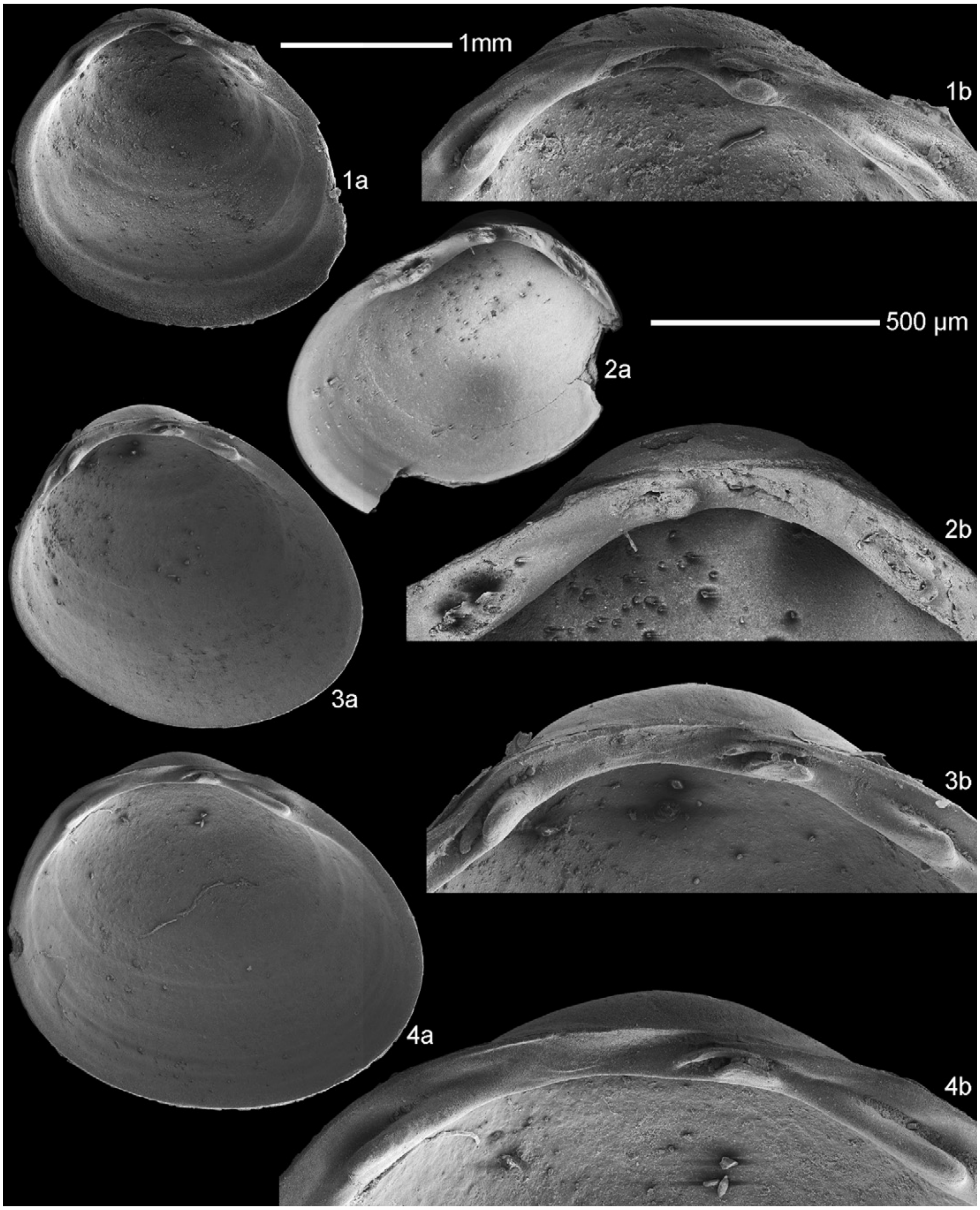

Fig. 12. SEM-images of some *Pisidium* species showing detailed features of the hinge plate. 1a – Internal view of a left valve of *Pisidium stewarti*; 1b – hinge plate of the same specimen showing the characteristic inverse ligament pit and two short, prominent cardinal teeth; 2a – internal view of a right valve of *Pisidium stewarti*; 2b – hinge plate of the same specimen with inverse ligament pit and one strongly bended cardinal tooth; 3a – Internal view of a left valve of *Pisidium subtruncatum*; 3b – hinge plate of the same specimen with two long and parallel cardinal teeth; 4a – Internal view of a left valve of *Pisidium casertanum*; 4b – hinge plate of the same specimen showing two prominent cardinal teeth, in which the upper cardinal tooth is located oblique posterior to the lower one; Figs. 1–4a = 1 mm scale, Figs. 1–4b = 500 µm scale.

existence of steppe habitats. They indicate not only dry but also warm conditions during the growing season. Insect assemblages from the nearby late Quaternary permafrost sequences of Bolshoy Lyakhovsky Island showed that steppe insects occurred in the late Quaternary only during warm stages, such as the Eemian (Andreev et al., 2004) and the early Holocene (Andreev et al., 2009). The meadow-steppe beetle *Phyllobius kolymensis* is currently known only from the upper reaches of the Kolyma River. The Siberian stipulated cinquefoil, *Potentilla stipularis*, the most abundant plant species in the Oyogos Yar record, is described from meadow steppes within relict tundra-steppe vegetation complexes in Yakutia and on the Chukchi Peninsula (Yurtsev, 1981, 2001). According to our own vegetation studies, the plant occurs in lowland and alpine steppes in Central Yakutia and in the Momsky and Chersky Mountain ranges (Kienast, unpublished data). It was also found in well-drained places in the southern tundra belt of Yakutia, e.g., at the top of a pingo in the Lena River Delta and on coarsely clastic substrate (rubble) in the vicinity of Tiksi. Thus, *P. stipularis* is characteristic of both steppes and *Dryas*–*Kobresia*-mats, which typically occur at such dry, exposed places in the arctic tundra and in the alpine belt of mountains. The remains of other plant species characteristic of *Dryas*–*Kobresia*-mats, e.g., *Kobresia myosuroides*, *Dryas octopetala s.l.*, *Rhododendron* sp., *Potentilla nivea* and *Ranunculus affinis*, indicate that such habitats existed in the Oyogos Yar lowlands during the Last

Interglacial. The interglacial existence of such dry habitats in arctic tundra is also indicated by the insects *Morychus viridis* and *Troglocollops arcticus*. The northernmost modern occurrence of the cryoxerophilous (cold steppe indicator) species *M. viridis* is in the central part of Wrangel Island, where it occurs on extra zonal relict steppe patches, which are characterised by a microclimate warmer and drier than the surrounding areas (Khruleva, 2009). Steppe patches and *Dryas*–*Kobresia*-mats likely merged and formed mosaics with woody thickets and saline *Puccinellia* meadows, as described in modern plant communities in the continental parts of SW Greenland (Böcher, 1954) and NE-Siberia (Yurtsev, 1981, 1982, 2001). The abundance of alkali grass (*Puccinellia* sp.) in the fossil plant spectrum indicates the existence of saline meadows and highlights the similarity of Oyogos Yar's paleo-vegetation with such modern tundra-steppe relict complexes.

