University of Groningen

Larix during the Mid-Pleniglacial (Greenland Interstadial 8) on Kotelny Island, northern Siberia

van Geel, Bas; Protopopov, Albert; Protopopova, Victoria; Pavlov, Innokenti; van der Plicht, Johannes; Reenen, van, Guido B.A.

Published in:
Boreas

DOI:
[10.1111/bor.12216](https://doi.org/10.1111/bor.12216)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2016

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

van Geel, B., Protopopov, A., Protopopova, V., Pavlov, I., van der Plicht, J., & Reenen, van, G. B. A. (2016). Larix during the Mid-Pleniglacial (Greenland Interstadial 8) on Kotelny Island, northern Siberia. *Boreas*, [10.1111/bor.12216]. <https://doi.org/10.1111/bor.12216>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Larix during the Mid-Pleniglacial (Greenland Interstadial 8) on Kotelny Island, northern Siberia

BAS VAN GEEL, ALBERT PROTOPOPOV, VICTORIA PROTOPOPOVA, INNOKENTI PAVLOV, JOHANNES VAN DER PLICHT AND GUIDO B. A. VAN REENEN

BOREAS

van Geel, B., Protopopov, A., Protopopova, V., Pavlov, I., van der Plicht, J. & van Reenen, G. B. A.: *Larix* during the Mid-Pleniglacial (Greenland Interstadial 8) on Kotelny Island, northern Siberia. *Boreas*. 10.1111/bor.12216. ISSN 0300-9483.

Needles, wood and pollen of *Larix*, recorded in a peat deposit from Kotelny Island, northern Siberia, indicate the local occurrence of larch around 38 000 cal. a BP, which is during the Middle Pleniglacial (Greenland Interstadial 8) of the Weichselian last glacial period. The pollen record, dominated by Cyperaceae, Poaceae, *Betula*, *Alnus*, *Salix* and *Artemisia*, indicates steppe-tundra conditions with some shrubs and trees. The distribution of *Larix* species plays an important role in the reconstruction of climatic conditions during the Weichselian in Siberia. Nowadays *Larix* does not occur on Kotelny Island and in the present situation the temperature may not be the limiting factor for *Larix*, but instead the long, snowy winters and the moist tundra vegetation. Our data may contribute to a better understanding of *Larix* refugia and Weichselian climatic conditions in northern Siberia.

Bas van Geel (B.vanGeel@uva.nl) and Guido B. A. van Reenen, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, 1098 XH Amsterdam, The Netherlands; Albert Protopopov and Innokenti Pavlov, Academy of Sciences of the Republic of Sakha (Yakutia), 33 Lenina ave., Yakutsk 677007, Russia; Victoria Protopopova, Institute for Biological Problems of Cryolithozone, Siberian Branch of RAS, 41 Lenina ave., Yakutsk 677980, Russia; Johannes van der Plicht, Centre for Isotope Research, University of Groningen, Nijenborgh 4, 9747 AG Groningen, The Netherlands; received 22nd August 2016, accepted 25th October 2016.

Our knowledge of climatic conditions and species distributions during the Weichselian is still rather limited. Carbon dioxide levels were much lower than today (~190 ppm compared with ~280 ppm in pre-industrial time) and the effects of lower CO₂ were lower photosynthetic rates and reduced water-use efficiency of plant species, with stronger negative effects on trees than on herbaceous species (Magyari *et al.* 2014 and references therein). CO₂-generated differences amongst species may have had effects on interspecific competition and this is a complication for climate reconstructions and for finding present-day analogues – if any – of vegetation types during glacial periods. According to Tarasov *et al.* (2009) it is due to a lack of wood macrofossils older than 10 ka from eastern Siberia between 108° and 145°E that there is no agreement on whether trees could persist there during the coldest phases of the last glacial period. We found needles, wood and pollen of *Larix*, preserved in a peat deposit at Kotelny Island, in northern Siberia, and the goal of the present study was to determine when, and under which ecological conditions *Larix* trees occurred at this site far north of the present tree line.

