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### Testate amoebae record from the Laptev Sea coast and its implication for the reconstruction of Late Pleistocene and Holocene environments in the Arctic Siberia

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### ABSTRACT

Our study aims to look for testate amobae (TA) in the surface and fossil sediments from the Cape Mamontov Klyk (73°60′-73°63′ N, 116°88′-117°18′ E), southern coast of the Laptev Sea, ca 150 km west of the Lena Delta and to discuss the potential of TA analysis for Glacial/Interglacial environmental reconstructions in Arctic Siberia. The radiocarbon age determination suggests that the studied sediments accumulated between ca 45,000 <sup>14</sup>C yr BP and present. A total of 98 TA taxa were identified in the 10 recent surface and 59 fossil samples. Results of taxonomical identification and ecological analysis of TA in the modern and fossil samples suggest that major changes in the soil moisture conditions took place. Our results show that soil-living taxa dominated the testate TA assemblages at the study sites during the past 45,000 years. The environmental conditions of the study area were most favourable (relatively warm and humid) during the Kargin Interstadial (ca 45,000-25,000<sup>14</sup>C yr BP). An opposite situation is reconstructed for the Sartan Stadial (ca. 25,000–15,000 <sup>14</sup>C yr BP). During the Kargin Interstadial, optimum conditions occurred between ca 44,000 and 40,000 <sup>14</sup>C yr BP characterised by highest TA abundances and taxa diversity. This initial optimal phase was followed by the interval with drier and colder conditions about 40,000–30,000 <sup>14</sup>C yr BP. The sediments dated between ca. 24,000 and 18,000 <sup>14</sup>C yr BP show low TA abundances and diversity, in agreement with the much colder and drier environments during the maximum phase of the last glacial. The onset of the Holocene is indicated by a broad representation of obligate hydrophilic taxa, especially from genus Difflugia, suggesting wet and relatively warm conditions. By comparison with other environmental proxies used in the studied sections as well as from the neighbouring arctic regions our results suggest that TA analysis can provide valuable information, contributing to the better understanding of the Late Quaternary climate and environments in Arctic Siberia.

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### 1. Introduction

The Arctic is more sensitive to climate change than most other 35 parts of our planet (ACIA, 2004). Here effects of the current warming 36 can obviously be seen from the present destruction of terrestrial and 37 sub-sea permafrost surfaces as well as the reduction of the sea-ice 38 cover. There are also many indications of various palaeoenvironmental 39 changes in lowland regions of Northeast Siberia during the Late 40 Quaternary that are available from multi proxy studies of permafrost 41 records (e.g. Andreev et al., 2002b; Schirrmeister et al., 2002a). 42 43 Northern Eurasia has long been known as an important region for 44 understanding the magnitude of climatic and environmental changes during the Late Quaternary and their consequences for other high-45

latitude regions (e.g. Velichko, 1984; Khotinskiy, 1984; Hubberten 46 et al., 2004; Lozhkin et al., 2007; Kienast et al., 2008). This area has 47 been lagged behind other regions in terms of high-resolution 48 palaeoclimatic studies. Therefore comprehensive multidisciplinary 49 and high-resolution palaeoecological studies are necessary in order to 50 understand the complex environmental changes that took place in the 51 Arctic periglacial environments in the past.

Permafrost sequences exposed around the Laptev Sea coast have 53 proven to represent informative archives of Late Quaternary 54 environmental and climate dynamics. One of the best preserved 55 sequences on the Laptev Sea coastal region has been studied using 56 a multi-proxy approach at Bykovsky Peninsula (e.g. Schirrmeister 57 et al., 2002a,b; Meyer et al., 2002; Andreev et al., 2002b; Bobrov 58 et al., 2004; Kienast et al., 2005; Sher et al., 2005). Environmental 59 changes from the Middle to the Late Weichselian and into the 60 Holocene have been reconstructed through multidisciplinary 61 studies. The two clearest results of these studies are (i) the 62 continuous existence of a treeless grass/herb-dominated vegetation 63

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Fig. 1. Map of the Arctic (I) and Laptev Sea region (II) showing the location of the studied section at Cape Mamontov Klyk (III).; 1 \_ Olenek channel; 2 \_ Bykovsky Peninsula; 3 \_ Bol'shoi Lyakhovsky Island; source for III: GoogleEarth software.