6. Discussion

6.1. Tree line, paleo-vegetation and novel biomes

In summary, the fossil record from Oyogos Yar allows for the reconstruction of a relatively open landscape of larch-birch forest tundra, interspersed with grasslands and thermokarst lakes. The presence of larch-birch woodlands in a region that is now occupied by high arctic tundra indicates a substantial northward shift of the tree line during the Last Interglacial. Larch was absent from interglacial deposits about 80 km NW of the Oyogos Yar site, as revealed by the lack of *Larix* macrofossils and pollen in coeval permafrost deposits that were exposed at the coast of the Bolshoy Lyakhovsky Island (Andreev et al., 2004; Kienast et al., 2008b, Wetterich et al., 2009). Based on the floristic composition of the local macroflora, Kienast et al. (2008b) suggested that the Eemian tree line was situated adjacent to that site. The abundance of *Larix* pollen and the macrofossil evidence of *Larix* and *A. incana* in Oyogos Yar deposits indicate that during the last warm stage, the northern tree line was located at or beyond today's mainland coast of the Dmitry Laptev Strait, at least 270 km north of its current position. This is the northernmost Last Interglacial macrofossil evidence of tree species in Yakutia, although larch remains were also described from other Eemian exposures in the tundra lowlands of Yakutia, e.g., in Achchagyy deposits at the Allaikha River west of the Indigirka River (Lavrushin, 1963; Kaplina et al., 1980b), the Bolshoy Khomus Yuryakh site east of the Indigirka River (Lozhkin and Anderson, 1995) and Duvanny Yar in the lower reaches of the Kolyma River (Giterman et al., 1982; Sher, 1991). Thus, boreal woodland expanded over all of the coastal lowlands of NE Siberia and at least to the modern coastline. Modern arctic tundra was completely replaced by forest-tundra on the mainland (Lozhkin and Anderson, 1995) and by subarctic shrub tundra on the New Siberian Archipelago, e.g., from the southern coast of Bolshoy Lyakhovsky (Andreev et al., 2004; Kienast et al., 2008b) to the northern coast of Kotelny Island (Alekseev, 1997). However, the reconstructed woodland differed from modern forest-tundra due to its more northerly distribution and its floristic composition. The Eemian vegetation was largely similar to the vegetation reconstructed for the early Holocene at the Laptev Strait (Andreev et al., 2009) when the region was inland due to delayed sea level rise (Bauch et al., 2001; Romanovskii et al., 2000). Early Holocene deciduous woodlands were structurally and functionally novel, compared to modern boreal forests, as they were dominated by shrub birches that formed tree-sized growth forms (Edwards et al., 2005). A similar situation can also be inferred for the Last Interglacial by the numerous birch remains in our record. Grichuk (1984) and Sher (1991) hypothesised that, unlike modern closed larch-dominated woodlands, birches prevailed in the Eemian boreal forest-tundra. The dominance of *Betula* over *Larix* in our macrofossil assemblage and in all of the Eemian pollen spectra from Arctic Yakutia confirms that hypothesis. The dominance of birches in modern northern boreal forests is frequently the result of long-lasting pasturing and other continuous disturbances (Dierßen, 1996). In the geological past, grazing (and browsing) by large herbivores might have had a similar effect. The fossil discovery of the tree alder *A. incana* also points to grazing. Away from river banks, *A. incana* benefits from the disturbing effect of grazing (Wilson, 1973; Ellenberg, 1996). Indeed, there is strong evidence that grazing took place in the study region during the Last Interglacial. High numbers of dung-inhabiting fungi spores in the pollen-spore spectrum point to the presence of numerous herbivores in the area. The high content of *Glomus*, an indicator of disturbed soils, is probably connected with the presence of grazing animals in the area during that interval. The most striking evidence for the survival of large mammals through the Last Interglacial is a mammoth tusk recovered *in situ* in an Eemian ice wedge cast at Oyogos Yar during the 2007 field campaign (Fig. 13; Schirrmeister et al., 2008b). Mammoth remains had already been found in Krest Yuryakh deposits along the Dmitry Laptev Strait (Ivanov, 1972). Mammoth and muskoxen remains have also been found in Last Interglacial deposits in the Arctic Yana lowlands (Lozhkin and Anderson, 1995). In the Oyogos Yar record, many plants that are characteristic of steppe, *Kobresia*-mats and

Fig. 13. Mammoth tusk in-situ preserved in an Eemian ice wedge peudomorph at Oyogos Yar proves that western Beringia was a mammoth refuge during interglacials prior to the Holocene.

saline *Puccinellia* meadows, indicate that potentially productive grassland communities existed continuously in NE Siberia throughout Pleistocene warm stages. The persistence of this potential feeding base for herbivores during preceding warm stages helps explain why large cold-adapted grazers survived earlier interglacials in Beringia.

6.2. Continental climate in Western Beringia during the Last Interglacial

The presence of steppes, *Kobresia*-mats and saline meadows in Arctic Siberia is characteristic of sea level low stands during cold stages (Kienast et al., 2005; Schirrmeister et al., 2008a; Wetterich et al., 2008a; Andreev et al., 2009), when today's coastal lowlands were situated further inland and became influenced by dry and very continental climate. Additionally, the extralimital aquatic, littoral and forest plants found in the Oyogos Yar record occur today mainly under a continental climate. The continental climate is distinguished by low net precipitation and a wide seasonal temperature range. There are many indications of high evaporation and low net precipitation in the ecological preferences of species in the fossil record. Plants and midge larvae typical of unstable littoral conditions indicate lake level fluctuations. Halophilic littoral plants and alkali grass (*Puccinellia*), also abundant in cold stage plant assemblages, were very abundant in our interglacial fossil record (Table 3). These indicate salinification as a result of high evaporation in closed (thermokarst) depressions. Plants associated with steppe communities and *Kobresia*-mats are closely tied to dry habitats. The other important feature of climatic continentality is the great seasonal temperature range, resulting in extremely cold winters and warm summers. Winter temperatures were reconstructed, based on paleobotanical data, to have been milder than today in the East Siberian Arctic during the Last Interglacial (CAPE, 2006). Such a reconstruction is problematic because low winter temperatures have no negative effect on the distribution of the plant species considered here, such as larch, alder and birch in East Siberia. These woody species occur today even at the coldest point of the Northern Hemisphere, near Oymyakon (63°, 27′N; 142°, 47′E), where the MTCO is about 16 °C lower than that of the arctic coastal tundra (Rivas-Martínez, 1996–2009). For this reason we omitted a reconstruction of MTCO. The main constraints on arctic biological communities are warmth and length of the growing season. The length of the growing season depends on the thickness of the snow cover, the duration of the snow melt and the power of warming in the spring. Warming and summer temperatures are associated with insolation and precipitation, which determines how much energy is spent on snow melting, evaporation and transformation in latent warmth. Beside orbital parameters, insolation depends on cloud cover. Precipitation, snow thickness and cloudiness are determined by the degree of influence of maritime or continental climate. Summer temperature is the factor limiting life in high latitudes, and can be accurately reconstructed using bioindicators. For example, larches need an MTWA of at least 12 °C to grow (Andreev, 1980). For quantitative MTWA reconstructions of the Last Interglacial, we have used three different methods for the various bioindicators in the Oyogos Yar record. Despite the use of differing approaches and proxies, the results agreed. The pollen-based BMA reconstruction resulted in a MTWA range between 11 °C and 17.6 °C with a most probable value of 13 °C. The mutual climatic range of plant species found in the macrofossil record falls between 12.7 and 13.6 °C for MTWA (Table 7). An MTWA of 12.9 ± 0.9 °C and a water depth of 1.00 ± 0.34 m were reconstructed using transfer functions based on the chironomid assemblages. Thus, independent of the approach to temperature reconstruction, the Oyogos Yar record reflects boreal temperature conditions with an MTWA slightly above 13 °C during the height of the Last Interglacial. The modern MTWA measured at the closest climate station Mys Shalaurova, 50 km north of the sampling site, is about 3 °C. At Svyatoy Nos, 70 km west of the site, the MTWA is about 4 °C (Rivas-Martínez, 1996–2009). We infer then that the modern MTWA of the study site falls between 3 and 4 °C. Given a modern mean value of 3.5 °C, the Eemian MTWA was thus 9–10 °C higher than today. This is much greater differential than the 4–5 °C temperature deviation previously estimated for the East Siberian Arctic (CAPE, 2006). What might be the reasons for such a temperature contrast to today? The orbitally controlled summer insolation over the high latitudes (60–90°N) during the peak of the Last Interglacial warmth was amplified by about 13%, compared to today (CAPE, 2006). Moreover, peak insolation coincided approximately with rapid ice sheet decay and consequent albedo decrease. The maximum energy supply was available to heat the ground (and was not spent in melting the ice sheets). However, the northward expansion of boreal forests and the associated summer warming was most pronounced in Siberia and less in North America (CAPE, 2006). That asymmetry may be explained by the intensified influx of warm Atlantic surface water into the Arctic Ocean (CAPE, 2006). An increased sea surface temperature of the Arctic Ocean would have resulted in more evaporated sea water and increased air moisture, leading to more precipitation and denser cloud cover above the coastal lowlands. Increased precipitation and dense cloud cover are in contrast to the dry conditions and very warm summers that are indicated by the fossil record from Oyogos Yar. Marine sediment proxy data, including planktic foraminiferal assemblages from the Nordic seas, clearly indicate a reduction in the northward flow of Atlantic surface water into the Arctic Ocean during the Last Interglacial (Bauch et al., 1999). It appears that less warm water reached the Arctic by ocean currents during Stage 5e than during the Holocene. It seems that the dry and very warm summer conditions in the NE Siberian Arctic during the Last Interglacial are the result of the climatic continentality that persisted beyond the penultimate deglaciation (after MIS 6) in the coastal lowlands of Yakutia.

