

Interglacial history of a palaeo-lake and regional environment: a multi-proxy study of a permafrost deposit from Bol'shoy Lyakhovsky Island, Arctic Siberia

Boris P. Ilyashuk^{1,*}, Andrei A. Andreev², Anatoly A. Bobrov³, Vladimir E. Tumskey⁴ and Elena A. Ilyashuk¹

¹Institute of North Industrial Ecology Problems, Kola Science Center, Russian Academy of Sciences, Fersman St. 14, 184209 Apatity, Russia; ²Alfred Wegener Institute for Polar and Marine Research, Research Unit Potsdam, Telegrafenberg A43, 14473 Potsdam, Germany; ³Faculty of Soil Science, Moscow State University, Vorobiev Gory, 119992 Moscow, Russia; ⁴Faculty of Geography, Moscow State University, Vorobiev Gory, 119992 Moscow, Russia; *Author for correspondence (e-mail: ilboris@yandex.ru)

Received 21 July 2005; accepted in revised form 6 December 2005

Key words: Chironomids, Last Interglacial, Palaeoenvironment, Pollen, Rhizopods, Yakutia

Abstract

Chironomid, pollen, and rhizopod records from a permafrost sequence at Bol'shoy Lyakhovsky Island (New Siberian Archipelago) document the development of a thermokarst palaeo-lake and environmental conditions in the region during the last Interglacial (MIS 5e). Open Poaceae and *Artemisia* associations dominated vegetation at the beginning of the interglacial period. Rare shrub thickets (*Salix*, *Betula nana*, *Alnus fruticosa*) grew in more protected and wetter places as well. Saalian ice wedges started to melt during this time, resulting in the formation of an initial thermokarst water body. The high percentage of semi-aquatic chironomids suggests that a peatland-pool initially existed at the site. A distinct decrease in semi-aquatic chironomid taxa and an increase in lacustrine ones point to a gradual pooling of water in the basin, which could in turn induce thermokarst and create a permanent pond during the subsequent period. The highest relative abundance of *Chironomus* and *Procladius* reflects unfrozen water remaining under the ice throughout the ice-covered period during the later stage of palaeo-lake development. The chironomid record points to three successive stages during the history of the lake: (1) a peatland pool; (2) a pond (i.e., shallower than the maximum ice-cover thickness); and (3) a shallow lake (i.e., deeper than the maximum ice-cover thickness). The trend of palaeo-lake development indicates that intensive thermokarst processes occurred in the region during the last Interglacial. Shrub tundra communities with *Alnus fruticosa* and *Betula nana* dominated the vegetation during the interglacial optimum. The climate was moister and warmer than present. The results of this study suggest that quantitative chironomid-based temperature reconstructions from Arctic thermokarst ponds/lakes may be problematic due to other key environmental factors, such as prolonged periods of winter anoxia and local hydrological/geomorphological processes, controlling the chironomid assemblages.

Introduction

Several palaeolimnological studies have now been completed in Northern Russia to address a variety

of environmental questions (e.g., Andreev et al. 2005; Ilyashuk et al. 2005; Ochiai and Kashiwaya 2005; Solovieva et al. 2005; Wetterich et al. 2005). Whereas the Quaternary history of NW-Eurasian

glaciations (from Scandinavia to the Taymyr Peninsula) has been well studied within the framework of the QUEEN project (Quaternary Environment of the Eurasian North) during the last years, the history of the mostly non-glaciated NE-Eurasian region, including Arctic Siberia, is still poorly documented. Quaternary permafrost sequences since the Saalian Glacial (corresponding to marine isotope stage MIS 7) are well exposed on the south coasts of Bol'shoy Lyakhovsky Island (New Siberian Archipelago). These were studied at the Zimov'e River key site as part of a joint German–Russian project on the 'Laptev Sea System' in 1999 (Schirmer et al. 2000).

Previous multidisciplinary studies of permafrost sequences resulted in the reconstruction of the palaeoenvironmental history of the region since the late Saalian time (MIS 7, prior to 200 ka) (Schirmer et al. 2000, 2002a; Kuzmina 2002; Meyer et al. 2002; Tumskey 2002; Andreev et al. 2004). Of special interest within this profile are the last Interglacial (MIS 5e, ca. 130–120 ka) deposits, which survived within the few buried ice wedge casts. This paper presents new interglacial chironomid, pollen, and rhizopod records of higher resolution from a 4 m long section of lacustrine sediments collected from an ice wedge cast (the so-called R35 section) situated west of the Zimov'e River. The results of this study will help in understanding the environment changes in Arctic Siberia during the last Interglacial.

Study area

The Bol'shoy Lyakhovsky Island belongs to the New Siberian Archipelago and is located between the Laptev Sea and the East Siberian Sea (Figure 1). The island extends between 73°10'–73°54' N 140°08'–144°20' E and covers 5300 km² with maximum elevation of 293 m a.s.l. The New Siberian Archipelago is located in a Cretaceous tectonic depression and the total thickness of the Cretaceous deposits in the archipelago area is 2–8 km (Zaitsev 1989). The 400–500 m surface layer of deposits is Neogene-Pleistocene clayey and sandy marine, alluvial and lake sediments (Zaitsev 1989).

The modern climate on the island is Arctic coastal. Winters are long (8 months), cold and dry, and summers are short and cool. Mean air

temperatures for January and July are –28 °C and 2 °C, respectively, with mean annual air temperature of –14 °C and mean annual precipitation of 100 mm, based on meteorological data collected at the closest weather station, Mys Shalaurova (73°11' N, 143°56' E; 21 m a.s.l.), situated in the south-eastern part of the Bol'shoy Lyakhovsky Island (<http://www.weatherbase.com/weather/weather.php3?s=074612&refer=>).

The island is in the continuous permafrost zone where the prevailing permafrost thickness is more than 500 m (Grigoriev et al. 1996), while the active layer thickness is about 30–40 cm. Soils in the area are mainly tundra-gley and peaty-gley. Moss-grass low-shrub tundra dominates the vegetation, with vascular plant species such as *Salix pulchra*, *Cassiope tetragona*, *Dryas punctata*, *Oxyria digyna*, *Alopecurus alpinus*, *Poa arctica*, *Carex ensifolia*, *C. rotundifolia* and *Eriophorum medium*.

The studied site is located on the southern coast of the island 3.5 km west of the Zimov'e River mouth (Figure 1) where the shoreline is formed as a natural coastal cliff up to 15 m in height a.s.l., allowing investigations into the depth without drilling equipment.

Methods

Field work

The first field work comprised a preliminary cryolithological description of the permafrost sequence in the R35 section and the surrounding sites as well as sampling. The R35 section (73°20' N, 141°16' E), consisting of a 400 cm thick profile of lacustrine sediments, was sampled every 40 cm (eleven samples S11–S1, 120–520 cm a.s.l.; Figure 2). As the sediments below the 120 cm a.s.l. were removed by modern wave erosion, it was not possible to sample one continuous profile. Additionally, samples from the non-lacustrine deposits surrounding the ice wedge cast (seven samples S31–S25, 130–370 cm a.s.l.) and from the transition horizon between the lacustrine and non-lacustrine deposits (sample S12, 180 cm a.s.l.; Figure 2) were collected in order to provide data for detailed interpretation vegetation changes. The frozen samples were

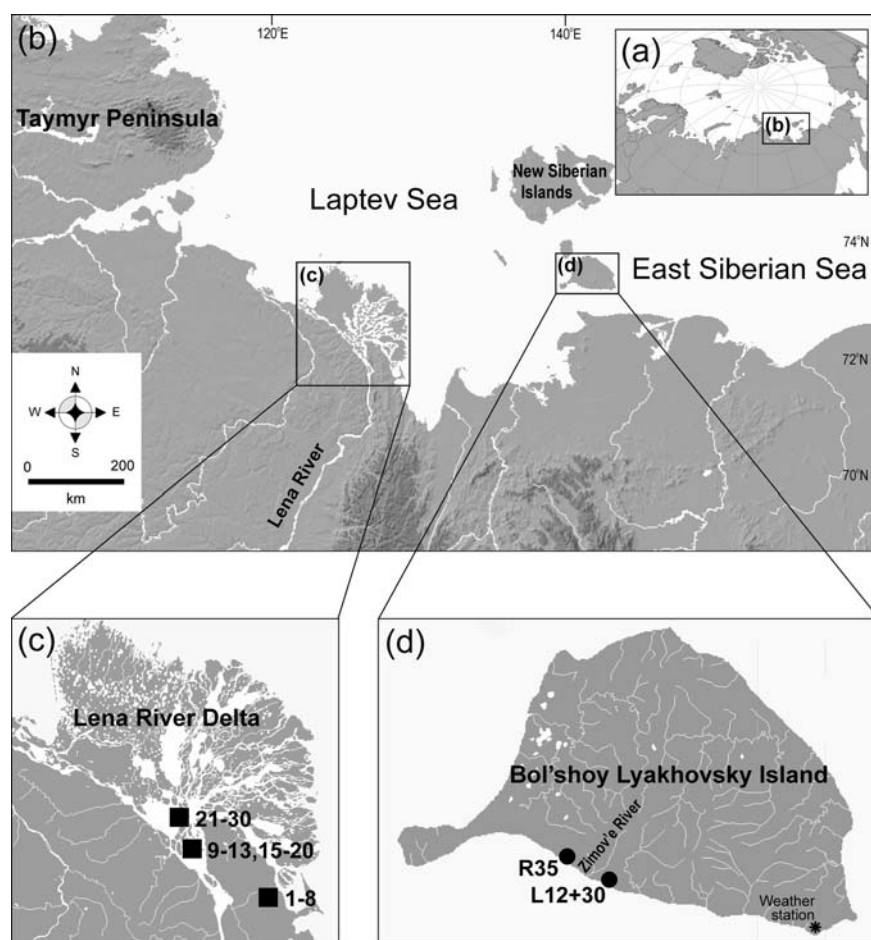


Figure 1. Maps of (a) the Arctic, (b) Laptev Sea region, (c) lower Lena River area, and (d) Bol'shoy Lyakhovskiy Island showing the location of the sampled interglacial R35 (this study) and L12 + 30 (previously studied; Andreev et al. 2004) sites. The lakes and ponds 1–13, 15–20 (previously studied; Porinchu and Cwynar 2000), and 21–30 (this study) sampled for surface chironomid remains are also shown.

collected in plastic bags, and then transported to the laboratory for further analysis.