(Andreev et al., 2002b), and (ii) very cold winters, attested by the
continuous growth of thick ice wedges and by their stable-isotope
composition (Meyer et al., 2002; Hubberten et al., 2004).

Recent studies in the Arctic regions show a complex response of 67 the environmental system to major climatic fluctuations during the 68 Late Pleistocene and Holocene. In such situations it is difficult, if at all 69

possible, to find a single proxy which provides complete information
 about the palaeoenvironment at local to regional scale. It is therefore
 important to find complementary records and proxies for multi disciplinary investigation of Late Quaternary sediments in the Arctic.

Testate amoebae (Cercozoa & Amoebozoa; hereafter TA) are small 74 single-celled organisms (7-450 µm) with a distinct organic shell 75(testa) and well-defined ecological preferences. They are distributed 76 77 worldwide in freshwater environments, in peat bogs, and mosses, but 78 they are also frequent in soils, especially in soils with a high organic 79 content. The empty shell remains intact after the death of the amoebae and allows precise taxonomic identification; in most cases to 80 species level (Beyens and Meisterfeld, 2001). An important advantage 81 for palaeoecological investigations is the short generation time, which 82 makes TA sensitive indicators of short-lived environmental changes. 83 This provides a basis for reconstruction of past environments and 84 climates. The occurrence of the fragile shells in fossil sequences also 85 reflects non-disturbed sediment accumulation without reworking. 86 Beyens and Chardez (1987) reported that the moisture content 87 determines the structure of TA communities. Therefore fossil TA 88 assemblages can be used to detect changes in local hydrological 89 conditions. TA have been widely studied in peat bogs (e.g. Schönborn, 90 91 1962; Tolonen, 1986), in particular in Sphagnum-moss habitats (e.g. 92 Charman, 2001; Gilbert et al., 2003, Schnitchen et al., 2003; Mitchell et al., 2004; Lamentowicz and Mitchell, 2005), and in lakes (Ogden 93 and Hedley, 1980). Most of the former studies have been done in 94Europe. In the Arctic terrestrial moss habitats were studied for TA in 95Greenland (Beyens et al., 1992; Trappeniers et al., 2002), Spitsbergen 96 97 (Beyens et al., 1986), Canada (Beyens et al., 1990) and Alaska (Beyens and Chardez, 1995). Smith (e.g. 1992, 1996) and Wilkinson (e.g. 1990, 98 1994) performed several case studies focusing on distribution and 99 100 ecology of terrestrial TA in the Antarctic soil environments.

Studies from aquatic environments have shown that TA are good 101 palaeoenvironmental indicators in freshwater environments. For 102 example Medioli and Scott (1988) noted that TA require a certain 103 minimum water temperature (6 °C) at some time during the year to 104 reproduce successfully. McCarthy et al. (1995) compared palaeotem- 105 peratures and precipitation amounts derived from pollen data with 106 the TA assemblages from the same sediment. Patterson et al. (1985) 107 found that the division between two major TA assemblages in some 108 small lakes appears to be a function of seasonal temperatures. 109 Dallimore et al. (2000) studied TA communities in lakes of the 110 Canadian Arctic in order to correlate modern TA assemblages to 111 varying environmental variables (e.g. summer lake temperature, 112 water conductivity) and in turn, to relate this information to past 113 assemblages from core material. In East Siberia the TA analysis of 114 lacustrine sediments of the Last Interglacial and the Holocene has 115 been reported from Bol'shoy Lyakhovsky Island in the Laptev Sea 116 (Andreev et al., 2004a,b; Andreev et al., in press), from Bykovsky 117 Peninsula. east of the Lena Delta (Bobrov et al., 2004), and from the 118 Olenek Channel, the westernmost outlet of the Lena Delta (Schirrme- 119 ister et al., 2003) where differences between Late Pleistocene and 120 Holocene environmental conditions as well as during Late Pleistocene 121 climate fluctuations are convincingly reflected by TA records. 122

### 2. Study area

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The study area, Cape Mamontov Klyk  $(73^{\circ}60'-73^{\circ}63'N, 116^{\circ}88'- 124)$   $(117^{\circ}18'E; Fig. 1)$ , is located at the Laptev Sea coast between the Anabar 125 Bay and the Olenek Bay, about 30 km to the north of the 126 Pronchishchev Ridge (about 270 m a.s.l.). The coastal lowland is a 127 gently inclined plain ca 25–35 m a.s.l. in elevation. Wide flat 128 watersheds with gentle slopes and shallow valleys characterize the 129