Table 7
MTWA requirements and coexistence interval of the vascular plant species that were identified in Eemian deposits at Oyogos Yar.

	UMean temperature of the warmest month in °C	
Taxon	Min	Max
Alnus hirsuta	12.7	18.4
Duschekia fruticosa	7.5	18.4
Potamogeton perfoliatus	12.2	18.4
Larix dahurica	7.8	18.4
Betula divaricata	9	18.4
Arctostaphylos uva-ursi	12.2	18.4
Betula exilis	6.5	17.8
Betula fruticosa	9.1	18.2
Callitriche hermaphroditica	8.4	17
Carex duriuscula	11.7	18.2
Carex supina s.l.	7.6	18.4
Dryas octopetala s.l.	3.2	18
Eriophorum brachyantherum	8.7	17.7
Juncus biglumis	2.3	16.4
Kobresia myosuroides	7.3	18.2
Potamogeton vaginatus	8.8	18
Potentilla stipularis	6.5	16.7
Ranunculus affinis	6.6	18
Sparganium hyperboreum	8.8	18.1
Alyssum obovatum	8.8	17.8
Rumex arcticus	5.2	16.4
Ranunculus nivalis	1.5	13.6
Allium schoenoprasum	7.8	18.2
Coexistence interval	12.7	13.6

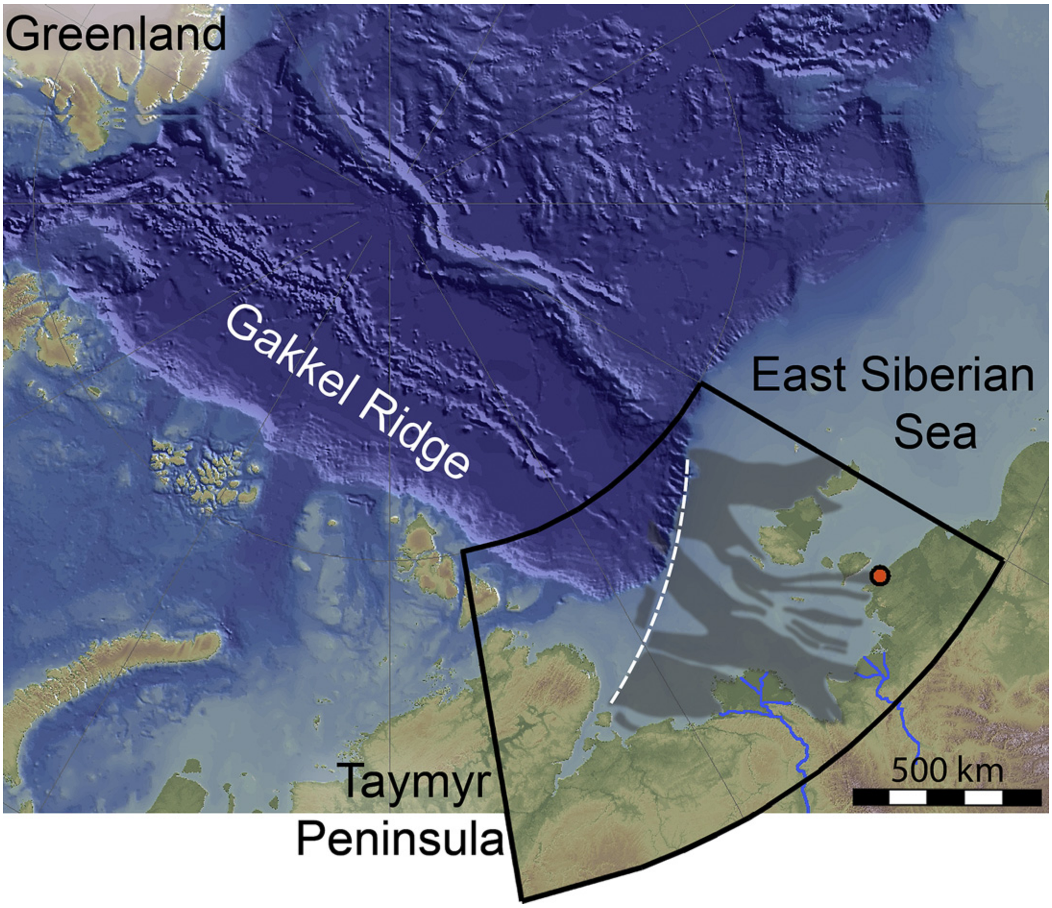

Fig. 14. Tectonic situation of the Laptev and East Siberian Shelves. The spreading processes arising from the mid-oceanic Gakkel Ridge proceed on the continental shelves. As result, intense subsidence processes occur along the rifting zone involving the formation of a series of deep basins (gray areas on the shelves derived from Drachev et al., 1998); White line, Khatanga–Lomonosov fracture.

6.3. Continentality and coastline setting

The degree of maritime or continental climate influence depends on the distance of the considered site to the sea. Climatic continentality during the late Pleistocene cold stages was connected with an inland position of today's coastal districts as a result of regressing shelf seas (Kienast et al., 2005). Consequently, the continental climate at Oyogos Yar during the Last Interglacial, as determined by fossil indicators, is inconsistent with the present-day coastal location of this site. Kienast et al. (2008b) suggested that due to the lack of Eemian marine deposits on the Yakutian mainland and based on continental climate characteristics that were reconstructed using paleobotanical data from the southern coast of Bolshoy Lyakhovsky Island, the Eemian coastline was located considerably farther north than today. Accordingly, the New Siberian Islands were part of the mainland during the cold stages and during the Last Interglacial. The isolated marine deposits on their northern coasts (Ivanenko, 1998) represent the mainland coast during the maximum sea level high stand at that time. The present coastal setting is the result of an exceptional Holocene transgression that exceeded the former marine advances due to tectonic subsidence. As a continuation of the mid-oceanic spreading zone along the Gakkel-Ridge, the shelf and coastal areas of the Laptev and East Siberian Seas are affected by extension and subsidence (Drachev et al., 1998, 2003; Franke et al., 2001, 2004), which have resulted in the formation of a series of neotectonic basins (Fig. 14). The shelf subsidence rate ranges by about 0.5 to 2 mm/year (Nikonov, 1977). Even at a mean subsidence rate of only 0.5 mm per year for the last 120,000 years, the shelf ground surface would currently be 60 m lower than during the Last Interglacial.[1] Owing to the extreme shallowness of the epicontinental Laptev and East Siberian Seas, such subsidence would result in an estimated mainland expansion of 400–500 km despite the higher sea levels inferred for the Last Interglacial in Beringia. The results in this paper are evidence of considerable tectonic subsidence since the Eemian. Terrestrial and freshwater organism remains were found at the modern coast at Oyogos Yar at only 3.5 m a.s.l. The fossil locality is in a topographic position that should have been inundated by sea water during the time of deposition, when global sea level was at least 6 m (Dumas et al., 2006) or, in Beringia, 10–15 m higher than today (Alekseev, 1997; Brigham-Grette and Hopkins, 1995). Additionally, the continental character of the reconstructed paleoclimate suggests the coastline was far removed. Generally, subsidence is compensated by sedimentation. After the Last Interglacial, sediments accumulated mainly during the Weichselian cold stage on the then-exposed Laptev Shelf and the adjacent coastal lowlands, forming 10 to 60-m thick ice-bonded permafrost (Romanovskii et al., 2000). Ice-bonded permafrost consists of up to 90% ice by volume (Ice Complex) and is therefore climatically very susceptible to melting. In the context of the thermal erosion that took place in the course of the Holocene warming, the late Quaternary sediment cover melted widely and