Chironomid analysis

Samples for chironomid analysis were only mixed with distilled water and neither treated with KOH nor sieved prior to sorting, following Walker (2001). The samples were sorted in a Bogorov counting tray under a dissecting microscope (25 \times magnification). Chironomid remains were picked out and mounted on glass slides in glycerol for microscopic identification. At least 50 chironomid head capsules were counted and identified in each sample, sufficient for inference analyses (Hierl and

Lotter 2001; Larocque 2001; Quinlan and Smol 2001a). Chironomid concentrations were calculated as head capsule abundance per gram dry sediment.

Taxonomic identification of the chironomid remains is primarily based on descriptions of genera provided in Hofmann (1971), Wiederholm (1983), and Makarchenko and Makarchenko (1999). Identifications of the chironomid head capsules to a more precise taxonomic level were carried out using the descriptions of Sæther (1975) for *Heterotrissocladius*; Kiknadze et al. (1991) and Shilova et al. (1993) for *Lipiniella*; Tang et al. (2004) for *Prosilocerus*; Heiri et al. (2004) for *Paratanytarsus*; Makarchenko and Makarchenko (1999) and Walker et al. (1993) for

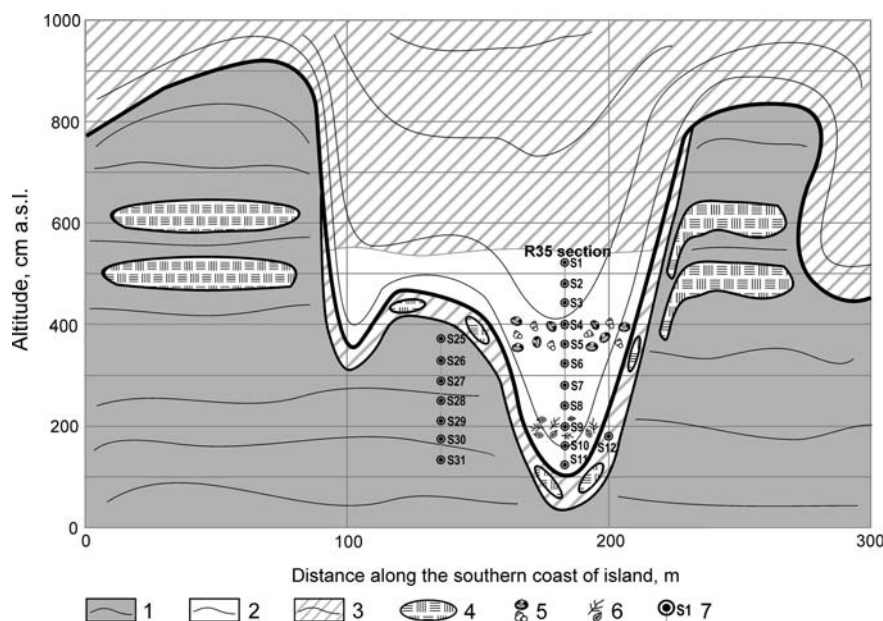


Figure 2. Illustration of the cliff at the southern coast of the Bol'shoy Lyakhovsky Island, showing cryolithological structure of the studied profile, and location of samples. Legend: (1) Late Saalian (>130 ka) grey loess-like silty sediments; (2) lacustrine and (3) non-lacustrine interglacial (ca. 130–120 ka) blue-grey silty sediments filling the ice wedge cast; (4) peat lens; (5) shells of freshwater molluscs; (6) plant fragments, and (7) sample number.

Parakiefferiella; Makarchenko and Makarchenko (1999) for *Acricotopus* and *Diamesa*. Most midge taxa could be identified to the generic or specific level, but in some cases, larger taxonomic groupings were necessary (e.g., *Cricotopus/Orthocladus*, *Limnophyes/Paralimnophyes*, *Eukiefferiella/Tvetenia*, *Metriocnemus/Thienemannia*).

Interglacial chironomid assemblages of the R35 section and of another locality (L12+30 section) ca. 4.7 km southeast studied earlier (Andreev et al. 2004) were quantitatively compared with the modern assemblages from surface (the uppermost 1 cm) sediment samples from a number of water bodies in the Laptev Sea region (Figure 1). In total, 29 modern assemblages from the tundra ponds and lakes of the lower Lena River area were used for the comparative analysis. The assemblages from 19 water bodies were collected and analyzed by Porinchu and Cwynar (2000). Their numbers (1–13 and 15–20, Figure 1) are according to the published dataset Porinchu and Cwynar (2000). As an average maximum ice-cover thickness of water bodies in the region is about 2 m (e.g., Huh et al. 1998), the studied water bodies were split into two types following Sheath (1986): ponds (up to 2 m deep) freezing to

the bottom during winter, and lakes (deeper than 2 m deep) with water remaining unfrozen under the ice-cover. Below lakes (i.e., deeper than the maximum ice-cover thickness), the permafrost thaws, and perennial thaw bulbs (taliks) form; below ponds (i.e., shallower than the maximum regional ice-cover thickness), only thin, seasonally thawing and freezing zones occur (Brewer 1958; Dyke 1991). The separation of ponds and lakes based on a ratio of depth to ice-cover thickness as in Sheath (1986) is common in arctic studies (e.g., Rouse et al. 1997). Among water bodies from the lower Lena River studied by Porinchu and Cwynar (2000) there are only three with the water depth ≤ 1.2 m (ponds 2, 3, and 17) and four with the depth of 1.5–2.0 m (ponds 1, 12, 15, and 18). Depth of the other studied water bodies (true lakes) ranges between 2.20 and 3.95 m (Porinchu and Cwynar 2000).

In order to improve the probability of good analogue matching, additional modern chironomid assemblages from surface sediment samples collected in 10 shallow (<1.2 m deep) circumneutral (pH = 6.5–7.5) intra- and inter-polygonal thermokarst ponds (ponds 21–30) in the Lena River Delta area, between 72°22'–72°23' N and 126°11'–

126°31' E (Figure 1, Wetterich 2003), were analyzed and also included in the comparative analysis. As reported by Meyer (2003), recent intense thermokarst processes in the region result in a formation of numerous intra- and inter-polygonal ponds with the depth not exceeding 1.2 m.

The pattern of similarity among the interglacial and modern chironomid assemblages was analyzed using non-metric multidimensional scaling (MDS), a multivariate method for ecological analysis (Clarke and Warwick 2001) available in the software package PRIMER for Windows version 5.2.4 (Clarke and Gorley 2001). Differences between the groups identified in MDS were analyzed using the ANOSIM procedure in the PRIMER package. Differences between the assemblages expressed as the Bray–Curtis dissimilarity coefficient (Bray and Curtis 1957) are used in all MDS analyses. The inter-sample distances were expressed as the average Bray–Curtis dissimilarity coefficient (D) using the SIMPER procedure in the PRIMER package. The taxonomy of the modern and fossil assemblages was harmonized before the analyses. To stabilize variances among chironomid taxa, percentage data were transformed using the natural logarithm ($\ln[x + 1]$) prior to all numerical analyses.

Pollen analysis

A standard HF technique was used for pollen preparation (Berglund and Ralska-Jasiewiczowa 1986). At least 200 pollen grains were counted in every sample. The relative frequency of pollen taxa was calculated from a sum of the terrestrial pollen taxa. Spore percentage was based on a sum of pollen and spores. The relative abundance of reworked taxa (Tertiary spores and redeposited Quaternary pollen) was based on a sum of pollen and redeposited taxa. The percentage of algae was based on a sum of pollen and algae, and the relative abundance of fungi – on a sum of pollen and fungi.

Rhizopod analysis

For rhizopod analysis, wet sediment samples of 15–20 g were sieved through a 500 μm mesh, and then rhizopod tests were concentrated with a centrifuge. A drop of the concentrate was placed on a slide, and then glycerol was added. A minimum of five subsamples were examined

at 200–400 \times magnification using a light microscope. For ecological interpretations, all identified rhizopod taxa were separated into three categories as hydro- and/or hygrophilous (water and/or moss inhabitants), soil, and eurytopic taxa, using the information regarding their modern biotope preferences provided in Chardez (1965).

Background and cryolithological description

Extremely ice-rich and perennially frozen sediment sequences with thick polygonal ice wedges, called “Ice Complex”, formed during the late Pleistocene, and are widely distributed in Arctic Siberia, especially in the coastal lowlands adjacent to Laptev and East Siberian seas (Romanovsky 1993). The R35 section belongs to a horizon that contains numerous ice wedge casts exposed for long distances along the south coast of Bol’shoy Lyakhovsky Island. This horizon, corresponding to the last Interglacial (ca. 130–120 ka), is underlain by late Saalian deposits and covered by Weichselian sequences as it has been determined by means of numerous $^{230}\text{Th}/\text{U}$ (Schirrmeister et al. 2002a), infrared stimulated luminescence and ^{14}C (Andreev et al. 2004) dates. For more details on the stratigraphic correlation of profiles from the Zimov’e River key site, see Schirrmeister et al. (2000). The late Saalian grey loess-like silty deposits underlie the ice wedge cast. Peat lenses of 0.2–0.3 m thickness immediately underlie the studied ice wedge cast (Figure 2). The 400 cm section (120–520 cm a.s.l.) consists of interglacial lacustrine blue–grey silty laminated sediments filling the ice wedge cast. The sediments from 360–400 cm a.s.l. contain numerous shells of freshwater molluscs, snails (*Pisidium* sp. and *Sphaerium corneum*) and mussels (*Valvata piscinalis*). The sediments from ca. 200 cm a.s.l. contain a layer with numerous plant remains. Lower down to the sea level, a wave cut hollow exists where the sediment was removed by modern coastal erosion.

Results

Chironomids

Modern assemblages from thermokarst ponds

A total of 32 chironomid taxa were identified in the surface samples from 10 shallow thermokarst ponds

of the Lena River Delta area (Figure 3). Among these taxa 23 were found in at least two or more ponds with a minimum relative abundance of 1%. Nine other taxa (*Boreoheptagyia*, *Cladotanytarsus mancus*-type, *Constempellina brevicosta*, *Corynoneura scutellata*-type, *Psectrocladius septentrionalis*-type, *Polypedilum*, *Protanypus*, *Psilometriocnemus europaeus*, and *Stictochironomus*) are very rare. The assemblages are dominated mainly by *Paratanytarsus penicillatus*-type, *Cricotopus/Orthocladius*, *Tanytarsus*, and *Chironomus anthracinus*-type. Other taxa, namely *Hydrobaenus*, *Psectrocladius sordidellus*-type, *Procladius*, and *Dicrotendipes*, are common with lower relative abundances. The concentration of chironomid remains covers a broad range (3.6–82.0 head capsules g^{-1} sediment).