Study area

Kotelny Island (Fig. 1) is a practically uninhabited territory belonging to the Sakha Republic (Yakutia) of the Russian Federation. It is the largest island of the Anzhu archipelago, located in the Arctic Ocean

between the Laptev Sea and the East Siberian Sea. When combining the bathymetry as shown in the map in Fig. 1B (after Rudenko *et al.* 2014) and the sea-level reconstructions by Lambeck *et al.* (2014) it is evident that the Kotelny area was connected with the Siberian mainland during the second half of the last glacial period. The present surface area of the island is 23 200 km². The landscape is mostly hilly, rising up to 361 m a.s.l. (Mt Malakatyn-Tas). Rivers on Kotelny Island are small and shallow, flowing in narrow valleys, except for the 205-km-long Balyktah River. The climate of the island is less continental than the climate of continental Yakutia. The duration of sunshine varies from 1500 to 1600 h per year. The radiation balance is negative from the beginning of October until the end of March, with a maximum of ~9.1 kcal cm⁻² in June. Winters last from September until June and mean January temperatures range from –32 to –35 °C, whereas mean July temperatures range from 6 to 8 °C. The rainiest months are July and August when 30% of the annual precipitation falls (Mozolevskaya 1963). Arctic deserts, tundras, flood-plain wetlands and peaty soils are common, and Kotelny Island is largely covered with Quaternary deposits with deep permafrost. Conditions are adverse for woody plants and the present-day tree line is located on the mainland, more than 500 km to the south (Fig. 1B). Characteristic of the tundra region is the formation of ‘baydzharahs’ (silty, peaty thermokarst frost mounds; Fig. 2A). Baydzharahs are 5–10 m high, with a diameter of 15–20 m at the base. The relatively dry frost

Fig. 1. A. Map showing the present Eurasian tree line (solid line) and the isotherms for the mean July surface air temperature of 10 and 15 °C (after MacDonald *et al.* 2008). B. Bathymetric map (after Rudenko *et al.* 2014) showing the position of Kotelny Island, the sample site of the *Larix* trunk, the modern tree line according to MacDonald *et al.* (2008) and Tchekbakova *et al.* (2005), and the Last Glacial Maximum shoreline, as based on the bathymetry.

mound surfaces play a role in the distribution of vegetation.

According to the geobotanical zonation the vegetation on Kotelny Island belongs to the zone of the arctic desert, but tundra vegetation dominates the landscape. The vegetation shows a pronounced bumpy cryogenic micro-relief. The most common types of tundra vegetation on Kotelny Island are the following (Gorodkov 1956; plant names according to current taxonomic nomenclature): shrub-herb tundra with baydzharahs dominated by *Alopecurus alpinus*, *Salix polaris* and the moss species *Aulacomnium turgidum*, *Hylocomium splendens* and *Orthothecium chryseum*. Trees and tall shrubs are absent. In the vegetation of polygonal

peatlands the following species may occur: *Dupontia fisheri*, *Pleuropogon sabinei*, *Alopecurus alpinus*, *Arcophila fulva*, *Carex aquatilis*, *Eriophorum angustifolium*, *Eriophorum scheuchzeri* and *Caltha palustris*. The tundra vegetation in the hills with polygonal soils is represented mostly by *Salix polaris*, *Alopecurus alpinus*, *Saxifraga oppositifolia*, *Saxifraga nivalis*, *Papaver radiculatum*, *Dryas octopetala*, *Cassiope tetragona*, *Luzula confusa*, *Ranunculus hyperboreus*, *Endocellion glaciale* and the mosses *Ditrichum flexicaule* and *Distichium capillaceum*. The vegetation cover of the island is made up mostly by the arctic shrub *Salix polaris*. The willow species *Salix glauca* and *Salix reptans* are occasionally encountered on southern slopes in the

Fig. 2. A. Landscape of Kotelny Island with baydzharahs (thermokarst frost mounds). B. *Larix* trunks in peat deposit. C. Cross-section of *Larix* trunk. D. Sampled trunk.

southern part of the island. In the northern part *Salix polaris* occurs, but its dominance diminishes with increasing altitudes. With the decrease of shrubs, the presence of arctic pioneer species, such as *Papaver radicum* and *Oxyria digyna* increases. The vegetation cover in the northern part of the island occurs in clusters within areas of bare soils. *Artemisia* species (mostly pioneers on dry soils) have not been observed on Kotelny Island.