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[1] Due to a miscalculation, the neotectonic subsidence was underestimated by a factor of 10 in Kienast et al. (2008a, b). A rate of 2 mm per year for 130,000 years would result in 260 m (not 26 m) subsidence!

rapidly away (Romanovskii et al., 2000). The compensating effect of sedimentation on the tectonic subsidence dwindled. During the Holocene, the rising sea could advance farther. At the beginning of the Holocene, the landscape and vegetation in Arctic Yakutia first developed in ways analogous to the Eemian with the formation of widespread thermokarst and initially persisting continentality (Kaplina, 1981; Andreev et al., 2004, 2009; Kienast et al., 2005, 2008b). Arctic lowlands were initially still situated inland due to the delay in global ice sheet decay and sea level rise. Later during the course of the Holocene transgression, the climate in Arctic Yakutia gradually became influenced by the advancing sea, bringing more precipitation, milder winters and cooler summers. The former areas of tundra steppe that had previously served as refuges for megaherbivores changed dramatically in character. Suitable habitats for the mammoth faunal complex ceased to exist. In the late Holocene, when the coastline reached its current position, plant communities maintained by climatic continentality disappeared from the landscape and were replaced by wet tundra vegetation (Kienast et al., 2005). The elements of the mammoth faunal complex became extinct during the course of the Holocene (Stuart et al., 2004; Sher et al., 2005).

7. Conclusions

The presented multi-proxy-based reconstruction of local environmental conditions during the Eemian interglacial shows a shallow thermokarst lake with a pronounced macrophyte zone and a disturbed littoral zone affected by seasonal flooding and drying. This lake existed within an open larch-birch forest-tundra, interspersed with xerophilous grassland vegetation. The fossil assemblages allow the following conclusions:

1. Thermokarst processes were widespread during the Eemian interglacial in the Yakutian coastal lowlands.
2. The tree line was shifted about 270 km north of its current position and at least to the modern mainland coast. This is indicated by the macrofossil remains of *Larix dahurica* and *Alnus incana* and a high pollen concentration of *Larix*.
3. The presence of numerous extralimital species indicates that the MTWA was about 13 °C, which is more than about 9 °C higher than today.
4. Low net precipitation is indicated by the evidence of lake level fluctuations, salinification and the presence of steppe and other dry upland habitats.
5. The reconstructed climate characteristics are typical of an inland climate and are consequently inconsistent with today's coastal position. An inland position of the study site during the Last Interglacial can be inferred.
6. The finding of terrestrial and freshwater fossils at a site on the modern coast and below the Eemian sea level is evidence of considerable tectonic subsidence after the Last Interglacial, resulting in a relative coastline shift of several hundred km southward since that period.
7. In NE Siberia, the marine transgression resulting from the Eemian eustatic sea level rise advanced less than it did during the Holocene despite higher global sea levels in the Eemian. The maritime influence on the modern climate in the study area, reflected by humid conditions, relatively mild winters and cool summers, is likely the consequence of a marine transgression that advanced farther during the Holocene.

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References

ACIA, 2005. Impacts of a Warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.

ACIS, 2008. ACIS – Arctic Climate Impact Science – An Update Since ACIA. WWF International Arctic Programme, Oslo, Norway.

Aleksandrova, V.D., 1980. The Arctic and Antarctic: Their Division into Geobotanical Areas. Cambridge University Press, Cambridge.

Alekseev, M.N., 1997. Paleogeography and geochronology 800 in the Russian eastern Arctic during the second half of the Quaternary. Quaternary International 41–42, 11–15.

Alm, G., 1914. Beiträge zur Kenntnis der nördlichen und arktischen Ostracodenfauna. Arkiv för Zoologi 9, 1–20 (in German).

Alonso, M., 1996. Crustacea Branchiopoda Fauna Iberica, vol. 7. Museo Nacional de Ciencias Naturales CSIC, Madrid.

Anderberg, A.-L., 1994. Resedaceae-Umbelliferae. Atlas of Seeds and Small Fruits of Northwest-European Plant Species with Morphological Descriptions, 4. Swedish Museum of Natural History, Stockholm, 281 pp.

Andreev, V.N., 1980. Vegetation and Soils of Subarctic Tundra. Academy of Science, Siberian Subbranch Biological Institute, Nauka, Novosibirsk.

Andreev, A.A., Grosse, G., Schirrmeister, L., Tarasov, P.E., Meyer, H., Kuzmina, S.A., Novenko, E.Y., Bobrov, A.A., Ilyashuk, B.P., Kuznetsova, T.V., Krbetschek, M., Kunitsky, V.V., 2004. Late Saalian and Eemian palaeoenvironmental history of the Bolshoy Lyakhovsky Island (Laptev Sea region, Arctic Siberia). Boreas 33 (4), 319–348.

Andreev, A.A., Grosse, G., Schirrmeister, L., Kuznetsova, T.V., Kuzmina, S.A., Bobrov, A.A., Tarasov, P.E., Novenko, E.Y., Meyer, H., Derevyagin, A.Y., Kienast, F., Bryantseva, A., Kunitsky, V.V., 2009. Weichselian and Holocene palaeoenvironmental history of the Bol'shoy Lyakhovsky Island, New Siberian Archipelago, Arctic Siberia. Boreas 38 (1), 72–110.

Barkova, M.V., 1971. Spore-pollen complexes from preglacial and first glacial Late Pleistocene deposits of the Yana-Indigirka region. Paleontologiya i Biostratigrafiya 31 (in Russian).

Bauch, H.A., Erlenkeuser, H., Fahl, K., Spielhagen, R.F., Weinelt, M.S., Andruleit, H., Henrich, R., 1999. Evidence for a steeper Eemian than Holocene sea surface temperature gradient between Arctic and sub-Arctic 826 regions. Palaeogeography, Palaeoclimatology, Palaeoecology 145 (1–3), 95–117.

Bauch, H.A., Mueller-Lupp, T., Taldenkova, E., Spielhagen, R.F., Kassens, H., Grootes, P.M., Thiede, J., Heinemeier, J., Petryashov, V.V., 2001. Chronology of the Holocene transgression at the North Siberian margin. Global and Planetary Change 31 (1–4), 125–139.

Bellmann, H., 1991. Spinnen, Krebse, Tausendfüßer. Steinbachs Naturführer 9. Mosaik Verlag, Munich, 287 pp. (in German).

Berggren, G., 1969. Cyperaceae. Atlas of Seeds and Small Fruits of Northwest-European Plant Species with Morphological Descriptions, 2. Swedish Natural Science Research Council, Stockholm, 107 pp.