Last Interglacial assemblages and their ordination along with modern ones

All samples from the R35 section contain well-preserved chironomid head capsules identified to 33 different taxonomic groups. Their concentration is low (1.2–4.0 head capsules g^{-1} sediment). Three chironomid stratigraphic zones, CZ-I,

CZ-II, and CZ-III, were identified by visual inspection of the diagram (Figure 4). The assemblage from the lowermost sample (120 cm a.s.l., CZ-I) is distinguished by a relatively high proportion of *Metriocnemus/Thienemania*, *Smittia*, and *Limnophyes/Paralimnophyes*. The CZ-II (ca. 140–220 cm a.s.l.) includes assemblages with a high relative abundance of *Chironomus plumosus*-type, *Cricotopus/Orthocladius*, and Orthoclaadiinae ind. Other taxa, such as *Limnophyes/Paralimnophyes*, *Georthocladius*, *Tanytarsus*, *Chironomus anthracinus*-type, *Procladius*, *Hydrobaenus*, and *Psectrocladius sordidellus*-type, are also present with a lower contribution in the assemblages of this zone. The CZ-III (ca. 220–520 cm a.s.l.) is characterized by a high proportion of *Chironomus plumosus*-type, *C. anthracinus*-type, *Procladius*, and *Sergentia coracina*-type. *Tanytarsus* and *Polypedilum* are present throughout much of the zone at relatively low abundance.

MDS based on dissimilarities in taxonomic composition generated an ordination of the interglacial and modern chironomid assemblages (Figure 5). The stress value is 0.18, which suggest a potentially useful 2-dimensional plot (Clarke

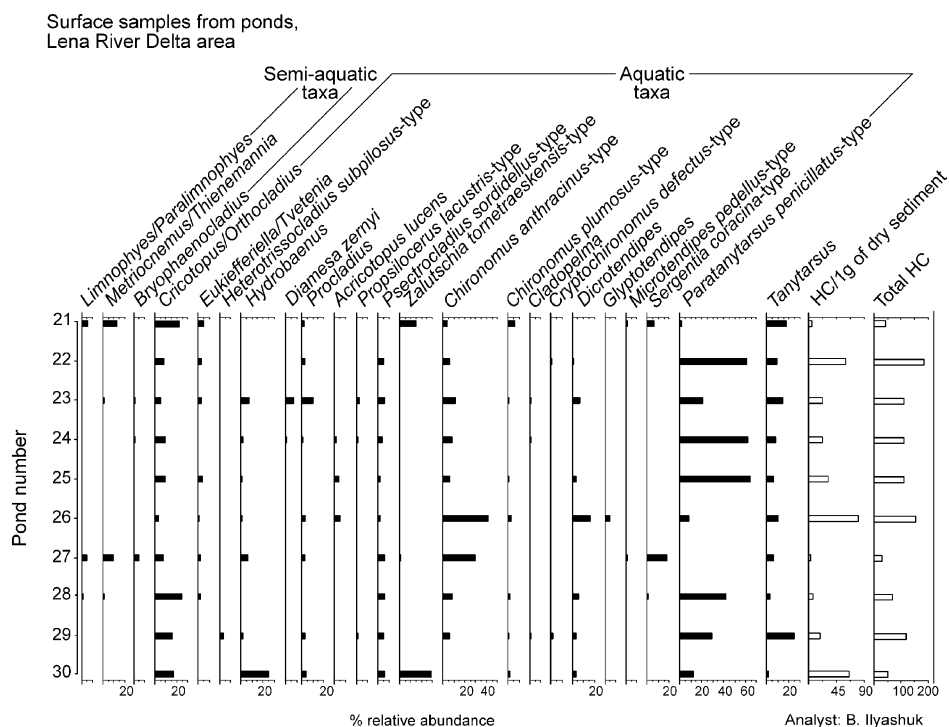


Figure 3. Percentage diagram showing the distribution of chironomid taxa in the surface sediment samples from thermokarst ponds, Lena River Delta area.

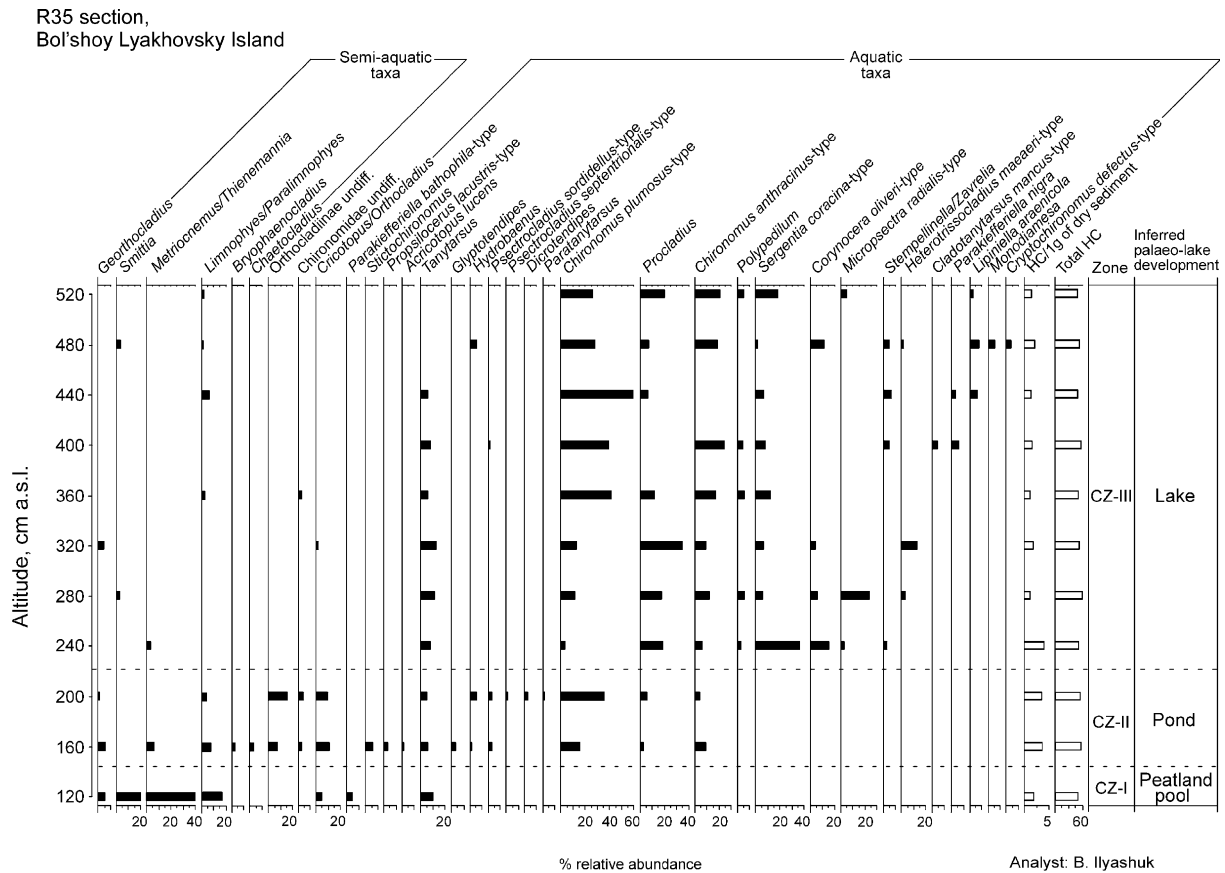


Figure 4. Chironomid percentage diagram for taxa recorded in the R35 section, Bol'shoy Lyakhovsky Island, including chironomid-inferred stages during the palaeo-lake development.

and Warwick 2001). Two somewhat distinct groups, assemblages of shallow (≤ 1.2 m deep) ponds and assemblages of deeper (> 1.2 m deep) ponds and lakes, are distinguishable among modern chironomids. A statistically significant difference was detected between the groups (ANOSIM R -value = 0.66, $p < 0.001$). The shallow pond assemblages are characterized by high average contribution of *Tanytarsini* (29.3%), *Cricotopus/Orthocladius* (17.2%), and *Chironomus* (15.0%). In comparison with the shallow ponds, the assemblages of the deeper ponds and lakes are distinguished by smaller contributions of *Tanytarsini* (21.1%), *Cricotopus/Orthocladius* (8.9%), and by a relatively high average contribution of *Sergentia* (9.7%) and *Zalutschia* (7.8%).

The MDS results (Figure 5) shows that the interglacial assemblage from the lowermost sample (120 cm a.s.l., CZ-I) of R35 section is very dissimilar ($D = 71\%$) to the modern assemblages

from both the shallow and the deeper water bodies. The CZ-II assemblages (160 and 200 cm a.s.l.) are less dissimilar ($D = 51\%$ and 39% , respectively) to the modern assemblages from the shallow ponds than from the deeper water bodies ($D = 64\%$ and 57% , respectively). The CZ-III (ca. 220–520 cm a.s.l.) assemblages grouped close together in the ordination diagram have high similarity of 58%. These assemblages are less dissimilar ($D = 62\%$) to the modern assemblages from the deeper water bodies than from the shallow ponds ($D = 67\%$).

The MDS ordination also shows that the interglacial assemblages from the Bol'shoy Lyakhovsky Island L12+30 section (400 and 430 cm a.s.l.) differ from the modern assemblage groups (Figure 5). The assemblage from 400 cm a.s.l. is more similar to the modern assemblages from deeper water bodies, but the assemblage from 430 cm a.s.l. is more similar to the modern