Material and methods

During fieldwork in 2014 Mr Semyon Yakovlev discovered trunks of *Larix* in peat mounds (Fig. 2B–D). The coordinates of the site are 75°23'17"N, 139°18'42"E. The presence of *Larix* on Kotelny Island is remarkable as the site is situated ~530 km north of the present tree line on the continent (Fig. 1A, B). One trunk was sampled for further study and the peat layer was sampled at the transition from the trunk to the roots. The preparation of microfossils of the peat samples was according to Fægri & Iversen (1989) and for the preparation of macrofossils we followed Mauquoy & van Geel (2007). Wood of the *Larix* trunk was dated at the AMS facility of the Centre for Isotope Research of the University of Groningen, The Netherlands. The sample was chemically pretreated using the standard acid–alkali–acid protocol (Mook & Streurman 1983). After the chemical pretreatment the samples were combusted

and turned into CO₂ by an elemental analyser (EA), coupled online with a stable isotope mass spectrometer (MS). The EA was also used for purification of CO₂. In addition, the EA/MS system enables precise measurements of the $\delta^{13}\text{C}$ -values. CO₂ was reduced to graphite by reacting under an excess of hydrogen gas (Aerts-Bijma *et al.* 2001). This graphite was pressed into the target holders that were placed in the ion source of an accelerator mass spectrometer (AMS). The Groningen AMS facility is based on a 2.5 MV accelerator, and measures the ¹⁴C concentration in the graphite (van der Plicht *et al.* 2000). The results are presented in conventional radiocarbon years (a BP), including correction for isotopic fractionation and usage of the conventional half-life (Mook & van der Plicht 1999). The ¹⁴C dates (reported in a BP) were calibrated into calendar ages (reported in cal. a BP) using the recommended calibration curve IntCal13 (Reimer *et al.* 2013).

Results

The *Larix* wood was radiocarbon dated to 33 600±150 a BP (GrA-62148), showing that the studied peat was formed during the Middle Pleniglacial of the Weichselian (last glacial period). Calibration using the recommended calibration curve IntCal13 (Reimer *et al.* 2013) yielded a calendar age of 38 380–37 850 cal. a BP (1-sigma range, numbers rounded to

the nearest 10). In Fig. 3 this age range is plotted on a relevant time interval of the Greenland ice-core record (after Rasmussen *et al.* 2014).

Two subsamples (A and B) of the peat deposit were analysed for microfossils (Table 1). The most common pollen taxa were Cyperaceae, Poaceae, *Betula*, *Alnus*, *Salix* and *Artemisia*. In addition, a variety of herbaceous taxa was recorded in low amounts, amongst which were *Papaver*, *Plantago*, *Polemonium*, *Potentilla* type and *Rumex*. We were not able to identify *Artemisia* pollen to species level, but the presence anyhow implies the occurrence of drier substrates than the present-day tundras (for a discussion about the ecological indicator value of *Artemisia* we refer to West 1996). Sample B was dominated by Ericales pollen whereas sample A had a relatively low amount of Ericales. Therefore we also show in Table 1 the percentages of sample B when Ericales were excluded from the pollen sum. Low percentages of *Larix* pollen were recorded in both samples. Some rare pollen grains of *Ilex* and *Ulmus* may have arrived after long-distance wind transport. The nearby or local occurrence of *Carex* is evident from the record of hyphopodia of *Clasterosporium caricinum* (HdV-126), which is known to be a parasite on *Carex* species (van Geel & Aptroot 2006). Algae are represented by *Pediastrum*, *Botryococcus* and Type HdV-128A, pointing to local aquatic conditions. Ascospores of *Sporormiella* and *Sordaria* type (van Geel & Aptroot 2006) were also present. These are coprophilous fungi and thus indicate the nearby deposition of faeces.