Berggren, G., 1981. Salicaceae–Cruciferae. Atlas of Seeds and Small Fruits of Northwest-European Plant Species with Morphological Descriptions, 3. Swedish Museum of Natural History, Stockholm, 261 pp.

Berglund, B.E., Ralska-Jasiewiczowa, M., 1986. Pollen analysis and pollen diagrams. In: Berglund, B. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. Interscience, New York, pp. 455–484.

Berman, D.I., Alfimov, A.V., Zhigulskaya, Z.A., Leirikh, A.N., 2007. Wintering and Cold Hardiness of Ants in North-East Asia. KMK Scientific Press Ltd, Moscow (in Russian).

Binney, H.A., Willis, K.J., Edwards, M.E., Bhagwat, S.A., Anderson, P., Andreev, A.A., Blaauw, M., Damblon, F., Haesaerts, P., Kienast, F.W., Kremenetski, K.V., Krivonogov, S.K., Lozhkin, A.V., Macdonald, G.M., Novenko, E.Y., Oksanen, P., Sapelko, T.V., Valiranta, M., Vazhenina, L., 2009. The distribution of late-Quaternary woody taxa in Eurasia: evidence from a new macrofossil database. Quaternary Science Reviews 28 (23-24), 2445–2464.

Böcher, T.W., 1954. Oceanic and continental vegetational complexes in Southwest Greenland. Meddelelser om Grønland 148 (1), 1–336.

Brigham-Grette, J., Hopkins, D.M., 1995. Emergent marine record and paleoclimate of the Last Interglaciation along the Northwest Alaskan Coast. Quaternary Research 43 (2), 159–173.

Brodin, Y., 1986. The postglacial history of Lake Flarken, interpreted from subfossil insect remains. Internationale Revue der gesamten Hydrobiologie 71, 371–432.

Brooks, S.J., Birks, H.J.B., 2000. Chironomid-inferred late-glacial and early-Holocene mean July air temperatures for Kråkenes Lake, western Norway. Journal of Paleolimnology 23, 77–89.

Brodersen, K.P., Anderson, J.N., Odgaard, B.V., 2001. Long-term trends in the profundal chironomid-fauna in nitrogen limited Lake Esrom, Denmark: a combined palaeolimnological/historical approach. Archiv für Hydrobiologie 150, 393–409.

Brooks, S.J., Langdon, P.G., Heiri, O., 2007. Using and identifying chironomid larvae in palaeoecology. QRA Technical Guide No. 10. Quaternary Research Association, London, UK.

Campos, P.F., Willerslev, E., Sher, A., Orlando, L., Axelsson, E., Tikhonov, A., Aaris-Sørensen, K., Greenwood, A.D., Kahlke, R.-D., Kosintsev, P., Krakhmalnaya, T., Kuznetsova, T., Lemey, P., MacPhee, R., Norris, C.A., Shepherd, K., Suchard, M.A., Zazula, G.D., Shapiro, B., Gilbert, M.T.P., 2010. Ancient DNA analyses exclude humans as the driving force behind late Pleistocene musk ox (*Ovibos moschatus*) population dynamics. Proceedings of the National Academy of Sciences 107 (12), 5675–5680.

CAPE-Last Interglacial Project, 2006. Last Interglacial Arctic warmth confirms polar amplification of climate change. Quaternary Science Reviews 25 (13–14), 1383–1400.

CAVM-Team, 2003. Circumpolar Arctic vegetation map. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Chapin III, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.L., Tape, K.D., Thompson, C.D.C., Walker, D.A., Welker, J.M., 2005. Role of land-surface changes in Arctic summer warming. Science 310 (5748), 657–660.

Chernov, Yu.I., 1972. Structure of The Animal Population of The Subarctic. Nauka, Moscow (in Russian).

Cranston, P.S., Oliver, D.R., Saether, O.A., 1983. The larvae of Othocladiinae (Diptera: Chironomidae) of the Holarctic region – keys and diagnoses. In: Wiederholm (Ed.), Chironomidae of The Holarctic Region, Part I – Larvae. Entomologica Scandinavica, Suppl. 19, pp. 149–291.

Crawford, R.M.M., Jeffree, C.E., Rees, W.G., 2003. 876 Paludification and forest retreat in northern oceanic environments. Annals of Botany 91 (Spec. Iss. Jan.), 213–226.

Danby, R.K., Hik, D.S., 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. Journal of Ecology 95 (2), 352–363.

DeMott, W.R., Kerfoot, W.C., 1982. Competition among cladocerans: nature of the interaction between Bosmina and Daphnia. Ecology 63, 1949–1966.

Dierßen, K., 1996. Vegetation Nordeuropas. Eugen Ulmer Verlag, Stuttgart, 838 pp.

Drachev, S.S., Kaul, N., Beliaev, V.N., 2003. Eurasia spreading basin to Laptev shelf transition: structural pattern and heat flow. Geophysical Journal International 152 (3), 688–698.

Drachev, S.S., Savostin, L.A., Groshev, V.G., Bruni, I.E., 1998. Structure and geology of the continental shelf of the Laptev Sea, Eastern Russian Arctic. Tectonophysics 298 (4), 357–393.

Dumas, B., Hoang, C.T., Raffy, J., 2006. Record of MIS 5 sea-level highstands based on U/Th dated coral terraces of Haiti. Quaternary International 145–146, 106–118.

Edwards, M.E., Brubaker, L.B., Lozhkin, A.V., Anderson, P.M., 2005. Structurally novel biomes: a response to past warming in Beringia. Ecology 86 (7), 1696–1703.

Ellenberg, H., 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Eugen Ulmer, Stuttgart, 1096 pp.

Flössner, D., 2000. Die Haplopoda und Cladocera (ohne Bosminidae) Mitteleuropas. Backhuys Publishers, Leiden, 428 pp.

Franke, D., Hinz, K., Oncken, O., 2001. The Laptev Sea rift. Marine and Petroleum Geology 18 (10), 1083–1127.

Franke, D., Hinz, K., Reichert, C., 2004. Geology of the East Siberian Sea, Russian Arctic, from seismic images: structures, evolution, and implications for the evolution of the Arctic Ocean Basin. Journal of Geophysical Research B: Solid Earth 109 (7).

Frey, D.G., 1959. The taxonomic and phylogenetic significance 902 of the head pores of the Chydoridae (Cladocera). Internationale Revue der gesamten Hydrobiologie 44, 27–50.

Frey, D.G., 1986. Cladocera analysis. In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. Wiley, Chichester, pp. 667–692.

Gill, J.L., Williams, J.W., Jackson, S.T., Lininger, K.B., Robinson, G.S., 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. Science 326 (5956), 1100–1103.

Giterman, R.E., Sher, A.V., Mathewes Jr., J.V., 1982. Comparison of the development of tundra-steppe environments in East and West Beringia: pollen and macrofossil evidence from key sections. In: Hopkins, D.M., Matthews Jr., J.V., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, pp. 43–73.

Glöer, P., 2002. Die Süßwassergastropoden Nord- und Mitteleuropas. Die Tierwelt Deutschlands, Bd. 73. Conch Books, 327 pp.

Glöer, P., Meier-Brook, C., 2003. Süßwassermollusken – Ein Bestimmungsschlüssel für die Bundesrepublik Deutschland. Deutscher Jugendbund für Naturbeobachtungen 13, Auflage, 134 pp.

Goulden, C.E., Frey, D.G., 1963. The occurrence and significance of lateral head pores in the genus Bosmina (Cladocera). Internationale Revue der gesamten Hydrobiologie 48, 513–522.

Grichuk, V.P., 1984. Late Pleistocene vegetation history. In: Velichko, A.A. (Ed.), Late Quaternary Environments of the Soviet Union. University of Minnesota Press, Minneapolis, pp. 155–178.