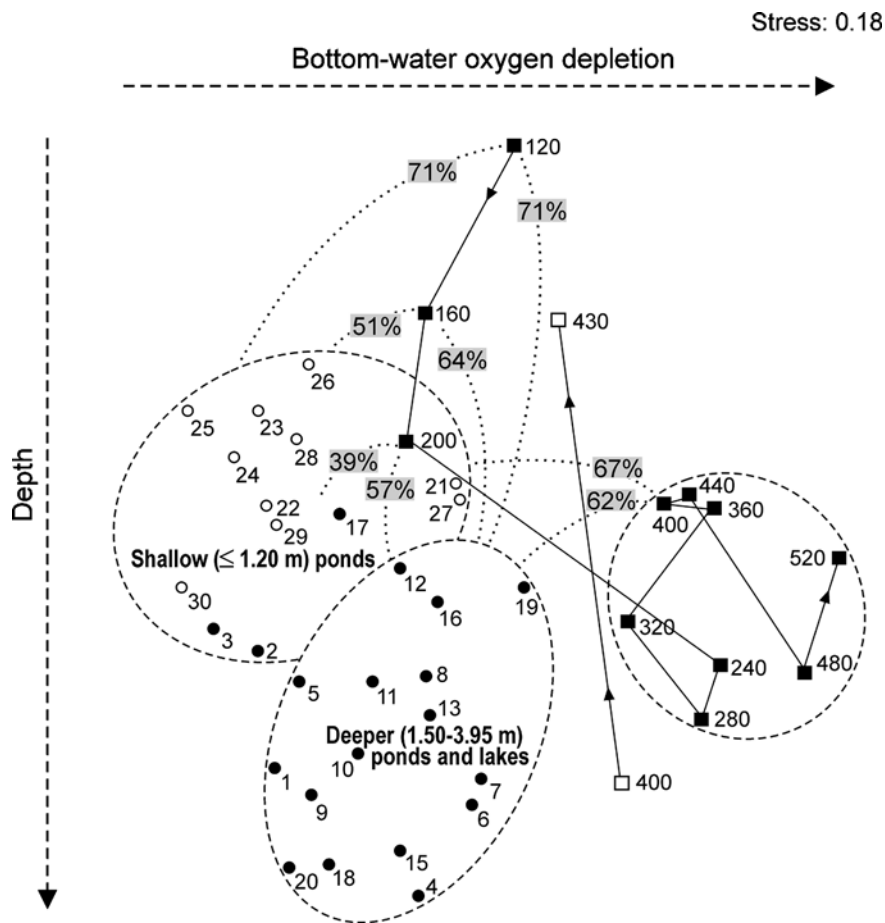


Figure 5. Multidimensional scaling of the Bol'shoy Lyakhovsky Island interglacial chironomid assemblages from the R35 (solid squares) and L12 + 30 (open squares; after Andreev et al. 2004) sections along with the modern chironomid assemblages from ponds and lakes of the lower Lena River area (solid circles; after Porinchu and Cwynar 2000) and ponds of the Lena River Delta area (open circles, this study). Percentages are the average Bray–Curtis dissimilarity between the interglacial and modern chironomid assemblages. Arrows indicate the directions of possible major environment variables (dashed line) and interglacial assemblage trajectories through time (solid line).

assemblages from the shallow ponds. Thus, the MDS results reveal the opposite development trends of two interglacial water bodies at the Bol'shoy Lyakhovsky Island (Figure 5).

Pollen

The pollen spectra from the loess-like silty deposits surrounding ice wedge cast (samples S31–S25; Figure 2) are characterized by the extreme low pollen concentration (less than 2500 grains per cm^3) and a large amount of reworked Pinaceae pollen. Rare Poaceae and Cyperaceae pollen with few other herb pollen types (Caryophyllaceae and Cichoriaceae) were found. Only a

sparse grass-sedge association with few other herbs existed during this period.

The spectrum from the transition horizon between the lacustrine sediments and surrounding loess-like silty deposits (sample S 12; Figure 2) is characterized by a high pollen concentration (20,000 grains per cm^3). Poaceae pollen dominate but Cyperaceae, Caryophyllaceae, Astraceae, *Artemisia* and *Betula* sect. *Nanae* also occur. Redeposited Pinaceae pollen is almost absent in the spectrum. The pollen spectrum reflects an open grass association with some dwarf shrubs.

The pollen spectra from the ice-wedge cast (samples S11–S1) are dominated by *Alnus fruticosa*, Poaceae, Cyperaceae and *Betula* pollen (Figure 6). The pollen concentration is generally higher (up to

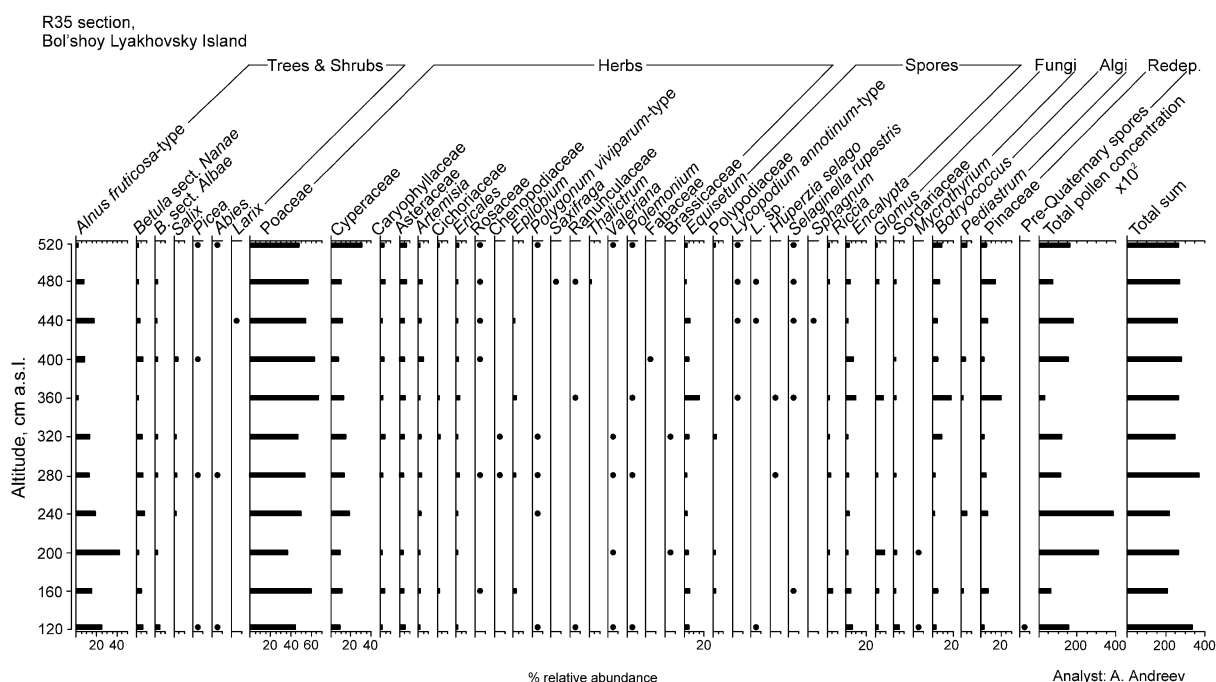


Figure 6. Pollen and spore percentage diagram; ● – less than 1%.

40,000 grains per cm^3) in the lower part, between 120 and ca. 340 cm a.s.l., which is also notable for a higher content of *Alnus fruticosa* and *Betula* pollen. The upper sediments display higher contents of redeposited Pinaceae, spores (especially *Equisetum* and *Encalypta*), remains of green algae colonies (*Botryococcus* and *Pediastrum*), and *Artemisia*, *Asteraceae* and *Poaceae* pollen. These spectra reflect shrub tundra vegetation around a water body.

Rhizopods

The sediments from the R35 section are characterized by a low density of rhizopod remains (1–11 rhizopod tests per sample) belong to 16 taxa (Figure 7). Generally, eurytopic taxa (e.g., *Centropyxis constricta* v. *minima*, *C. sylvatica*, and *Plagiopyxis minuta*) are present. However, hydro-/hygrophilous *Cyclopyxis kahli*, *C. orbicularis* taxa, *Nebela bigibbosa*, and *Arcella discoides*, which are commonly associated with wet *Sphagnum* and/or green moss microhabitats, and hydrophilous taxa, namely *Diffugia brevicola*, *D. cratera*, *D. penardi*, and *Pontigulasia elisa*,

were also found in the sediments. Soil rhizopods are represented only by two taxa (Figure 7).

Discussion

Chironomid notes: Last Interglacial and modern records, ecological preferences

In the early discussions (e.g., Hofmann 1988) concerning to the significance of chironomid analysis for palaeoecological studies, it was noted that chironomid fossil remains are usually abundant only in late-glacial and postglacial lake sediments and that these assemblages can reflect the environmental conditions in the former lakes. There are also numerous reports (e.g., Frey 1962; Matthews et al. 1990; Bennike and Böcher 1992; Matthews and Telka 1997; Bennike and Jepsen 2000) about single finds of chironomid remains in the last Interglacial deposits. The importance of these single remains for palaeoecological interpretations is problematic. However, the new chironomid records from the last Interglacial sites in Greenland (Bennike et al. 2000; Brodersen and Bennike 2003) and on the Bol'shoi Lyakhovskiy Island (Andreev et al. 2004) revealed

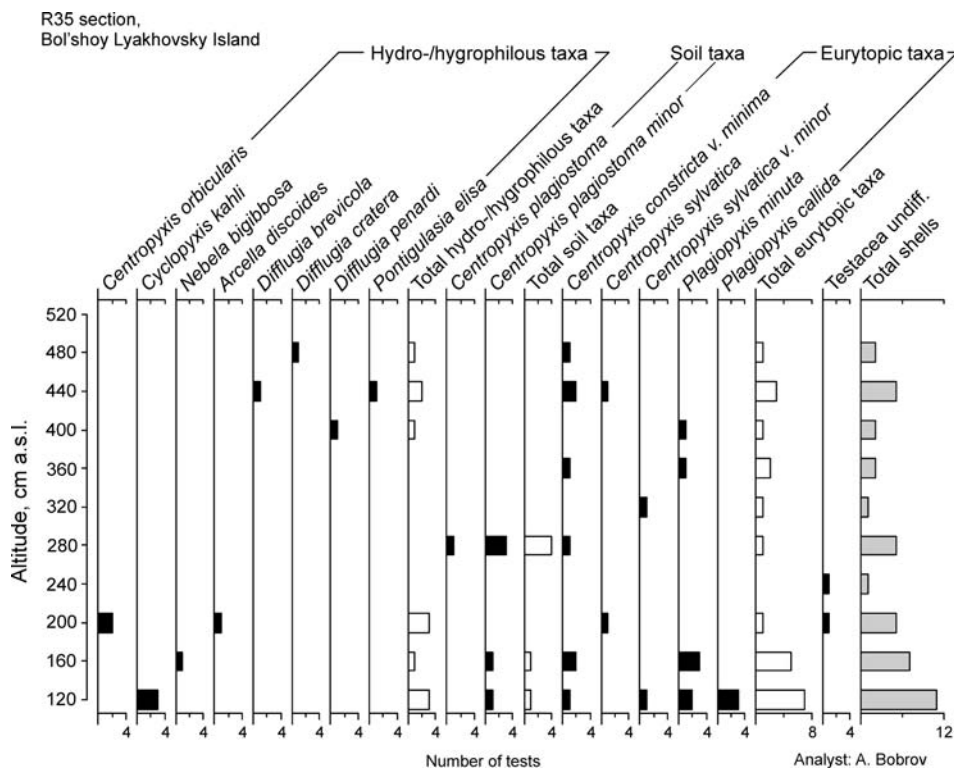


Figure 7. Diagram showing the stratigraphic distribution of rhizopod taxa recorded in the R35 section.

relatively rich chironomid assemblages, which can be used for palaeoenvironmental inferences. The chironomid record from the R35 section is also representative assemblages of the interglacial fauna.