The peat was also studied for macrofossils. It mainly consisted of well-preserved bryophytes. The following

wet-growing taxa were identified: *Amblystegium riparium*, *Calliergon giganteum*, *Dicranum cf. elongatum*, *Drepanocladus aduncus*, *Homalothecium lutescens*, *Meesia triquetra* and an unidentified species of Pottiaceae. In addition, needles of *Larix* sp. (Fig. 4A, B), wood-epidermis of *Larix* (Fig. 4C), remains of *Betula* sp. (Fig. 4F, G) and a seed of *Callitriche* (Fig. 4E) were found. Statoblasts of the bryozoan *Cristatella mucedo* (Fig. 4H) in various states of preservation occurred regularly.

Discussion

Larix and the other recorded taxa most probably lived in the Kotelny area during Greenland Interstadial-8c (Fig. 3). An age of Greenland Stadial-9 is also possible, but less probable. The dominance of wet-growing and aquatic moss species of alkaline environments (Nyholm 1975; Crum & Anderson 1981; Vitt & Buck 2001) at the sampling site, and the presence of algae, *Callitriche* and *Cristatella mucedo* all point to an aquatic to semi-aquatic habitat as the local environment of the sampling site. According to Økland & Økland (2000) *Cristatella mucedo* has a circumpolar holarctic distribution, but so far it has not been found on the arctic islands of Svalbard and Novaya Zemlya. Lacourt (1968) mentioned that the present-day occurrence of *Cristatella mucedo* in northern Europe is limited by the timber line and, based on Lacourt's data, van Geel *et al.* (1981) used the presence of *C. mucedo* as an extra indication for a relatively warm phase during the early Holocene in the Netherlands. However, Økland & Økland (2000) studied the present

Fig. 3. Selected part of the Greenland ice-core record (adapted from Rasmussen *et al.* 2014) showing in the lower part the 20-year average oxygen isotope values in permil from GRIP (red), GISP2 (green) and NGRIP (blue) on the GICC05modelext time scale. The upper part shows Ca^{2+} values in ppb. Interstadials are illustrated by grey shading (light grey indicates cold sub-events). The 1-sigma range of the *Larix* wood radiocarbon date from Kotelny is plotted on the same time scale. Note that the Greenland ice-core chronology is plotted in thousands of b2k (calendar ages relative to 2000). This 50-year difference with the calibrated ^{14}C age (cal. a BP, calendar age relative to 1950) was taken into account.

Table 1. Microfossil spectra of two samples (A and B) from peat, stratigraphically corresponding with the *Larix* trunk shown in Fig. 2D.

Kotelny Island, peat	A		B		% excl. Ericales
	n	%	n	%	
<i>Artemisia</i>	43	13.8	10	1.8	3.1
<i>Alnus</i>	43	13.8	38	6.7	11.7
Apiaceae	—	—	1	0.2	0.3
Asteraceae Tubuliflorae	2	0.6	2	0.4	0.6
<i>Betula</i>	37	11.9	48	8.5	14.8
Brassicaceae	2	0.6	2	0.4	0.6
Caryophyllaceae	1	0.3	2	0.4	0.6
Chenopodiaceae	1	0.3	—	—	—
Cyperaceae	52	16.7	67	11.8	20.6
Ericales	5	1.6	242	42.6	74.5
<i>Ilex</i>	+	+	—	—	—
<i>Larix</i>	4	1.3	3	0.5	0.9
cf. <i>Papaver</i>	1	0.3	1	0.2	0.3
<i>Pinus</i> -type	13	4.2	17	3.0	5.2
<i>Plantago</i> sp.	—	—	2	0.4	0.6
Poaceae	97	31.2	115	20.3	35.4
<i>Polemonium</i>	—	—	1	0.2	0.3
<i>Potentilla</i> -type	4	1.3	3	0.5	0.9
Ranunculaceae	1	0.3	1	0.2	0.3
Rosaceae undiff.	1	0.3	—	—	—
<i>Rumex</i> sp.	—	—	3	0.5	0.9
<i>Salix</i>	5	1.6	9	1.6	2.8
<i>Ulmus</i>	+	+	—	—	—
Pollen sum	311		567		325
cf. <i>Equisetum</i>	1	0.3	—	—	—
Monolete psil. fern spores	7	2.3	1	0.2	0.3
Monolete verrucate fern sp.	—	—	1	0.2	0.3
<i>Lycopodium</i> (reticulate)	—	—	1	0.2	0.3
<i>Sphagnum</i>	4	1.3	—	—	—
Type HdV-128A	42	13.5	80	14.1	24.6
<i>Botryococcus</i>	4	1.3	2	0.4	0.6
<i>Pediastrum</i>	18	5.8	21	3.7	6.5
<i>Clasterosporium caricinum</i> (HdV-126)	4	1.3	41	7.2	12.6
<i>Sordaria</i> -type (HdV-55A)	—	—	3	0.5	0.9
<i>Sporormiella</i> (HdV-113)	4	1.3	5	0.9	1.5