Guiot, J., 1990. Methodology of the last climatic cycle reconstruction in France from pollen data Palaeogeography. Palaeoclimatology, Palaeoecology 80 (1), 49–69.

Hess, M., 1993. Benthische und epiphytische Makroinvertebraten-Gemeinschaften. In: Fittkau, E.J., Colling, M., Hess, V., Hoffman, G., Orendt, C., Reiff, N., Riss, W., Colling, H.W.M. (Eds.), Biologische 928 Trophieindikation im Litoral von Seen. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft 7, Munich, 184 pp. (in German).

IQW, 2009. Index Herbariorum: Herbarium Senckenbergianum Weimar. Available from: http://sweetgum.nybg.org/ih/herbarium.php?irn=154437.

Ivanenko, G.V., 1998. Map of Quaternary deposits. S-53–55 (New Siberian Islands), State Geological Map of the Russian Federation (New Series). St. Petersburg Cartographic Factory VSEGEI, St. Petersburg.

Ivanov, O.A., 1972. Stratigraphy and correlation of Neogene and Quaternary deposits in the subarctic plains of East Yakutia. Problemy izucheniya chetvertichnogo perioda (Problems in the study of the Quaternary period). Nauka, Moscow.

Iversen, J., 1944. Viscum, Hedera und Ilex as Climate Indicators. Geologiska Foreningens i Stockholm Forhandlingar 66, 463–483.

Jessen, K., 1955. Key to Subfossil Potamogeton. Botanisk Tidsskrift 52, 1–7.

Juggins, S., 2007. C2 Version 1.5: Software for Ecological and Palaeoecological Data Analysis and Visualisation [Program]. University of Newcastle, Newcastle upon Tyne.

Kahlke, R.-D., 1999. The History of the Origin, Evolution and Dispersal of the Late Pleistocene Mammuthus–Coelodonta Faunal Complex in Eurasia (Large Mammals). Fenske, Rapid City, pp. 1–219.

Kaplina, T.N., 1981. Istoriya merzlykh tolshch cevernoy Yakutii v pozdnyom kaynozoye (The history of permafrost in North Yakutia during the late Cenozoic). In: Dubikov, G.I., Baulin, V.V. (Eds.), Istoriya razvitiya mnogolyetnemerzlykh porod Yevrazii (The History of The Development of Perennially Frozen Deposits in Eurasia). Nauka, Moscow, pp. 153–181.

Kaplina, T.N., 1987. Zakonomernosti razvitiya kriolitogeneza v pozdnyom kainozoye na akkumulyativnykh ravninakh Severo-Vostoka Azii (Regularity of cryolithogenesis developing on accumulation plains in north-eastern 954 Asia during the Late Cenozoic). Thesis of doctor of Science, Yakutsk (in Russian).

Kaplina, T.N., Lozhkin, A.V., 1982. The age of the ice complex in the coastal lowlands of Yakutia. Izvestiya AN SSSR. Seria Geograficheskaya 2, 84–95.

Kaplina, T.N., Giterman, R.E., Lakhtina, O.V., Abrashov, B.A., Kiselev, S.V., Sher, A.V., 1978. Duvanny Yar – key section of Late Pleistocene deposits in the Kolyma lowland. Bulletin of The Commission of Studies of The Quaternary Period 48, 49–65.

Kaplina, T.N., Lyakhtina, O.V., Rybakova, N.O., 1980a. The history of landscapes and permafrost sequences in the Kolyma lowlands according to radiocarbon dating, cryolithological and palynological data (exemplified at the profile Stanchikovy Yar at the Maly Anyuy River). Geochronologiya chetvertichnogo perioda. Nauka, Moscow (in Russian).

Kaplina, T.N., Sher, A.V., Giterman, R.E., Zazhigin, S.V., Kiselev, S.V., Lozhkin, A.V., Nikitin, V.P., 1980b. The key Section of Pleistocene deposits on the Allaikha River (lower reach of the Indigirka River). Byulleten komissii po izucheniyu chetvertichnogo perioda 50, 73–95.

Kats, N.Y., Kats, S.V., Kipiani, M.G., 1965. Atlas and Keys of Fruits and Seeds Occurring in The Quaternary Deposits of The USSR. Nauka, Moscow, 366 pp.

Kayalainen, V.I., Kulakov, Y.N., 1966. Kvoprosy paleogeografii Yana-Indigirskoi nizmenosti v Neogeno-Chetvertichnom periode (On questions of Paleogeography in the Yana-Indigirka coastal lowlands during the Neogene-Quaternary period). In: Saks, V.N. (Ed.), Chetvertichnyi period v Sibiri (Quaternary Period in Siberia). Nauka, Moscow, pp. 274–283 (in Russian).

Khruleva, O.A., 2009. Steppe-tundra groups of Arthropoda of the Wrangel Island. In: Babenko, A.B., Matveeva, N.A., Makarova, O.L., Golovach, C.I. (Eds.), Species and Communities in Extreme Environments. KMS 979 Scientific Press, Moscow-Sofia, pp. 124–167 (in Russian).

Kienast, F., Schirrmeister, L., Siegert, C., Tarasov, P., 2005. Palaeobotanical evidence for warm summers in the East Siberian Arctic during the last cold stage. Quaternary Research 63 (3), 283–300.

Kienast, F., Schirrmeister, L., Wetterich, S., 2008a. Vegetation differentiation across a topographic Yedoma – Alas Transect in the High Arctic Tundra of Oyogos Yar, East Siberia. In: Kane, D.L., Hinkel, K.M. (Eds.), Ninth International Conference on Permafrost. Institute of Northern Engineering, University of Alaska Fairbanks, Fairbanks, Alaska, pp. 937–940.

Kienast, F., Tarasov, P., Schirrmeister, L., Grosse, G., Andreev, A.A., 2008b. Continental climate in the East Siberian Arctic during the Last Interglacial: implications from palaeobotanical records. Global and Planetary Change 60 (3–4), 535–562.

Killeen, I., Aldridge, D., Oliver, G., 2004. Freshwater bivalves of Britain and Ireland. In: Occasional Publication, 82. National Museum of Wales. 114pp.

Kiselev, S.V., 1981. Late Cenozoic Coleoptera of North-East Siberia. Nauka, Moscow.

Kiselev, S.V., Nazarov, V.I., 2009. Late cenozoic insects of Northern Eurasia. Paleontological Journal Supplement 43 (7), 1–128. Pleiades Publishing, Ltd.

Konishchev, V.N., Koleshnikov, S.F., 1981. Osobennosti stroeniya i sostava pozdnekainozoiskikh otlozheniyakh b obnazhenii Oyagosskii Yar. (Specifics of structure and composition of late Cenozoic deposits in the section of Oyogos Yar). Problemy Kriolitologii (Problems of Cryolithology). Moscow State University Publishers, Moscow, pp. 107–117.

Korhola, A., Rautio, M., 2001. Cladocera and other branchiopod crustaceans. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments. Zoological Indicators, vol. 4. Kluwer Academic 1004 Publishers, Dordrecht, Boston, London, pp. 5–41.

Krasnoborov, I.M., Malyshev, L.I., 2003. Salicaceae – Amaranthaceae. In: Flora of Siberia, 5. Science Publishers, Inc., Enfield (NH), USA, 305 pp.

Kuiper, J.G.J., 1962. Etude critique de Pisidium vincentianum. Institut royal des Sciences naturelles de Belgique 46, 1–19.

Kuiper, J.G.J., 1968. Die spätpleistozänen Pisidien des ehemaligen Ascherslebener Sees. Archiv für Molluskenkunde 98 (1/2), 23–38 (in German).

Lavrushin, Y.A., 1963. The Alluvium of The Lowland Rivers in The Subarctic Zone and The Periglacial of Inland Glaciations. Trudy IG AN SSSR, Moscow, 87 pp. (in Russian).