All taxa found in the R35 section can be separated into two groups as semi-aquatic (semi-terrestrial) and aquatic taxa (Figure 4), using the information about their modern biotope preferences according to (Brundin (1949), Strenzke (1950), Pankratova (1970), Dowling and Murray (1981), Wiederholm (1983), Rosenberg et al. (1988, 2001), Pinder (1995), Oliver and Dillon (1997), Makarchenko and Makarchenko (1999), Zinchenko (2002), and Dettinger-Klemm (2003). *Bryophaenocladus*, *Georthocladus*, *Limnophyes/Paralimnophyes*, *Chaetocladus*, *Metriocnemus/Thienemannia*, and *Smittia* are semi-aquatic (semi-terrestrial) taxa frequently associated with moist habitats (wet moss and waterlogged peaty soils) in lowlands and close to temporary or permanent water bodies. Such habitats are widespread in the arctic tundra zone. Sendstad et al. (1977) and Pinder (1995) noted that the distinction between

semi-aquatic, semi-terrestrial and terrestrial habitats is often difficult when larvae occur in permanently wet habitats. Larvae of the other chironomid taxa are true aquatic inhabitants, which can occur across a wide range of standing water bodies including lakes, ponds, and peatland pools.

Many of the taxa recorded in the R35 section were also found in the Greenland and Canadian last Interglacial deposits. For example, semi-aquatic *Chaetocladus* and *Smittia* are reported from northwestern Greenland (Brodersen and Bennike 2003), and *Metriocnemus* from eastern Greenland (Bennike et al. 2000). True aquatic taxa, such as *Chironomus* and *Glyptotendipes*, were found in last Interglacial deposits of Canada, Yukon Territory (Matthews et al. 1990; Matthews and Telka 1997). Remains of *Chironomus* were also found in eastern Greenland (Bennike et al. 2000). *Psectrocladius*, *Sergentia*, *Diamesa*, *Cricotopus/Orthocladus*, *Hydrobaenus*, and *Corynocera oliveri*-type are recorded from the last Interglacial deposits of eastern and/or northwestern Greenland (Bennike et al. 2000; Brodersen and Bennike 2003).

Generally, the chironomid palaeofauna recorded in the R35 section is quite similar to the modern chironomid fauna of the Laptev Sea Region. Out of 33 fossil taxa, only five taxa, namely *Chaetocladius*, *Smittia*, *Georthocladius*, *Monodiamesa*, and *Lipiniella*, do not occur in the studied modern assemblages. Most likely the semi-aquatic taxa *Chaetocladius*, *Smittia* and *Georthocladius* were not recorded in the modern assemblages because they were collected only from relatively large water bodies and not from wet terrestrial habitats. Nevertheless larvae of *Chaetocladius* and *Smittia* are widespread through the arctic zone of Russia (Pankratova 1970) and Canada (Oliver and Dillon 1997). *Georthocladius* remains were recorded in surface lake sediments from subarctic Fennoscandia (Olander et al. 1997). The true aquatic larvae *Monodiamesa* and *Lipiniella* are also common in the Arctic. For example, *Monodiamesa* occurs in the tundra lakes in Arctic Russia (Makarchenko 1985) and Canada (Walker et al. 2003). *Lipiniella* is common throughout the Arctic Russia (Belyanina et al. 1992), including the Lena River Delta area (Shilova et al. 1993), and also occurs in north-western Canada (Pinder and Reiss 1983).

Chironomid successions and inferred palaeo-lake history

The high percentage of semi-aquatic taxa in the lowermost sample (120 cm a.s.l., CZ-I) suggests that a peatland palaeo-biotope existed at the site, when the water body started to form. The aquatic *Tanytarsus* and *Cricotopus/Orthocladius*, which can be abundant in open-water zones of peatlands (Rosenberg et al. 1988, 2001), may indicate the presence of pools in the peatland.

The MDS results suggest that the interglacial site represents a shallow (≤ 1.2 m deep) pond environment during the subsequent stage (CZ-II, ca. 140–220 cm a.s.l.) of the palaeo-lake development. The CZ-II assemblages are characterized by a distinct decrease in semi-aquatic taxa and an increase in lacustrine ones. These significant changes may be related to a gradual pooling of water in the basin, which could in turn induce thermokarst and create a permanent pond (Mackay 1992). This conclusion agrees with the suggestion of Walker (1990) that the ratio of soil-inhabiting chironomids to lacustrine ones may

provide a useful index of pond permanence. The pond assemblages are dominated by *Chironomus*, a taxon indicative of low oxygen availability and prolonged periods of anoxia (e.g., Quinlan et al. 1998; Quinlan and Smol 2001b; Little and Smol 2001). The presence of semi-aquatic taxa in the assemblages reflects the existence of semi-aquatic habitats encircling the pond.

The duration and thickness of seasonal ice cover are key factors controlling the winter oxygen depletion in arctic shallow aquatic ecosystems (Hobbie 1984). Ice prevents oxygen exchange between underlying waters and the atmosphere, and may commonly result in depletion of dissolved oxygen throughout a prolonged ice-covered period. In shallow arctic lakes, where only a small portion of the water column remains unfrozen, severe anoxia commonly occurs in underlying water towards the end of the ice-covered period (Hobbie 1984; Welch and Bergman 1985). In arctic ponds, the water column freezes to the bottom over the winter. Many chironomid species, except Tanypodinae (Danks 1971), are adapted to severe Arctic environment and noted as freeze-tolerant taxa (Greze 1947; Danks 1971; Danks et al. 1994; Lencioni 2004). Moreover, the oxygen depletion may also occur in ponds at the beginning of the ice-covered period, when the thickness of ice cover does not exceed depth of a pond (Nagell and Brittain 1977; Hobbie 1980). Larvae of *Chironomus* and *Procladius*, which have a high oxygen-regulator capacity (Brodersen et al. 2004) and tolerance to low oxygen concentrations (Quinlan et al. 1998; Quinlan and Smol 2001b; Little and Smol 2001), are common in the Arctic ponds and lakes (Oliver 1968; Danks and Oliver 1972a; Danks and Oliver 1972b; Walker 1988; Walker 1990; Porinchu and Cwynar 2000; Brodersen et al. 2001; Quinlan et al. 2005; this study, Figure 3).

The highest relative abundance of *Chironomus* and *Procladius* (taxa able to survive anoxia through long periods) during the third stage of the palaeo-lake development (CZ-III, ca. 220–520 cm a.s.l.) suggests that the severest bottom-water anoxia existed during this stage. It may indicate that unfrozen water remained under the ice throughout the ice-covered period. Moreover, the high proportion of freeze-intolerant Tanypodinae (Danks 1971), also suggests unfrozen water remained under the ice. Thus, we assume that the palaeo-pond (i.e., shallower than the maximum

ice-cover thickness) was transformed to the palaeo-lake (i.e., deeper than the maximum ice-cover thickness) at the beginning of CZ-III.

As pollen-based climate reconstructions from the Bol'shoy Lyakhovsky Island indicate significantly higher summer air temperatures during the last Interglacial optimum than present (Andreev et al. 2004), it is possible to suppose that the thickness of ice-cover of interglacial water body decreased and the ice-covered period shortened in response to the warming. In addition, amelioration of climate leads to an increase of active layer depth of the permafrost system and an enlargement of water bodies (Rouse et al. 1997). Accordingly, due to the instability of a permafrost landscape during the warming, it is difficult to determine the exact causes of limnological changes in the thermokarst water body. The results of MDS ordination show that the CZ-III assemblages are dissimilar to the modern pond and lake chironomid assemblages from of the region. The dissimilarity is due to the very high abundance of anoxia-tolerant taxa *Chironomus* and *Procladius* in the interglacial lake. Two orthogonal gradients of environment variables can be interpreted from the MDS ordination: a vertical depth gradient, and a horizontal gradient of the water-bottom oxygen depletion (Figure 5).

Thus, the changes in the R35 chironomid assemblages suggest three successive types of freshwater systems through the palaeo-lake history: a peatland pool (CZ-I), a pond (CZ-II), and a shallow lake (CZ-III) (Figure 4). This chironomid-inferred trend in the development of the interglacial palaeo-lake agrees fairly well with the development of thermokarst lakes in the Laptev Sea Region during the late Pleistocene–Holocene warming (ca. 12–7 ky BP) (Schirrmeister et al. 2002b) and at present time (Meyer 2003). Moreover, the inferred hydrologic events in studied interglacial palaeo-lake coincide with a pattern of hydrologic events that were inferred from multi-stratigraphic study of a classic interglacial palaeo-lake in northern Denmark (Björck et al. 2000).

Unfortunately, the studied profile does not cover the latest stages of the palaeo-lake, so it is not possible to infer the complete palaeo-lake history. Probably the water body disappeared due to drainage event(s) at the shallow lake stage. As reported by Sellmann et al. (1975) and Mackay (1992), thermokarst lakes can drain, sometimes

within a few hours, due to thawing of ice wedges blocking an outlet.

General interpretation of palaeoenvironment during the last Interglacial

During the last Interglacial optimum, sea level was ca. 5–6 m higher than present, based on dating of emergent coral reefs on tectonically stable coastlines (Harmon et al. 1983; Muhs et al. 1994; Lambeck and Chappell 2001). The isotopic record from the NorthGRIP ice core of Greenland suggests significantly warmer (ca. 5 °C) climate during the last Interglacial compared to the present (Schmidt et al. 2004). Carbon dioxide concentrations were higher (Rundgren and Bennike 2002). Data from the Vostok ice core of Antarctica also indicate that climate was warmer, and atmospheric concentrations of carbon dioxide and methane were higher than the highest pre-industrial Holocene levels (Petit et al. 1999). Global simulations of the last Interglacial climate together with local palaeodata suggest it may have been ca. 1 °C warmer (global annual mean) compared with the modern pre-industrial climate, with particularly warm temperatures in the Northern Hemisphere summers (Kubatzki et al. 2000).

Our study also provides clear evidence of humid and warm (interglacial) palaeoenvironmental conditions in Arctic Siberia during an interval significantly older than the Holocene. The studied section fits very well to the stratigraphy of the well-dated sequence in the Zimov'e key section (Schirrmeister et al. 2002a; Andreev et al. 2004), located in few hundred meters to the east, where this interval was referred to the last Interglacial based on the local stratigraphy and age determinations of the deposits (Andreev et al. 2004). The results of palaeoecological studies support this stratigraphic interpretation.