distribution and ecology of *C. mucedo* in Norway, and based on their data they concluded that the occurrence in northern areas indicates a tolerance of cold climates. The species has been recorded on the Kola Peninsula, and in Greenland (Fredskild & Røen 1982), and in Norway it was found in many localities north of the Arctic Circle and some localities were even north of 70°N. Økland & Økland (2000) concluded that the present occurrence up to 71°03'N is a global maximum. However, our Kotelny record shows that *C. mucedo* occurred at least up to 75°N during the last ice age (c. 38 000 cal. a BP).

Larix pollen is known for its short-distance dispersal and poor preservation (Tarasov *et al.* 2009 and references therein). Even if pollen is preserved then there are only a few distinctive morphological characteristics, and mistakes can easily occur because some small invertebrate egg shells show similarities with *Larix*

pollen. Macrofossils such as wood, needles and cones are the best evidence for the presence of *Larix*. The distribution of *Larix* species plays an important role in the reconstruction of climatic conditions during the Weichselian in Siberia (Tarasov *et al.* 2009). The present-day extension of *Larix* in the Arctic is mainly limited by the mean July isotherm of 10–12 °C (MacDonald *et al.* 2000; see Fig. 1A), but according to Pisaric *et al.* (2001) individual larch specimens can survive in a grass-shrub landscape even under mean July temperatures of about 8 °C. Permafrost is not a limiting factor for *Larix*, as it grows on frozen shallow soils with seasonally active layer depths of 10–30 cm (Pozdnyakov 1993 referenced in Müller *et al.* 2010). Migrations from southern refugia to the north may have occurred during temporary mild climatic conditions of the last ice age, but based on molecular research Abbott *et al.* (2000) hypothesized high-latitude, local 'cryptic refugia' where trees could persist during colder phases of the last glacial period (see also Bennett & Provan 2007). Müller *et al.* (2010) also suggested that larch may have survived during the last 50 ka in locally favourable micro-habitats in northeast Asia. Based on their study of a sediment core from Lake Billyakh, Müller *et al.* (2010) highlighted the presence of *Larix*, growing locally about 170–140 km south of the Arctic Circle, prior to the Holocene. According to Müller *et al.* (2010, and references therein) the results of palaeobotanical and isotope studies led to the reconstruction of a continental climate during the Weichselian, characterized by relatively high summer temperatures, a long snow-free period, extremely low winter temperatures and low precipitation. Kienast *et al.* (2005) used palaeobotanical data to conclude that relatively warm summers occurred in the East Siberian Arctic during the last glacial period.

The macro-remains of *Larix* and *Betula* of our Kotelny site point to nearby stands of vegetation of these woody taxa. Considering the pollen record, *Alnus* may have played a role as well, but no *Alnus* macrofossils were recorded. Nowadays the distribution of *Larix dahurica* in Yakutia is up to ~71°N (map by Sokolov *et al.* 1977 in Tchebakova *et al.* 2005), which is ~530 km south of our sampling site at Kotelny Island. The present northern fringe of the distribution of *Larix* borders the tundra zone along the northern Siberian coast. According to Tchebakova *et al.* (2005) the potential for migration to the north as a consequence of 'global warming' is limited ultimately by the Arctic Ocean. However, based on our new data and existing literature we suppose that the present mean July temperatures are not the limiting factor for the present northern distribution limit of *Larix*, but the wet tundra conditions with much snow, and thus a short growing season, compared to relatively dry climatic conditions of the last ice age. In any case, the