**Fig. 2.** Stratigraphic scheme of the main studied site of Cape Mamontov Klyk with position of investigated sections. Explanations for geomorphological terms used in this study: thermo-erosional valley: dendritic u-shaped valleys with flat floor, very moist, often with surface water and little ponds, dense grass/sedge vegetation; width about 50 m; thermokarst depression: deep ground subsidence area due to permafrost melting often with large extent (100 m to several km), dominated by wet tundra vegetation (mosses, grass), lakes may occur in the depressions; thermokarst mounds: intra-polygon sediment blocks surrounding the perimeter of ice wedges that have melted; Yedoma: frozen sequences of organic and mineral soils containing large amounts of ground ice, erosional relicts of Late Pleistocene surface; Alas: steep-sided depression formed by the melting of permafrost, it may contain a lake.

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t1.1 Table 1

Selected geochemical characteristics, radiocarbon ages, and short lithological description of analysed samples; samples marked with \* containing no testate amoebae shells

t1.2 t1.3	Sample	Profile/unit 1/transition	Height (m a.s.l.)	pН	TOC (wt.%)	C/N	Radiocarbon age ( <sup>14</sup> C yr BP)	Lithology
t1.4	MaK-1-9*	A to B	4.30	-	0.29	0.68	>44,520	Fine-sand silt, grass roots
t1.5	MaK-1-12	1/B	5.30	-	11.10	24.48	40,410+1230/-1070	Peaty palaeosol
t1.6	MaK-1-13	1/B	5.50	7.4	1.76	8.14	-	Silty interlayer
t1.7	MaK-1-14	1/B	5.70	-	3.18	11.17	-	Peaty palaeosol, peat inclusion
t1.8	MaK-2-1*	1/A	6.20	7.3	0.21	2.34	>37,100	Sand, organic free
t1.9	MaK-2-3	1/B	7.40	6.5	15.30	24.96	-	Peaty palaeosol, cryoturbated, peat inclusion
t1.10	MaK-2-4	1/B	7.80	6.6	3.02	10.46	-	Fine sand silt, interlayer, plant remains
t1.11	MaK-2-5	1/B	8.10	-	2.82	10.00	-	
t1.12	MaK-2-6	1/B	8.30	6.0	9.90	18.65	42,260+1860/-1510	Peaty palaeosol, cryoturbated, peat inclusion
t1.13	MaK-2-7*	1/B	8.70	7.9	0.98	7.37	-	Fine sand silt, interlayer, plant remains, net-like structures
t1.14	MaK-2-8	1/B	9.20	7.4	0.83	5.35	-	Fine sand to silt
t1.15	MaK-2-9	1/B	9.80	6.8	13.50	15.48	44,310+1260/-1090	Peaty palaeosol, cryoturbated, peat inclusion
t1.16	MaK-3-1*	1/B	4.90	-	1.20	6.57	-	Fine sand, peat inclusions
t1.17	MaK-3-3*	1/B 1/D	5.90	- 70	1.96	9.78	-	Reworked, refrozen slope material?, peat inclusion
t1.18	MaK 2 7	1/B 1/D	0.90	7.0	4.07	11.82	-	Palaeosol, fine-sand sift, sinali, discontinuous peat inclusion
t1.19	MaK 2 10	1/B 1/D	7.00	0.7	4.80	10.00	43,510+1010/-900	Pedly palaeosol, see Mark 3–5
t1.20	MaK-3-10	1/B 1/P	8.40	7.2	2.50	0.00	-	Palaeosol, plant remains
+1.22	$M_{2}K = 2 \cdot 12^{-1}$	1/D 1/P	10.20	7.5	0.81	2.95	-	
+1.92	$M_2 K_2 = 16$	1/D 1/P	10.50	6.7	2.72	0.07	43,020+1700/-1400	Peaty palaeosol, peat inclusions
t1.25 +1.94	$M_{2}K_{3}_{17}$	1/B	12.40	0.7	3.55	0.J0 8 01	- 31 250 + 1080/- 950	Peaty palaeosol, peat inclusions
t1.24 +1.25	$M_{2}K_{-5-3}$	1/D 1/C	14.30	67	3.02	8.08	$24.600 \pm 170/-160$	Palaeosol, peat inclusion, wood remains (twigs, roots)