The grass and sedge dominated pollen spectra from the deposits surrounding the ice wedge cast are very similar to the late Saalian spectra deposited during a stadial (MIS 6, ca. 170–130 ka) (Andreev et al. 2004). The extremely low pollen concentrations most likely reflect sparse grass-sedge vegetation cover and unfavourable environmental conditions during the latest Saalian.

The pollen-rich spectrum from the transition horizon points to open grass associations with some *Artemisia*, *Betula nana*, Cyperaceae and Asteraceae. The relatively high content of *Betula nana* pollen indicates that dwarf birch might have grown in protected places close to the site. The climate was warm enough to result in melting of the Saalian ice wedges and formation of an initial water body below at the beginning of the last Interglacial (MIS 5e). Similar environmental conditions were also reconstructed from a few other pollen spectra found in the lowermost layers of the interglacial ice wedge casts there (Andreev et al. 2004).

The lacustrine sediments from the ice wedge cast content rather high amounts of *Alnus fruticosa* and *Betula nana* pollen (Figure 6) confirming that shrub tundra dominated vegetation around the palaeo-lake. These data are in good correlation with other last Interglacial records from the area (Andreev et al. 2004). The climate was relatively moist and warm. Quantitative pollen-based climate reconstruction (Andreev et al. 2004) performed on the pollen records from the sediment attributed to the last Interglacial optimum suggests mean July temperatures were at least 4–5 °C higher than today on the Bol'shoy Lyakhovsky Island. Reconstruction of the annual sum of mean-day temperatures above 5 °C (GDD5) also suggests that summers were warmer (GDD5 = 150–230 °C) than today (GDD5 = 0 °C) (Andreev et al. 2004).

The larger amounts of Poaceae and *Artemisia* pollen, slight decrease of *Alnus* and *Betula* from pollen spectra, as well as higher numbers of reworked Pinaceae pollen in the upper part of the section, may reflect a significant deterioration of climate at the beginning of the last Interglacial termination.

Pollen records from sites beyond the limit of radiocarbon dating with high percentages of tree and shrub pollen are relatively well known in northern Yakutia (e.g., Rybakova 1962; Barkova 1970; Rybakova and Kolesnikov 1983; Pirumova and Rybakova 1984; Sher 1991; Lozhkin and Anderson 1995). Generally, such records are assumed to date from the last Interglacial (MIS 5e) or even to the middle Weichselian (MIS 3) based on radiocarbon dates, stratigraphic position, and local geology. However, only a few of these records are dated at all and at a high resolution,

making the chronological correlation of the reconstructed environmental fluctuations difficult. The age estimation of deposits older than 40 ka based on radiocarbon dating are especially speculative, because it may lead to the wrong conclusions. Probably, all 'warm' middle Weichselian pollen records from the region dated around 40 ka are the last Interglacial ones.

The results of chironomid-based inferences suggest that the opposite processes (Figure 5), such as gradual pooling of water with the formation of thermokarst lakes (R35 section) and gradual drying up of other lakes (L12+30 section), occurred on the Bol'shoy Lyakhovsky Island during the last Interglacial. Local hydrological conditions in each site, such as an alteration in the lake drainage pattern, probably led to the difference in direction of these processes. Thus, the results suggest intensive thermokarst processes, which agree fairly well with the pollen-based inferred climate warming in the region.

High-latitude lakes and ponds are extremely responsive to climate change, because even slight warming results in decreased ice cover and, hence, longer growing seasons for aquatic organisms (Rouse et al. 1997; Smol et al. 2005). It has been shown that chironomid assemblages from the Arctic ponds respond remarkably to recent climate warming (Quinlan et al. 2005). Unfortunately, quantitative chironomid-based temperature reconstructions from the R35 section are not applicable owing to the relatively high dissimilarity of fossil and modern chironomid assemblages as well as inferred local hydrological/geomorphological factors controlling the chironomid fauna in the palaeo-lake. Similar drawbacks hampered the use of chironomids in the last Interglacial temperature inferences in Northwest Greenland (Brodersen and Bennike 2003).

Research on testate amoebae during the past few years has resulted in great progress on realizing the potential of this group as an important new class of palaeoenvironmental indicator (Patterson and Kumar 2002 and references therein; Bobrov et al. 2004; Boudreau et al. 2005). Unfortunately, only single rhizopod remains were found in our study, and some rhizopod-based palaeoenvironment inferences are problematic. The R35 rhizopod record may reflect only a wide variety of biotopes (e.g., disturbed soils, peatlands, pools, shallow ponds and lakes) characterizing the Arctic

thermokarst landscape during relatively warm periods.

Conclusion

Palaeoenvironmental records clearly indicate that humid and warm conditions existed during the last Interglacial. Open grass associations dominated vegetation at the beginning of the interglacial period. Climate was rather warm (similar to modern conditions), resulting in the partial melting of Saalian ice wedges. Shrub tundra with *Alnus fruticosa* and *Betula nana s.l.* dominated the vegetation in the area during the middle of the last Interglacial climatic optimum, when summer temperatures were higher than at present.

The chironomid palaeofauna recorded in the studied section is similar to the modern chironomid fauna of the Laptev Sea Region. The chironomid record documents the development of the interglacial water body. The high percentage of semi-aquatic chironomids in the lowermost sample suggests that a peatland-pool initially existed at the site, when the water body started to form. Afterwards, the chironomid assemblages are characterized by a distinct decrease in semi-aquatic taxa and an increase in lacustrine taxa. These changes point to a gradual pooling of water in basin, which could in turn induce thermokarst and create a permanent pond. The presence of semi-aquatic taxa in the assemblages reflects an existence of semi-aquatic habitats encircling the pond. The highest relative abundance of *Chironomus* and *Procladius*, taxa able to survive anoxia through long periods, during the later stage of the palaeo-lake development, suggests that the severest bottom-water anoxia existed during this stage. It may indicate that unfrozen water remained under the ice throughout the ice-covered period. The high proportion of freeze-intolerant Tanyptodinae also suggests that unfrozen water remained under the ice. Thus, the changes in the chironomid record point to three successive types of water bodies through the palaeo-lake history: a peatland pool, a pond (i.e., shallower than the maximum ice-cover thickness), and a shallow lake (i.e., deeper than the maximum ice-cover thickness). The lake development trend indicates that intensive thermokarst processes occurred in the region during the last Interglacial.

The results of this study show that chironomids are valuable indicators of hydrological and geomorphological processes, and they have considerable potential for Quaternary palaeoenvironmental studies within the Arctic thermokarst landscape. However, quantitative chironomid-based temperature reconstructions from high Arctic thermokarst ponds and shallow lakes may be problematic owing to other key environmental factors, such as prolonged periods of winter anoxia and local hydrological/geomorphological processes, controlling the chironomid fauna.

Acknowledgements

This study was funded by the German Ministry of Science and Technology through the German-Russian science cooperation "Laptev Sea System". The chironomid study was supported via a grant awarded by DAAD to B.I. We especially thank David Porinchi (Department of Geography, Ohio State University) and Les Cwynar (Department of Biology, University of New Brunswick) for allowing the use of the surface chironomid data from the lower Lena River region, and Sebastian Wetterich (Alfred Wegener Institute for Polar and Marine Research, Potsdam) for supplying the surface sediment samples from the Lena River Delta area. We are grateful to Tatiana Kuznetsova (Faculty of Geology, Moscow State University) for help with fieldwork, and to Elena Taldenkova (Faculty of Geography, Moscow State University) for identification of the molluscs. We would also like to thank Lutz Schirrmeister (Alfred Wegener Institute for Polar and Marine Research, Potsdam) for many valuable comments and suggestions during the preparation of the manuscript, and John Smol and two anonymous referees for their constructive criticisms resulting in the present form of the paper.

References

- Andreev A.A., Grosse G., Schirrmeister L., Kuzmina S.A., Novenko E.Yu., Bobrov A.A., Tarasov P.E., Ilyashuk B.P., Kuznetsova T.V., Krbetschek M., Meyer H. and Kunitsky V.V. 2004. Late Saalian and Eemian palaeoenvironmental history of the Bol'shoy Lyakhovsky Island (Laptev Sea region, Arctic Siberia). *Boreas* 33: 319–348.
- Andreev A.A., Tarasov P.E., Ilyashuk B.P., Ilyashuk E.A., Cremer H., Hermichen W.-D., Wischer F. and Hubberten H.-W. 2005. Holocene environmental history recorded in the