Fig. 4. Macrofossils from sampled peat. A. *Larix*, needles. B. Needle epidermis of *Larix*, showing row of stomata. C. *Larix*, wood epidermis. D. Unidentified seed. E. *Callitriche* sp., seed. F. *Betula* sp., seed. G. *Betula* sp., leaf fragment. H. *Cristatella mucedo*, statoblasts in various shapes of decomposition.

occurrence of *Larix* at Kotelny Island, which was connected to the Siberian mainland during the Weichselian, is remarkable and fits with the existing evidence for appropriate (dry, steppic) environmental conditions for plants and animals ('mammoth steppe') during the Weichselian (Kienast *et al.* 2011). Table 2 shows the main differences between the tundra and steppe environments as based on Guthrie (2001). The transition from the last ice age to the Holocene was characterized by temperature increase, co-occurring with an increase of precipitation during and after the melting of the ice sheet in northwest Europe (Guthrie 2001). The

transition from steppe to tundra conditions at the start of the Holocene had major, and for some plant and animal species negative, effects on their northern distribution limits. In other words, the environmental conditions during the Weichselian were non-analogous to any modern conditions and therefore climate and vegetation reconstructions are complicated when using the present climatic envelopes of various taxa as a reference and tool for the reconstruction of the past. According to Kienast *et al.* (2011) the main constraints on arctic communities are warmth and length of the growing season, which depend on the thickness

Table 2. Contrasting environmental factors (Guthrie 2001) of present-day tundras and the cold steppes of the last glacial period.

Steppe	Tundra
Climate dry: food also available during winter.	Climate humid: peaty layer on top of mineral soil and thick snow cover during winter.
Early start of growing season. Snow absent, or only thin snow cover, so sunshine quickly melts the snow.	Late start of plant growth in spring because melting of thick snow cover takes time.
Fast recycling of nutrients (a lot of dung produced by herbivores).	Slow and incomplete recycling of nutrients.
Thick unfrozen part of the soil during summer, and therefore high nutrient availability for plants.	Unfrozen part of soil during summer relatively thin and therefore low nutrient availability for plants.
Dominance of grasses: excellent food for grazing herbivores. The growing point of grasses is just near their roots, so grazing does not do harm to grasses (grazing stimulates growth).	Many tundra plant species are not palatable and their growing points are at the end of the stems (vulnerable to grazing).

of the snow cover, the duration of the snow-melt and the power of warming in spring. The vegetation in the Kotelny area may have served as food resources for herbivore populations, and grazing may also have had effects on the vegetation composition (cf. Zimov 2005) but the palaeontological record from Kotelny, unfortunately, is still rather limited (Markova *et al.* 2013).

Conclusions

Nowadays the northern boundary of *Larix* trees is about 530 km south of the recorded presence of *Larix* in the Kotelny Island area as it was around 38 000 years ago. Considering the record of microfossils, macro-remains and the age of the studied samples, the occurrence of *Larix* fits with the climatic steppe conditions (climatic continentality) that occurred in the non-glaciated area of the eastern Siberian Arctic. Based on our palaeobotanical data we conclude that a mosaic of meadow and steppe communities dominated the Kotelny area around 38 000 years ago, where larch, and also birch and alder, occurred.

Acknowledgements. – The authors thank Jan van Arkel for the photography of the macrofossils and for preparing the maps. Pavel Tarasov kindly provided the bathymetric map as published by Rudenko *et al.* (2014). We thank A. G. Brown and an anonymous reviewer for useful suggestions that helped to improve the manuscript.

References

Abbott, R. J., Smith, L. C., Milne, R. I., Crawford, R. M. M., Wolff, K. & Balfour, J. 2000: Molecular analysis of plant migration and refugia in the Arctic. *Science* 289, 1343–1346.