+1.26	$M_2K_5_4$	1/C	14.50	6.6	107	5.00	24,000 170/ 100	Silty sand grass roots weakly laminated sand laminae
t1.20	MaK-6-4*	1/C	16.00	- 0.0	2.02	6.27	20.640+90	Sandy silt, grass roots
t1 28	MaK-8-3	1/C	15.80	_	2.02	732	_	Peaty palaeosol neat inclusion wood remains
t1 20	MaK-8-4*	1/C	16 30	67	4 93	12 41	_	Peaty palaeosol, peat inclusion, wood remains
t1.20	MaK-9-3	1/C	20.90	67	4.06	10.84	_	Fine-sand silt wood remains
t1 31	MaK-9-4	1/C	20.30	64	3 53	9.54	_	Fine-sand silt, wood remains
t1 32	MaK-9-5	1/C	21.90	_	4 90	13 41	16 510 + 60	Fine-sand silt, wood remains
t1.33	MaK-10-5	1/D	24.30	6.7	21.80	16.53	9480±40	Cryoturbated palaeosol, peat inclusion
t1.34	MaK-10-7	1/D	24.90	_	11.10	15.25	_	Peaty palaeosol, peat inclusion
t1.35	MaK-10-8	1/D	25.20	7.2	7.89	13.81	9510±45	Cryoturbated palaeosol, peat inclusion
t1.36	MaK-10-10*	1/D	25.75	6.6	10.54	14.58	_	Palaeosol, peat inclusion
t1.37	MaK-10-11	1/D	26.00	-	16.10	14.69	2785±30	Palaeosol, peat inclusion
t1.38	MaK-11-2*	sub-profile	2.50	-	3.50	10.58	11,060±45	Sandy silt, plant remains
t1.39	MaK-11-6	sub-profile	4.20	-	2.13	10.31	2075±30	Silty fine sand, laminated, grass roots
t1.40	MaK-11-7	sub-profile	4.90	5.5	1.99	9.57	-	Peaty palaeosol, peat inclusions
t1.41	MaK-11-8*	sub-profile	5.20	-	3.81	11.57	-	Peaty soil, peat inclusions
t1.42	MaK-11-9	sub-profile	5.50	5.8	6.41	12.85	-	Peat inclusion
t1.43	MaK-11-10	sub-profile	5.80	-	6.55	12.82	-	Fine sand to silt
t1.44	MaK-11-11	sub-profile	6.00	-	7.48	14.07	-	Transition layer, soil
t1.45	MaK-12-1	2/C	0.50	6.6	6.13	10.89	27,220+310/-300	Peaty palaeosol, peat inclusion
t1.46	MaK-12-2	2/C	0.75	-	8.22	13.44	-	Peaty palaeosol, peat inclusion
t1.47	MaK-12-4	2/C	1.00	6.6	8.52	15.58	-	Peaty palaeosol, peat inclusion
t1.48	MaK-12-5	2/C	1.25	6.3	5.58	13.08	-	Cryoturbated palaeosol, peat inclusion
t1.49	MaK-13-7	2/C	4.30	7.4	3.34	9.30	24,150±120	Fine-sand silt, few organic, wood remains
t1.50	MaK-14-4	sub-profile	1.40	5.6	14.15	11.73	1480±20	Alas deposit, interbedding peaty layers (2-4 cm)
t1.51	MaK-14-5	sub-profile	1.70	-	3.47	11.01	-	Alas deposit, sand-peat interbedding
t1.52	MaK-14-6	sub-profile	2.00	5.3	3.57	11.54	-	Alas deposit, sand-peat interbedding
t1.53	MaK-14-7*	sub-profile	2.30	-	6.18	15.82	-	Alas deposit, sand-peat interbedding, more peaty
t1.54	MaK-14-8	sub-profile	2.60	5.5	4.88	14.34	3720±30	Alas deposit, peaty soil
t1.55	MaK-14-9*	sub-profile	2.90	-	4.20	14.11	-	Alas deposit, cryoturbated peat soil, peat inclusion
t1.56	MaK-15-5*	2/C	6.60	-	2.26	9.31	21,890±90	Fine-sand to silt, wood (twigs, roots)
t1.57	MaK-16-5*	2/C	9.30	-	1.81	9.06	20,180±80	Fine-sand to silt, wood (twigs, roots)
t1.58	MaK-17-3	2/C	11.50	-	2.49	10.24	18,920±70	Peaty palaeosol, wood remains
t1.59	MaK-17-7*	2/C	13.60	7.0	2.06	9.46	17,700+70/-60	Palaeosol
t1.60	MaK-19-3*	2/C	15.30	-	1.41	7.17	16,350±90	Sand, few wood remains, finely distributed plant remains
t1.61	MaK-19-4	2/0	15.60	7.5	5.06	13.37	-	Palaeosol, many wood remains, organic-rich spots
t1.62	MaK-19-7*	2/C	17.10	7.5	2.61	11.32	14,545±50	Sandy slit