- Lake Lyadhej-To sediments, Polar Urals, Russia. *Palaeogeogr. Palaeoclim. Palaeoecol.* 223: 181–203.
- Barkova M.B. 1970. Spore–pollen complexes of pre-glacial and first glacial epochs of Late Pleistocene sediments of Yana-Indigirka Rivers lowland. *Uchenye zapiski NIIGA* 31: 40–46 (in Russian).
- Belyanina S.I., Loginova N.V., Sergeeva I.V., Gavrikova V.V. and Filinkova T.N. 1992. To the fauna Chironomidae from North regions of the USSR. In: Nartshuk E.P. (ed.), *Systematic, Zoogeography and Karyology of Two-winged Insects (Insecta: Diptera)*. Zoological Institute RAS, St. Petersburg, pp. 21–23 (in Russian).
- Bennike O. and Böcher J. 1992. Early Weichselian interstadial land biotas at Thule, Northwest Greenland. *Boreas* 21: 111–117.
- Bennike O. and Jepsen H.F. 2000. A new interglacial sequence from Washington Land, northern Greenland. *Polar Res.* 19: 267–270.
- Bennike O., Björck S., Böcher J. and Walker I.R. 2000. The Quaternary arthropod fauna of Greenland: a review with new data. *Bull. Geol. Soc. Denmark* 47: 111–134.
- Berglund B.E. and Ralska-Jasiewiczowa M. 1986. Pollen analysis and pollen diagrams. In: Berglund B.E. (ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. Interscience, New York, pp. 455–484.
- Björck S., Noe-Nygaard N., Wolin J., Houmark-Nielsen M., Hansen H.J. and Snowball I. 2000. Eemian Lake development, hydrology and climate: a multi-stratigraphic study of the Hollerup site in Denmark. *Quat. Sci. Rev.* 19: 509–536.
- Bobrov A.A., Andreev A.A., Schirmeister L. and Siegert C. 2004. Testate amoebae (Protozoa: Testacealobosea and Testaceaflosea) as bioindicators in the Late Quaternary deposits of the Bykovsky Peninsula, Laptev Sea, Russia. *Palaeogeogr. Palaeoclim. Palaeoecol.* 209: 165–181.
- Boudreau R.E.A., Galloway J.M., Patterson R.T., Kumar A. and Michel F.A. 2005. A paleolimnological record of Holocene climate and environmental change in the Temagami region, northeastern Ontario. *J. Paleolimnol.* 33: 445–461.
- Bray J.R. and Curtis J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* 27: 325–349.
- Brewer M.C. 1958. The thermal regime of an Arctic lake. *T. Am. Geophys. Union* 39: 278–284.
- Brodersen K.P. and Bennike O. 2003. Interglacial Chironomidae (Diptera) from Thule, Northwest Greenland: matching modern analogues to fossil assemblages. *Boreas* 32: 560–565.
- Brodersen K.P., Lindegaard C. and Anderson N.J. 2001. Holocene temperature and environmental reconstruction from lake sediments in the Søndre Strømfjord region, southern West Greenland. *Geol. Greenland Survey Bull.* 189: 59–64.
- Brodersen K.P., Pedersen O., Lindegaard C. and Hamburger K. 2004. Chironomids (Diptera) and oxy-regulatory capacity: An experimental approach to paleolimnological interpretation. *Limnol. Oceanogr.* 49: 1549–1559.
- Brundin L. 1949. Chironomiden und andere Bodentiere der Südschwedischen Urgebirgsseen. *Rep. Inst. Freshwater Res. Drottningholm* 30: 1–914.
- Chardez D. 1965. *Ecologie generale des Thecamoebiens (Rhizopoda, testacea)*. Bulletin de l'Institut Agronomique et des Stations de Recherches Gembloux 3: 306–341.
- Clarke K.R. and Gorley R.N. 2001. *PRIMER v5: User manual/tutorial*. PRIMER-E, Plymouth, 91 pp.
- Clarke K.R. and Warwick R.M. 2001. *Change in marine communities: an approach to statistical analysis and interpretation*, 2nd edition. PRIMER-E, Plymouth, 172 pp.
- Danks H.V. 1971. Overwintering of some north temperate and arctic Chironomidae. II. Chironomid biology. *Can. Entomol.* 103: 1875–1910.
- Danks H.V. and Oliver D.R. 1972a. Seasonal emergence of some high arctic Chironomidae (Diptera). *Can. Entomol.* 104: 661–686.
- Danks H.V. and Oliver D.R. 1972b. Diel periodicities of emergence of some high arctic Chironomidae (Diptera). *Can. Entomol.* 104: 903–916.
- Danks H.V., Kukul O. and Ring R.A. 1994. Insect cold-hardiness: insights from the Arctic. *Arctic* 47: 391–404.
- Dettinger-Klemm P.-M.A. 2003. *Chironomids (Diptera, Nematocera) of Temporary Pools – an Ecological Case Study*. Ph.D. thesis. Phillips-Universität Marburg, Marburg and Lahn.
- Dowling C. and Murray D.A. 1981. The distribution of the Chironomidae (Diptera) in two Irish blanket bog. *Proc. R. Ir. Acad.* 81B: 53–61.
- Dyke L.D. 1991. Temperature changes and thaw of permafrost adjacent to Richards Island, Mackenzie Delta, N.W.T. *Can. J. Earth Sci.* 28: 1834–1842.
- Frey D.G. 1962. Cladocera from the Eemian interglacial of Denmark. *J. Paleontol.* 36: 1133–1155.
- Greze V.N. 1947. Anabiosis and productivity of zoobenthos in Taymyr Lake. *Zool. Zh.* 26: 3–8 (in Russian).
- Grigoriev M.N., Imaev V.S., Koz'min B.M., Kunitski V.V., Larionov A.G., Mikulenko K.I., Skryabin R.M. and Timirshin K.V. 1996. *Geology, Seismicity and Cryogenic Processes in Western Arctic Yakutia*. Scientific Center SD RAS, Yakutsk, pp. 84 (in Russian).
- Harmon R.S., Mitterer R.M., Kriausakul N., Land L.S., Schwarcz H.P., Garrett P., Larson G.J., Vacher H.L. and Rowe M. 1983. U-series and amino-acid racemization geochronology of Bermuda: Implications for eustatic sea-level fluctuation over the past 250,000 years. *Palaeogeogr. Palaeoclimat. Palaeoecol.* 44: 41–70.
- Hieri O. and Lotter A.F. 2001. Effect of low counts sums on quantitative environmental reconstructions: an example using subfossil chironomids. *J. Paleolimnol.* 26: 343–350.
- Heiri O., Ekrem T. and Willassen E. 2004. Larval head capsules of European *Micropsectra*, *Paratanytarsus* and *Tanytarsus* (Diptera: Chironomidae: Tanytarsini), Version 1.0. (<http://www.io.uu.nl/~palaeo/Chironomids/Tanytarsini/intro.htm>).
- Hobbie J.E. (ed.) 1980. *The Limnology of Tundra Pond*. Hutchinson and Ross, Stroudsburg, 515 pp.
- Hobbie J.E. 1984. Polar limnology. In: Taub F.B. (ed.), *Ecosystems of the World: Lakes and Reservoirs*. Elsevier, Amsterdam, pp. 63–106.
- Hofmann W. 1971. Zur Taxonomie und Palökologie subfossiler Chironomiden (Dipt.) in Seesedimenten. *Arch. Hydrobiol.* 6: 1–50.
- Hofmann W. 1988. The significance of chironomid analysis (Insecta: Diptera) for paleolimnological research. *Palaeogeogr. Palaeoclim. Palaeoecol.* 62: 501–509.

- Huh Y., Tsoi M.-Y., Zaitsev A. and Edmond J.M. 1998. The fluvial geochemistry of the rivers of Eastern Siberia: I. Tributaries of the Lena River draining the sedimentary platform of the Siberian Craton. *Geoch. Cosmoch. Acta* 62: 1657–1676.
- Ilyashuk E.A., Ilyashuk B.P., Hammarlund D. and Larocque I. 2005. Holocene climatic and environmental changes inferred from midge records (Diptera: Chironomidae, Chaoboridae, Ceratopogonidae) at Lake Berkut, southern Kola Peninsula, Russia. *Holocene* 15: 897–914.
- Kiknadze I.I., Shilova A.I., Kerkis I.E., Shobanov N.A., Zelentov N.I., Grebenyuk L.P., Istomina A.G. and Prasolov V.A. 1991. Karyotypes and morphology of the tribe Chironomini larvae: Atlas. Nauka, Novosibirsk, 115 pp. (in Russian).
- Kubatzki C., Montoya M., Rahmstorf S., Ganopolski A. and Claussen M. 2000. Comparison of the last interglacial climate simulated by a coupled global model of intermediate complexity and an AOGCM. *Clim. Dynam.* 16: 799–814.
- Kuzmina S.A. 2002. Quaternary Insects of Yakutian Coastal Lowlands. Ph.D. thesis, Paleontological Institute RAS, Moscow, (in Russian).
- Lambeck K. and Chappell J. 2001. Sea level change through the last glacial cycle. *Science* 292: 679–686.
- Larocque I. 2001. How many chironomid head capsules are enough? A statistical approach to determine sample size for palaeoclimatic reconstructions. *Palaeogeogr. Palaeoclim. Palaeoecol.* 172: 133–142.
- Lencioni V. 2004. Survival strategies of freshwater insects in cold environments. *J. Limnol.* 63(Suppl. 1): 45–55.
- Little J.L. and Smol J.P. 2001. A chironomid-based model for inferring late-summer hypolimnetic oxygen in southeastern Ontario lakes. *J. Paleolimnol.* 26: 259–270.
- Lozhkin A.V. and Anderson P.M. 1995. The last interglacial in northeast Siberia. *Quat. Res.* 43: 147–158.
- Mackay J.R. 1992. Lake stability in an ice-rich permafrost environment: examples from the western Arctic coast. In: Roberts R.D. and Bothwell M.L. (eds), *Aquatic Ecosystems in Semi-arid Regions: Implications for Resource Management*. Environment Canada, Saskatoon, NHRI Symposium Series 7: 1–22.
- Makarchenko E.A. 1985. Chironomids of the Far East SSSR. The subfamilies Podonominae, Diamesinae, and Prodiamesinae (Diptera, Chironomidae). DVNC AN SSSR, Vladivostok, 200 pp. (in Russian).
- Makarchenko E.A. and Makarchenko M.A. 1999. Chironomidae. Non-biting midges. In: Tsalolikhin S.J. (ed.), *Key to Freshwater Invertebrates of Russia and Adjacent Lands: Higher Insects: Diptera*, Vol. 4. Zoological Institute RAS, St. Petersburg, pp. 210–295 and 670–857 (in Russian).
- Matthews J.V. Jr. and Telka A. 1997. Insect fossils from the Yukon. In: Danks H.V. and Downes J.A. (eds), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods). Ottawa, pp. 911–962.
- Matthews J.V. Jr., Schweger C.E. and Janssens J.J. 1990. The last (Koy-Yukon) interglaciation in the northern Yukon Territory: evidence from Unit 4 at Ch'ijee's Bluff exposure, Bluefish Basin. *Géographie Phys. Quat.* 44: 341–362.
- Meyer H. 2003. Studies on recent cryogenesis. *Rep. Polar Res. Bremerhaven* 466: 29–48.
- Meyer H., Siegert C., Derevyagin A., Schirrmeister L. and Hubberten H.-W. 2002. Paleoclimate reconstruction on Big Lyakhovsky Island, North Siberia – hydrogen and oxygen isotopes in ice wedges. *Permafrost and Periglacial Processes* 13: 91–103.
- Muhs D.R., Kennedy G.L. and Rockwell T.K. 1994. Uranium-series ages of marine terrace corals from the Pacific coast of North America and implications for last interglacial sea level history. *Quat. Res.* 42: 72–87.
- Nagell B. and Brittain J.E. 1977. Winter anoxia – a general feature of ponds in cold temperature regions. *Int. Revue Hydrobiol.* 62: 821–824.
- Ochiai S. and Kashiwaya K. 2005. Climato-hydrological environment inferred from Lake Baikal sediments based on an automatic orbitally tuned age model. *J. Paleolimnol.* 33: 303–311.
- Olander H., Korhola A. and Blom T. 1997. Surface sediment Chironomidae (Insecta: Diptera) distributions along an eotonal transect in subarctic Fennoscandia: developing a tool for palaeotemperature reconstructions. *J. Paleolimnol.* 18: 45–59.
- Oliver D.R. 1968. Adaptations of Arctic Chironomidae. *Ann. Zool. Fennici* 5: 111–118.
- Oliver D.R. and Dillon M.E. 1997. Chironomids (Diptera: Chironomidae) of the Yukon Arctic North Slope and Herschel Island. In: Danks H.V. and Downes J.A. (eds), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, pp. 615–635.
- Pankratova V.Ya. 1970. Larvae and pupae of non-biting midges of the subfamily Orthoclaadiinae (Diptera, Chironomidae = Tendipedidae) of the USSR fauna. *Opredeliteli Fauny SSSR* 102: 1–343. (in Russian).
- Patterson R.T. and Kumar A. 2002. A review of current testate rhizopod (thecamoebian) research in Canada. *Palaeogeogr. Palaeoclim. Palaeoecol.* 180: 225–251.
- Petit J.R., Jouzel J., Raynaud D., Barkov N.I., Barnola J.-M., Basile I., Bender M., Chappellaz J., Davisk M., Delaygue G., Delmotte M., Kotlyakov V.M., Legrand M., Lipenkov V.Y., Lorius C., Pépin L., Ritz C., Saltzman E. and Stevenard M. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399: 429–436.
- Pinder L.C.V. 1995. The habitats of chironomid larvae. In: Armitage P.D., Cranston P.S. and Pinder L.C.V. (eds), *The Chironomidae: Biology and Ecology of Non-biting Midges*. Chapman and Hall, London, pp. 107–135.
- Pinder L.C.V. and Reiss F. 1983. The larvae of Chironominae (Diptera: Chironomidae) of the Holarctic region – Keys and diagnoses. *Entomol. Scand. Suppl.* 19: 293–436.
- Pirumova L.G. and Rybakova N.O. 1984. The main stages of the Late Cenozoic sedimentation in Northern Yakutia (according to data of spore-pollen and diatom analyses). In: Korotkiy A.N. (ed.), *Paleogeograficheskie rubezhi i metody ikh izucheniya*. DVNTS, Vladivostok, pp. 63–81. (in Russian).
- Porinchu D.F. and Cwynar L.C. 2000. The distribution of freshwater Chironomidae (Insecta: Diptera) across treeline