- Aerts-Bijma, A. T., van der Plicht, J. & Meijer, H. A. J. 2001: Automatic AMS sample combustion and CO₂ collection. *Radiocarbon* 43, 293–298.
- Bennett, K. D. & Provan, J. 2007: What do we mean with 'refugia'? *Quaternary Science Reviews* 27, 2449–2455.
- Crum, H. A. & Anderson, L. E. 1981: *Mosses of eastern North America. Vols 1 and 2*, Columbia University Press, New York. Vol. 1: 663 pp., Vol. 2: 1328 pp.
- Fægri, K. & Iversen, J. 1989: *Textbook of Pollen Analysis*. 328 pp. Wiley, Chichester.
- Fredskild, B. & Røen, U. 1982: Macrofossils in an interglacial peat deposit at Kap København, North Greenland. *Boreas* 11, 181–185.
- van Geel, B. & Aptroot, A. 2006: Fossil ascomycetes in Quaternary deposits. *Nova Hedwigia* 82, 313–329.
- van Geel, B., Bohncke, S. J. P. & Dee, H. 1981: A palaeoecological study of an upper Late Glacial and Holocene sequence from 'De Borchert', The Netherlands. *Review of Palaeobotany and Palynology* 31, 367–448.
- Gorodkov, B. N. 1956: Vegetation and soils on Ostrov Kotelny (Novosibirsk Archipelago). In Tikhomirov, B. A. (ed.): *The Vegetation of the Soviet Far North and its Utilization* 2, 7–132. Publishing House of the Academy of Sciences of the USSR, Moscow.
- Guthrie, R. D. 2001: Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews* 20, 549–574.
- Kienast, F., Schirmer, L., Siegert, C. & Tarasov, P. 2005: Palaeobotanical evidence for warm summers in the East Siberian Arctic during the last cold stage. *Quaternary Research* 63, 283–300.
- Kienast, F., Wetterich, S., Kuzmina, S., Schirmer, L., Andreev, A. A., Tarasov, P., Nazarova, L., Kossler, A., Frolova, L. & Kunitzky, V. V. 2011: 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. *Quaternary Science Reviews* 30, 2134–2159.
- Lacourt, A. W. 1968: A monograph of the freshwater Bryozoa - Phylactolaemata. *Zoologische Verhandlungen* 93, 3–159.
- Lambeck, K., Rouby, H., Purcell, A., Sun, Y. & Sambridge, M. 2014: Sea level and global ice volumes from the Last Glacial Maximum to the Holocene. *PNAS* 111, 15296–15303.
- MacDonald, G. M., Kremenetski, K. V. & Beilman, D. W. 2008: Climate change and the northern Russian treeline zone. *Philosophical Transactions of the Royal Society B* 363, 2285–2299.
- MacDonald, G. M., Velichko, A. A., Kremenetski, C. V., Borisova, O. K., Goleva, A. A., Andreev, A. A., Cwynar, L. C., Riding, R. T., Forman, S. L., Edwards, T. W. D., Aravena, R., Hammarlund, D., Szeicz, J. M. & Gattaulin, V. N. 2000: Holocene treeline history and climate change across Northern Eurasia. *Quaternary Research* 53, 302–311.
- Magyari, E. K., Kunes, P., Jakab, G., Sümegi, P., Pelánková, B., Schäbitz, F., Braun, M. & Chytrý, M. 2014: Late Pleniglacial vegetation in eastern-central Europe: are there modern analogues in Siberia? *Quaternary Science Reviews* 95, 60–79.
- Markova, A. K., Puzachenko, A. Y., van Kolfschoten, T., van der Plicht, J. & Ponomarev, D. V. 2013: New data on changes in the European distribution of the mammoth and the woolly rhinoceros during the second half of the Late Pleistocene and the early Holocene. *Quaternary International* 292, 4–14.
- Mauquoy, D. & van Geel, B. 2007: Mire and peat macros. In Elias, S. A. (ed.): *Encyclopedia of Quaternary Science* 3, 2315–2336. Elsevier, Amsterdam.
- Mook, W. G. & van der Plicht, J. 1999: Reporting ¹⁴C activities and concentrations. *Radiocarbon* 41, 227–239.
- Mook, W. G. & Streurman, H. J. 1983: Physical and chemical aspects of radiocarbon dating. *PACT Publications* 8, 31–55.
- Mozolevskaya, A. K. 1963: *Agroclimatological Reference Book on the Yakutian ASSR*. 146 pp. Gidrometeoizdat, Leningrad (in Russian).
- Müller, S., Tarasov, P. E., Andreev, A. A., Tütken, T., Gartz, S. & Diekmann, B. 2010: Late Quaternary vegetation and environments in the Verkhoyansk Mountains region (NE Asia) reconstructed from a 50-kyr fossil pollen record from Lake Billyakh. *Quaternary Science Reviews* 29, 2071–2086.