relief. The coastal lowland is drained to the sea by several small streams. The studied section (Fig. 2) is located at the lowland's cliff (10 to 25 m a.s.l.) formed by frozen deposits and ice wedges. The section extends, from the Nuchcha Dziele River mouth ca 2.2 km eastwards close to the navigation signal of Cape Mamontov Klyk.

The continental Arctic climate of this region is characterized by long cold winters and short cool summers. The mean annual air temperature is about -14 °C. The mean January temperature is about -22 °C and the mean July temperature 5 to 6 °C. Mean annual precipitation is 230-270 mm with 75% of it falling as rain during the summer months. In general, the snow cover stays from the end of September to the end of June. The snow cover is thin but locally reaches up to 50 cm. The study area belongs to the zone of continuous permafrost reaching 400–600 m 142 (Yershov, 1989). The mean annual ground temperature is about -11 to 143 -12 °C. The active layer varies in depth from 20 to 50 cm in July. 144

This area belongs to the northern tundra vegetation zone (Atlas 145 Arktiki, 1985). The CAVM Team (2003) classifies it further to the 146 nontussock-sedge, dwarf-shrub, moss tundra characterized by hemi 147 prostrate and dwarf shrubs (<40 cm high) and a well-developed moss 148 layer (5–20 cm thick). Prostrate and hemi prostrate dwarf shrubs 149 include *Betula exilis, Salix arctica, S. polaris, S. reticulata,* and *Dryas.* 150 Among other common taxa are sedges (*Carex arctisibirica, C. bigelowii,* 151 and *Eriophorum*), grasses (e.g. *Arctagrostis latifolia, Poa arctica*), forbs 152 (e.g. *Silene, Sagina nivalis, Senecio frigidus, Saxifraga oppositifolia,* 153

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Table 2 (continued)

### t2.1 Table 2

List of testate amoebae taxa in Late Pleistocene and Holocene deposits and their habitat preference (after Chardez, 1965)