Leemans, R., Cramer, W., 1991. The IIASA Climate Database for Mean Monthly Values of Temperature, Precipitation and Cloudiness on A Global Terrestrial Grid. International Institute of Applied Systems Analysis, Luxemburg (updated version).

Lozhkin, A.V., Anderson, P.M., 1995. The Last Interglaciation in Northeast Siberia. Quaternary Research 43 (2), 147–158.

Malyschev, L.I., 2000. Lycopodiaceae–Hydrocaritaceae. Flora of Siberia, 1. Science Publishers, Enfield, NH, USA, 190 pp.

Malyschev, L.I., 2006. Pyrolaceae–Lamiaceae. Flora of Siberia, 11. Science Publishers, Enfield, NH, USA, 310 pp.

Malyschev, L.I., Peschkova, G.A., 2001a. Araceae–Orchidaceae. Flora of Siberia, 4. Science Publishers, Enfield, NH, USA, 239 pp.

Malyschev, L.I., Peschkova, G.A., 2001b. Cyperaceae. 1029 Flora of Siberia, 3. Science Publishers, Enfield, NH, USA, 277 pp.

Malyschev, L.I., Peschkova, G.A., 2003. Portulacaceae–Ranunculaceae. Flora of Siberia, 6. Science Publishers, Enfield, New Hampshire, USA, 301 pp.

Malyschev, L.I., Peschkova, G.A., 2004. Berberidaceae–Grossulariaceae. Flora of Siberia, 7. Science Publishers, Enfield, NH, USA, 318 pp.

Makarchenko, E.A., Makarchenko, M.A., 1999. Chironomidae. In: Tsalolikhin, S.J. (Ed.), Key to Freshwater Invertebrates of Russia and Adjacent Lands, vol. 4. Zoological Institute RAS, St. Petersburg, pp. 210–295, pp. 670–857 (in Russian).

Massaferro, J., Brooks, S., 2002. The response of chironomids to Late Quaternary climate change in the Taitao Peninsula, southern Chile. Journal of Quaternary Science 17, 101–111.

Meisch, C., 2000. Freshwater Ostracoda of Western and Central Europe. Spektrum Akademischer Verlag, Heidelberg, Berlin, 522 pp.

Nazarova, L., Kumke, T., Pestryakova, L., Hubberten, H.-W., 2005. Chironomid fauna of Central Yakutian lakes (Northern Russia) in palaeoenvironmental investigations. Chironomus 18, 25–27.

Nazarova, L.B., Pestryakova, L.A., Ushnitskaya, L.A., Hubberten, H.-W., 2008. Chironomids (Diptera: Chironomidae) in lakes of Central Yakutia and their indicative potential for paleoclimatic research. Sibirskii Ekologicheskii Zhurnal 15 (3), 141–150 (in Russian).

Nakagawa, T., Tarasov, P.E., Nishida, K., Gotanda, K., Yasuda, Y., 2002. Quantitative pollen-based climate reconstruction in central Japan: application to surface and Late. Quaternary spectra Quaternary Science Reviews 21 (18-19), 2099–2113.

Nazarova, L., Herzschuh, U., Wetterich, S., Kumke, T., Pestryakova, L., 2011. Chironomid-based inference models for estimating mean July air temperature and water depth from lakes in Yakutia, northeastern Russia. Journal of Paleolimnology 45 (1), 57–71.

Nikonov, A.A., 1977. Holocene and Contemporary Movements of The Earth Crust. Nauka, Moscow, 240 pp.

Pejler, B., 1975. On Long-term Stability of Zooplankton Composition. Institute of Freshwater Research, Drottningholm (Report No. 54) pp. 107–117.

Peschkova, G.A., 2006. Geraniaceae–Cornaceae. Flora of Siberia, 10. Science Publishers, Enfield, NH, USA, 314 pp.

Péwé, T.L., 1973. Ice wedge casts and past permafrost distribution in North America. Geoforum 4 (3), 15–26.

Piechocki, A., 1989. The Sphaeriidae of Poland (Bivalvia, Eulamellibranchia). Annales Zoologici 42 (12), 249–318.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13, 131–144.

Pietrzeniuk, E., 1977. Ostracoden aus Thermokarstseen und Altwässern in Zentral-Jakutien. Mitteilungen aus dem Zoologischen Museums in Berlin 53, 331–362 (in German).

Pinder, L.C.V., Reiss, F., 1983. The larvae of Chironominae (Diptera: Chironomidae) of the Holarctic region. Keys and diagnoses. Entomol Scand Suppl 19, 293–435.

Polozhij, A.V., Malyschev, L.I., 2004. Rosaceae. Flora of Siberia, 8. Science Publishers, Enfield, NH, USA, 197 pp.

Rivas-Martínez, S., 1996–2009. Climate diagrams. Worldwide Bioclimatic Classification System. Phytosociological Research Center, Spain. http://www.globalbioclimatics.org/plot/diagram.htm.

Rjabov, F.P., Dyga, A.K., Kirilenko, A.S., Derkachenko, V.I., Aleshkina, R.S., 1980. Selfpurification and Bioindication of Polluted Waters. Nauka, pp. 227–231.

Romanovskii, N.N., 1958. Merzlotnye struktury v Chetvertichnykh otlozhenyakh. (Permafrost structures in Quaternary deposits). Proceedings of the Academy of Sciences of the USSR, Series Geology 3, 185–189 (in Russian).

Romanovskii, N.N., 1961. On the structure of the 1081 alluvial plain in the Yana-Indigirka coastal lowlands and the conditions of its formation. Merzlotnye Issledovaniya (Geocryological Studies). Moscow State University Publishing. Moscow (in Russian).

Romanovskii, N.N., et al., 2000. Thermokarst and land–ocean interactions, Laptev Sea region, Russia. Permafrost and Periglacial Processes 11 (2), 137–152.

Sarmaja-Korjonen, K., 2002. Multi-proxy data from Kaksoislammi Lake in Finland: dramatic changes in the late Holocene cladoceran assemblages. Journal of Paleolimnology 28, 287–296.

Schirrmeister, L., Grosse, G., Kunitsky, V.V., Meyer, H., Derevyagin, A.Y., Kuznetsova, T., 2003. Permafrost, periglacial and paleo-environmental studies on New Siberian Islands. Reports on Polar and Marine Research 466, 195–314.

Schirrmeister, L., Grosse, G., Kunitsky, V., Magens, D., Meyer, H., Dereviagin, A., Kuznetsova, T., Andreev, A., Babiy, O., Kienast, F., Grigoriev, M., Overduin, P.P., Preusser, F., 2008a. Periglacial landscape evolution and environmental changes of Arctic lowland areas for the last 60.000 years (western Laptev Sea coast, Cape Mamontov Klyk). Polar Research 27 (2), 249–272.

Schirrmeister, L., Wetterich, S., Kunitsky, V., Tumskoy, V., Dobrynin, D., Dereviagin, A., Opel, T., Kienast, F., Kuznetsova, T., Gorodinski, A., 2008b. Palaeoenviromental studies on the Oyogos Yar coast; Studies of Eemian (Krest Yuryakh Suite) and pre Eemian (Kuchchugui, Bychchagy Suite) sections. Reports on Polar and Marine Research 584, 85–99.

Schirrmeister, L., Wetterich, S., Kunitsky, V.V., Tumskoy, V.E., Dobrynin, D., Derevyagin, A.Y., Opel, T., Kienast, F., Kuznetsova, T., Gorodinsky, A., 2008c. Palaeoenviromental studies on the Oyogos Yar coast. Reports on Polar and Marine Research 584, 85–154.