- near the lower Lena River, Northeast Siberia, Russia. *Arct. Antarct. Alp. Res.* 32: 429–437.
- Quinlan R. and Smol J.P. 2001a. Setting minimum head capsule abundance and taxa deletion criteria in chironomid-based inference models. *J. Paleolimnol.* 26: 327–342.
- Quinlan R. and Smol J.P. 2001b. Chironomid-based inference models for estimating end-of-summer hypolimnetic oxygen from south-central Ontario shield lakes. *Freshwater Biol.* 46: 1529–1551.
- Quinlan R., Smol J.P. and Hall R.I. 1998. Quantitative inferences of past hypolimnetic anoxia in south-central Ontario lakes using fossil midges (Diptera: Chironomidae). *Can. J. Fish. Aquat. Sci.* 55: 587–596.
- Quinlan R., Douglas M.S.V. and Smol J.P. 2005. Food web changes in arctic ecosystems related to climate warming. *Glob. Change Biol.* 11: 1381–1386.
- Romanovsky N.N. 1993. Fundamentals of the Cryogenesis of the Lithosphere. Moscow State University, Moscow, 336 pp. (in Russian).
- Rosenberg D.M., Wiens A.P. and Bilyji B. 1988. Chironomidae (Diptera) of peatlands in northwestern Ontario, Canada. *Holarct. Ecol.* 11: 19–31.
- Rosenberg D.M., Wiens A.P., Bilyji B. and Armstrong L. 2001. Peatland Chironomidae (Diptera): effects of flooding on emergence from Lake 979, Experimental Lakes Area, Ontario. *J. N. Am. Benthol. Soc.* 20: 448–467.
- Rouse W.R., Douglas M.S.V., Hecky R.E., Hershey A.E., Kling G.W., Lesack L., Marsh P., McDonald M., Nicholson B.J., Roulet N.T. and Smol J.P. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. *Hydrol. Process.* 11: 873–902.
- Rundgren M. and Bennike O. 2002. Century-scale changes of atmospheric CO₂ during the last interglacial. *Geology* 30: 187–189.
- Rybakova N.O. 1962. Micropaleobotanical characteristics of Quaternary deposits in Arctic Yakutia. *Vestnik Moskovskogo Universiteta* 6: 55–63. (in Russian).
- Rybakova N.O. and Kolesnikov S.F. 1983. New evidence on the Upper Cenozoic deposits in the coastal lowlands of Yakutia. *Byulleten' Moskovskogo obshestva ispytatelye prirody. Otdelenie geologii* 60: 83–88. (in Russian).
- Sæther O.A. 1975. Nearctic and Palaearctic *Heterotrissocladius* (Diptera: Chironomidae). *Bull. Fish. Res. Bd Can.* 193: 1–67.
- Schirmermeister L., Kunitsky V., Grosse V., Meyer H., Kuznetsova T., Kuzmina S., Tumskey V., Derevyagin A., Akhmadeeva I. and Syromyatnikov I. 2000. Quaternary deposits of Bol'shoy Lyakhovsky Island. *Rep. Polar Res. Bremerhaven* 354: 113–168.
- Schirmermeister L., Oezen D. and Geyh M.A. 2002a. ²³⁰Th/U dating of frozen peat, Bol'shoy Lyakhovsky Island (North Siberia). *Quat. Res.* 57: 253–258.
- Schirmermeister L., Siegert C., Kunitzky V.V., Grootes P.M. and Erlenkeuser H. 2002b. Late Quaternary ice-rich permafrost sequences as a paleoenvironmental archive for the Laptev Sea region in northern Siberia. *Int. J. Earth Sci.* 91: 154–167.
- Schmidt K.G., Dahl-Jensen D., Johnsen S.J. and NorthGRIP members 2004. A high resolution climate record from the NorthGRIP deepice core. 34th International Arctic Workshop, Program and Abstracts. Institute of Arctic and Alpine Research, University of Colorado at Boulder, pp. 150–152.
- Sellmann P.V., Brown J., Lewellen R.I., McKim H. and Merry C. 1975. The classification and geomorphic implications of thaw lakes on the Arctic Coastal Plain, Alaska. Special Report 344. US Army Cold Regions Research and Engineering Laboratory, Hanover, New Hampshire.
- Sendstad E., Solem J.O. and Aagaard K. 1977. Studies of terrestrial chironomids (Diptera) from Spitsbergen. *Norw. J. Entomol.* 24: 91–98.
- Sheath R.G. 1986. Seasonality of phytoplankton in northern tundra ponds. *Hydrobiologia* 138: 75–83.
- Sher A.V. 1991. Problems of the last interglacial in Arctic Siberia. *Quat. Int.* 10–12: 215–222.
- Shilova A.I., Kerkis I.E. and Kiknadze I.I. 1993. *Lipiniella prima* sp. n. (Diptera, Chironomidae), larva and karyotype. *Net. J. Aquat. Ecol.* 26: 197–201.
- Smol J.P., Wolfe A.P., Birks H.J.B., Douglas M.S.V., Jones V.J., Korhola A., Pienitz R., Rühland K., Sorvari S., Antoniades D., Brooks S.J., Fallu M.-A., Hughes M., Keatley B.E., Laing T.E., Michelutti N., Nazarova L., Nyman M., Paterson A.M., Perren B., Quinlan R., Rautio M., Saulnier-Talbot E., Siitonen S., Solovieva N. and Weckström J. 2005. Climate-driven regime shifts in the biological communities of arctic lakes. *Proc. Natl. Acad. Sci. USA* 102: 4397–4402.
- Solovieva N., Jones V.J., Nazarova L., Brooks S.J., Birks H.J.B., Grytnes J.-A., Appleby P.G., Kauppila T., Kondratenok B., Renberg I. and Ponomarev V. 2005. Palaeolimnological evidence for recent climatic change in lakes from the northern Urals, arctic Russia. *J. Paleolimnol.* 33: 463–482.
- Strenzke K. 1950. Systematik, Morphologie und Ökologie der terrestrischen Chironomiden. *Arch. Hydrobiol. Suppl.* 18: 207–414.
- Tang H., Guo Y., Wang X. and Sæther O.A. 2004. The pupa and larva of *Prosilocerus taihuensis* (Wen, Zhou & Rong) (Diptera: Chironomidae), with complete keys to all immatures of the genus *Prosilocerus*. *Aquat. Insects* 26: 265–272.
- Tumskey V.E. 2002. Thermokarst and its Role in the Development of the Laptev Sea Region in the Late Pleistocene and Holocene. Ph.D. thesis, Moscow State University, Moscow, (in Russian).
- Walker I.R. 1988. Late-Quaternary Palaeoecology of Chironomidae (Diptera: Insecta) from Lake Sediments in British Columbia. Ph.D. thesis, Simon Fraser University, Burnaby, B.C., Canada.
- Walker I.R. 1990. Modern assemblages of arctic and alpine Chironomidae as analogues for late-glacial communities. *Hydrobiologia* 214: 223–227.
- Walker I.R. 2001. Midges: Chironomidae and related Diptera. In: Smol J.P., Birks H.J.B. and Last W.M. (eds), *Tracking Environmental Change Using Lake Sediments. Vol. 4, Zoological Indicators*. Kluwer Academic Publisher, Dordrecht, pp. 43–66.
- Walker I.R., Oliver D.R. and Dillon M.E. 1993. The larva and habitat of *Parakiefferiella nigra* Brundin (Diptera: Chironomidae). *Net. J. Aquat. Ecol.* 26: 527–531.
- Walker I.R., Levesque A.J., Pienitz R. and Smol J.P. 2003. Freshwater midges of the Yukon and adjacent Northwest Territories: a new tool for reconstructing Beringian paleoenvironments? *J. N. Am. Benthol. Soc.* 22: 323–337.

- Welch H.E. and Bergman M.A. 1985. Water circulation in small arctic lakes in winter. *Can. J. Fish. Aquat. Sci.* 43: 506–520.
- Wetterich S. 2003. Recent freshwater ostracods in the Lena Delta. *Rep. Polar Res. Bremerhaven* 466: 64–67.
- Wetterich S., Schirmermeister L. and Pietrzeniuk E. 2005. Freshwater ostracodes in Quaternary permafrost deposits in the Siberian Arctic. *J. Paleolimnol.* 34: 363–376.
- Wiederholm T. (ed.) 1983. Chironomidae of the Holarctic Region, Keys and Diagnoses. Part 1 – Larvae. *Entomol. Scand. Suppl.* 19: 1–457.
- Zaitsev V.N. 1989. Environmental conditions in Yana-Kolyma region. In: Ershov E.D. (ed.), *Geokriologia SSSR. Vostochnaya Sibir' i Dal'nii Vostok*. Nedra, Moscow, pp. 240–249. (in Russian).
- Zinchenko T.D. 2002. Chironomids of surface waters in the mid- and lower Volga basin (Samara district). IEVB RAS, Tolyatti, 174 pp. (in Russian).