Species	Frequency (%)	Frequency (%)		
	Pleistocene	Holocene	Surface samples	_
Arcella arenaria v. compressa Chardez	z 10.3	18.2	0.97	М
A. artocrea Leidy		9.1	0.19	Sh
A. c.f. <i>crenulata</i> Deflandre	3.4			ShM
A. discoides v. scutelliformis Playfair A. rotunda v. aplanata Deflandre	6.9		0.39	vv ShM
A. sp.	3.4			-
Bullinularia gracilis Thomas	3.4	0.0		MS
B. Inaica Penara Trigonopyvis arcula (Leidy) Penard	10.3	0.6		IVIS MS
<i>T. minuta</i> Schönborn & Peschke	3.4			S
Centropyxis aculeata (Ehrenberg Stein	) 3.4			W
C. aculeata f. A	3.4			W
C. aerophila Deflandre	86.2	63.6	5.41	М
C. aerophila v. minuta Chardez	86.2	72.7	0.58	WMS
C. aerophila v. sphagnicola Deflandre	41.4	45.5		ShM
C. cassis (Wallich) Deflandre	3.4	27.3	0.19	ShMS
C. constricta y minima Docloitro	51.7 70.2	18.2	0.70	IVIS
C. discoides (Penard) Deflandre	34	05.0	12.10	W/
<i>C</i> gibba Deflandre	3.4			ShM
C. orbicularis Deflandre	20.7	18.2	0.19	WShM
C. plagiostoma Bonnet, Thomas	86.2	45.5	0.39	S
C. plagiostoma f. A major	37.9		0.58	S
C. plagiostoma f. B minor	48.3	54.5	3.86	S
C. plagiostoma Bonnet, Thomas v. oblonga Chardez		9.1		S
C. plagiostoma v. terricola Bonnet, Thomas	3.4	54.5		S
<i>C. platystoma</i> (Penard) Deflandre <i>C. pontigulasiformis</i> Beyens, Chardez	6.9	27.3	0.19 0.19	WMS WM
& and De Bock	96.7	70 7	4.05	c
C. sylvatica v. globulosa Bonnet	34	12.1	4.05	S
C sylvatica v microstoma Bonnet	379	91		S
C. sylvatica v. minor Bonnet, Thomas	86.2	63.6	0.39	ShS
C. sp. 1	3.4			_
C. sp. 2		9.1		-
Cyclopyxis arcelloides Penard	3.4			WShM
C. eurystoma Deflandre	44.8	36.4	1.16	S
C. eurystoma v. parvula	72.4	81.8	11.39	S
<i>C kahli</i> Deflandre	672	18.2		WSP2
C c f <i>kahli</i> Deflandre f A (minor)	69	10.2		WShS
C. sp.	6.9			-
Plagiopyxis bathystoma Bonnet	10.3			S
P. callida Penard	20.7	9.1		WShMS
P. declivis Thomas	3.4			ShS
P. minuta Bonnet	3.4		0.39	MS
P. penardi Thomas	31.0	36.4		WS
Heleopera petricola Leidy	20.7			WSh
H. petricola v. ametrystea Penard H. petricola v. humicola	3.4			S
buillet & Huuilds	3.4			14/14
n. sphught Lefuy Nebela higibbosa Penard	5.4		0.10	W/ShM
N collaris (Ehrenberg) Leidy	34	18.2	0.19	ShM
N. lageniformis Penard	3.4	10.2	0.39	ShM
N. parvula Cash	6.9			ShM
N. penardiana Deflandre		9.1		W
N. tincta (Leidy) Awerintzew	3.4	9.1	9.85	ShM
N. tincta f. stenostoma Jung			0.58	ShMS
N. sp.	6.9	10.0		-
Argynnia sp.	31.0	18.2		WSh
Schoenbornia humicola (Schönborn	3.4 )		5.02	S
Decloitre				
Sch. viscicula Schönborn			0.39	S
Difflugia bryophila (Penard) Jung	3.4	10.0		ShM
D. CIULETU LEIUY	3.4	10.2		VV

Species	Frequency (%)			Ecology	t2.69
	Pleistocene	Holocene	Surface samples		t2.70
D. difficilis Thomas		18.2		W	t2.71
D. globulus Wallich	37.9	36.4	1.93	WSh	t2.72
D. lucida Penard	20.7	9.1		WSh	t2.73
D. mammilaris Penard	6.9			W	t2.74
D. microstoma (Thomas)	3.4			W	t2.75
D. minuta Rampi	10.3	9.1		Sh	t2.76
D. oblonga Ehrenberg		9.1		W	t2.77
D. oblonga v. longicollis Gassowsky		9.1		W	t2.78
D. penardi Hopkinson	6.9	9.1		W	t2.79
D. pristis Penard	6.9			W	t2.80
D. c.f. pyriformis Perty	3.4			W	t2.81
D. sp. 1	3.4			_	t2.82
D. sp. 2	3.4			_	t2.83
Phryganella acropodia (Hert. & Less.) Hopkinson	55.2	27.3	0.97	WMS	t2.84
Ph. acropodia c.f. v. australica Playfair	13.8	45.5		W	t2.85
Ph. hemisphaerica Penard		9.1		WShM	t2.86
Paraquadrulla irregularis Archer	3.4			М	t2.87
Assulina muscorum Greef			2.90	М	t2.88
Valkanovia delicatula (Valkanov)			0.39	ShM	t2.89
Euglypha ciliata (Ehrenberg) Wailes			0.19	WShM	t2.90
E. ciliata f. glabra Wailes			9.46	WShMS	t2.91
E. cuspidata Bonnet			0.39	S	t2.92
E. dolioliformis Bonnet			0.19	MS	t2.93
E. laevis (Ehrenberg) Perty			5.41	WShMS	t2.94
E. strigosa f. glabra Wailes			2.32	ShMS	t2.95
Corvthion dubium Taranek			0.77	WShM	t2.96
Trinema enchelys (Ehrenberg) Leidy			0.58	WShM	t2.97
T. lineare (Ehrenberg) Leidy			6.56	WShMS	t2.98
T. penardi Thomas-Chardez			1.93	MS	t2.99
Pseudodifflugia c.f. gracilis	3.4	27.3		W	t2.100
Schlumberger					
P. gracilis v. terricola Bonnet &	6.9	9.1		S	t2.101
I nomas	10.2	0.1			10.100
lestacea sp. 1	10.3	9.1		-	t2.102
lestacea sp. 2				-	t2.103
lestacea sp. 3			0.19	-	t2.104
N, species	68	42	40		t2.105
S soil Sh Snhamum M other	mossos W/	wator			+9 106