- Nyholm, E. 1975: *Illustrated Moss Flora of Fennoscandia II. Musci. Fascimile I*. 799 pp. Swedish Natural Science Research Council, Lund.
- Økland, K. A. & Økland, J. 2000: Freshwater bryozoans (Bryozoa) of Norway: distribution and ecology of *Cristatella mucedo* and *Paludicella articulata*. *Hydrobiologia* 421, 1–24.
- Pisarcic, M. F. J., MacDonald, G. M., Velichko, A. A. & Cwynar, L. C. 2001: The Lateglacial and Postglacial history of the northwestern limits of Beringia, based on pollen, stomata and tree stump evidence. *Quaternary Science Reviews* 20, 235–245.
- van der Plicht, J., Wijma, S., Aerts, A. T., Pertuisot, M. H. & Meijer, H. A. J. 2000: The Groningen AMS facility: status report. *Nuclear Instruments and Methods B172*, 58–65.
- Pozdnyakov, L. K. 1993: *Forest Science on Permafrost*. 192 pp. Nauka, Novosibirsk (in Russian).
- Rasmussen, S. O., Bigler, M., Blockley, S. P., Blunier, T., Buchardt, S. L., Clausen, H. B., Cvijanovic, I., Dahl-Jensen, D., Johnsen, S. J., Fischer, H., Gkinis, V., Guillevic, M., Hoek, W. Z., Lowe, J. J., Pedro, J. B., Popp, T., Seierstad, I. K., Steffensen, J. P., Svensson, A. M., Vallelonga, P., Vinther, B. M., Walker, M. J. C., Wheatley, J. J. & Winstrup, M. 2014: A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quaternary Science Reviews* 106, 14–28.
- Reimer, P. J., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Bronk Ramsey, C., Buck, C. E., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Hafflidason, H., Hajdas, I., Hatté, C., Heaton, T. J., Hoffmann, D. L., Hogg, A. G., Hughen, K. A., Kaiser, K. F., Kromer, B., Manning, S. W., Niu, M., Reimer, R. W., Richards, D. A., Scott, E. M., Southon, J. R., Staff, R. A., Turney, C. S. M. & van der Plicht, J. 2013: IntCal 13 and Marine13 Radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55, 1869–1887.
- Rudenko, O., Tarasov, P. E., Bauch, H. A. & Taldenkova, E. 2014: A Holocene palynological record from the northeastern Laptev Sea and its implications for palaeoenvironmental research. *Quaternary International* 348, 82–92.
- Sokolov, S. Y., Svyazeva, O. A. & Kubli, B. A. 1977: *Ranges of Trees and Bushes of the USSR*. 164 pp. Nauka, Leningrad (in Russian).
- Tarasov, P., Müller, S., Andreev, A., Werner, K. & Diekmann, B. 2009: Younger Dryas *Larix* in eastern Siberia: a migrant or survivor? *PAGES News* 17, 122–123.
- Tchebakova, N. M., Rehfeldt, G. E. & Parfenova, E. I. 2005: Impacts of climate change on the distribution of *Larix* spp. and *Pinus sylvestris* and their climatypes in Siberia. *Mitigation and Adaptation Strategies for Global Change* 11, 861–882.
- Vitt, D. H. & Buck, W. R. 2001: *Bryophyta Flora of North-America*. Available at: <http://www.mobot.org/plantscience/BFNA/bfna-menu.htm> (accessed 03.15.2016).
- West, F. H. (ed.) 1996: *American Beginnings. The Prehistory and Palaeoecology of Beringia*. 576 pp. University of Chicago Press, Chicago.
- Zimov, S. A. 2005: Pleistocene Park: return of the mammoth's ecosystem. *Science* 308, 796–798.