Schirrmeister, L., Kunitsky, V., Grosse, G., Wetterich, S., Meyer, H., Schwamborn, G., Babiy, O., Derevyagin, A. and Siegert, C. Sedimentary characteristics and origin of the Late Pleistocene Ice Complex on north-east Siberian Arctic coastal lowlands and islands - A review. Quaternary International, in press,

Schuur, E.A.G., Vogel, J.G., Crummer, K.G., Lee, H., Sickman, J.O., Osterkamp, T.E., 2009. The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. Nature 459, 556–559.

Screen, J.A., Simmonds, I., 2010. The central role of diminishing sea ice in recent Arctic temperature amplification. Nature 464, 1334–1337.

Sher, A.V., 1991. Problems of the Last Interglacial in Arctic Siberia. Quaternary International 10–12, 215–222.

Sher, A.V., 1997. A brief overview of the Late-Cenozoic history of the Western Beringian lowlands. In: Edwards, M.E., Sher, A.V., Guthrie, R.D. (Eds.), Terrestrial Paleoenvironmental Studies in Beringia, Proceedings of A Joint Russian–American Workshop, June 1991. The Alaska Quaternary Center, Fairbanks, Alaska, pp. 3–6.

Sher, A.V., Kuzmina, S.A., Kuznetsova, T.V., Sulerzhitsky, L.D., 2005. New insights into the Weichselian environment and climate of the East Siberian Arctic, derived from fossil insects, plants, and mammals. Quaternary Science Reviews 24 (5, 6), 533–569.

Sher, A.V., Kuzmina, S.A., Kiselyov, S.V., Korotyaev, B.A., Alfimov, A.V., Berman, D.I., 2006. QUINSIB–The Database on Quaternary Insects of North-Eastern Siberia.

Smirnov, N.N., 1974. Fauna of the U.S.S.R.: Crustacea. In: Chydoridae, vol. 1. Israel Program for Scientific Translations, Jerusalem, Number 2644 pp.

Smirnov, N.N., 1996. Cladocera: the Chydorinae and Sayciinae (Chydoridae) of the world. Guides to The Identification of The Microinvertebrates of Continental Waters of The World. SPB Academic Publishing, Amsterdam, 197 pp.

Stow, D.A., Hope, A., McGuire, D., Verbyla, D., Gamon, J., Huemmrich, F., Houston, S., Racine, C., Sturm, M., Tape, K., Hinzman, L., Yoshikawa, K., Tweedie, C., Noyle, B., Silapaswan, C., Douglas, D., Griffith, B., Jia, G., Epstein, H., Walker, D., Daeschner, S., Petersen, A., Zhou, L., Myneni, R., 2004. Remote sensing of vegetation and land-cover change in Arctic Tundra 1131 ecosystems. Remote Sensing of Environment 89 (3), 281–308.

Streble, H., Krauter, D., 2002. Das Leben im Wassertropfen. Mikroflora und Mikrofauna des Süßwassers. Franck–Kosmos Verlag, Stuttgart, 428 pp. (in German).

Stuart, A.J., Kosintsev, P.A., Higham, T.F.G., Lister, A.M., 2004. Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. Nature 431 (7009), 684–689.

Svendsen, J.I., Alexanderson, H., Astakhov, V.I., Demidov, I., Dowdeswell, J.A., Funder, S., Gataullin, V., Henriksen, M., Hjort, C., Houmark-Nielsen, M., 2004. Late Quaternary ice sheet history of northern Eurasia. Quaternary Science Reviews 23 (11–13), 1229–1271.

Tape, K., Sturm, M., Racine, C., 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12 (4), 686–702.

Tarasov, P., Bezrukova, E., Karabanov, E., Nakagawa, T., Wagner, M., Kulagina, N., Letunova, P., Abzaeva, A., Granoszewski, W., Riedel, F., 2007. Vegetation and climate dynamics during the Holocene and Eemian interglacials derived from Lake Baikal pollen records. Palaeogeography, Palaeoclimatology, Palaeoecology 252 (3, 4), 440.

Tarasov, P., Granoszewski, W., Bezrukova, E., Brewer, S., Nita, M., Abzaeva, A., Oberhänsli, H., 2005. Quantitative reconstruction of the Last Interglacial vegetation and climate based on the pollen record from Lake Baikal, Russia. Climate Dynamics 25 (6), 625–637.

Tsuyuzaki, S., Sento, N., Fukuda, M., 2010. Baidzharakhs (relic mounds) increase plant community diversity by interrupting zonal vegetation distribution along the Arctic Sea, northern Siberia. Polar Biology 33 (4), 565–570.

Vavrus, S., Waliser, D., Schweiger, A., Francis, J., 2009. Simulations of 20th and 21st century Arctic cloud amount in the global climate models assessed in the IPCC AR4. Climate Dynamics 33 (7), 1099–1115.

Vinokurov, N.N., 1979. True Bugs (Heteroptera) Insects of Yakutia. VMGO, Nauka, Leningrad (in Russian).

Voeikov Main Geophysical Observatory, 1980. Climatic atlas of Asia. In: WMO, UNESCO (Eds.), Goscomgidromet USSR. Gidrometeoizdat, Leningrad.

Walker, I.R., Mathewes, R.W., 1989. Chironomidae (Diptera) remains in surficial lake sediments from the Canadian Cordillera: analysis of the fauna across an altitudinal gradient. Journal of Paleolimnology 2, 61–80.

Weber, H.E., Moravec, J., Theurillat, J.-P., 2000. International code of phytosociological nomenclature, third edition. Journal of Vegetation Sciences vol. 11, 739–768.

Wetterich, S., Kuzmina, S., Andreev, A.A., Kienast, F., Meyer, H., Schirrmeister, L., Kuznetsova, T., Sierralta, M., 2008a. Palaeoenvironmental dynamics inferred from late Quaternary permafrost deposits on Kurungnakh Island, Lena Delta, Northeast Siberia, Russia. Quaternary Science Reviews 27 (15–16), 1523–1540.

Wetterich, S., Schirrmeister, L., Meyer, H., Siegert, C., 2008b. Thermokarst lakes in Central Yakutia (Siberia) as habitats of freshwater Ostracods and archives of palaeoclimate. In: Kane, D.L., Hinkel, K.M. (Eds.), Ninth International Conference on Permafrost. University of Alaska Fairbanks, Institute of Northern Engineering, pp. 1945–1950.

Wetterich, S., Schirrmeister, L., Meyer, H., Viehberg, F.A., Mackensen, A., 2008c. Arctic freshwater ostracods from modern periglacial environments in the Lena River Delta (Siberian Arctic, Russia): geochemical applications for palaeoenvironmental reconstructions. Journal of Paleolimnology 39 (4), 427–449.

Wetterich, S., Schirrmeister, L., Andreev, A.A., Pudenz, M., Plessen, B., Meyer, H., Kunitsky, V.V., 2009. Eemian and Late Glacial/Holocene palaeoenvironmental records from permafrost sequences at the Dmitry Laptev Strait (NE Siberia, Russia). Palaeogeography, Palaeoclimatology, Palaeoecology 279 (1–2), 73–95.

Wiederholm, T., 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. Entomologica Scandinavica, Suppl. 19.

Wilson, D.G., 1973. Notable plant records from the Cromer forest bed series. New Phytologist 72 (5), 1207–1234.

Yurtsev, B.A., 1981. Reliktovye Stepnye Kompleksy Severo-Vostochnoy Asii, Problemy rekonstruktsii krioxeroticheskikh landshaftov Beringii (Relict steppe Complexes in Northeastern Asia, Problems of the reconstruction of Beringia's kryoxeric landscapes). Nauka, Novosibirsk, 168 pp.

Yurtsev, B.A., 1982. Relics of the xerophyte vegetation of Beringia in Northeastern Asia. In: Hopkins, D.M., Matthews, J.V., Schweger Jr., C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, pp. 157–177.

Yurtsev, B.A., 2001. The Pleistocene "Tundra-Steppe" and the productivity paradox: the landscape approach. Quaternary Science Reviews 20 (1–3), 165–174.