soil, Sh — Sphagnum, M — other mosses, W — wate

Pedicularis lanata), mosses and liverworts (Tomenthypnum nitens, 154 Hylocomnium splendens, Aulacomnium turgidum), and lichens (Tham- 155 nolia, Peltigera, Cladonia). 156

#### 3. Data and analytical methods

#### 3.1. Sediments and chronology

Two large vertical composite profiles were studied at the coastal 159 cliff consisting mostly of frozen sediments accumulated in polygonal 160 centres of ice wedge polygon systems (Fig. 2). The sub-profiles are 161 mostly exposed in so-called thermokarst mounds between large ice 162 wedges. Additionally, deposits from a thermo-erosional valley and 163 from a thermokarst depression were collected. After cleaning the 164 profile wall the soil morphology of the sections were described in the 165 field. Then about 0.5-1 kg of frozen sediment was collected with a 166 hammer or a small axe and stored in sealed plastic bags for multiproxy 167 analysis, including TA analysis, and radiocarbon dating.

In the laboratory the content of total organic carbon (TOC) and 169 total nitrogen (TN) were measured with a CNS elementary analyser 170 (Elementar vario EL III). pH measurements of the filtrated water 171 extract were done with a pH-meter (WTW multilab 540) in the 172 laboratory. Organic material from 32 samples was extracted for 173 Accelerated Mass Spectrometry (AMS) dating at the Leibniz Labora- 174 tory (Nadeau et al., 1997, 1998). For TA analysis we tried to select dated 175 samples. The age estimation of non-dated sediment samples was done 176

t2.68

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6

Table 3

Ecological preference/ habitat	TA groups	TA taxa
Eurybiotic soil	Centropyxis plagiostoma group	C. plagiostoma
	(5 taxa)	C. plagiostoma f. A major
		C. plagiostoma f. B minor
		C. plagiostoma v. oblongo
		C. plagiostoma v. terricol
	Plagiopyxis group (3 taxa)	P. callida
		P. minuta
		P. penardi
Sphagnophilic and moss	Arcella group (4 taxa)	Arcella arenaria v.
		compressa
		A. artocrea
		A. c.f. crenulata
		A. rotunda v. aplanata
	Heleopera group (3 taxa)	Heleopera petricola
		H. petricola v. amethyste
		H. sphagni
	Nebela group (5 taxa)	N. collaris
		N. lageniformis
		N. parvula
		N. penardiana
		N. tincta
	Difflugia group 2 (4 taxa)	Difflugia bryophila
		D. globulus
		D. lucida
		D. minuta
Aquatic	<i>Difflugia</i> group 1 (8 taxa)	D. cratera
		D. difficilis
		D. mammilaris
		D. microstoma
		D. oblonga
		D. oblonga v. longicollis
		D. penardi
		D. pristis
		D. c.f. pyriformis

Taxa with similar ecological preferences were grouped into three ecological groups. (see t3.37 also Fig. 3.)

using a simple altitude-age correlation according to Schirrmeister et al. (in press).

In order to compare fossil and modern TA assemblages we 179collected ten modern surface soil samples (ca 500 g) from different 180 permafrost formations and habitats in the study area. Detailed 181 sedimentological and geomorphological descriptions as well as results 182 of more comprehensive palaeoecological and geochronological inves-183 tigations of the studied sections are presented in separate papers 184 (Schirrmeister et al., 2004, in press). Here we focus on the additional 185 data sets, which are relevant to the TA study. 186

187 3.2. TA analysis

Three grams of each representative and carefully mixed fossil or 188 modern surface sample were prepared for TA analysis. The samples 189 190were first suspend in distilled water and passed through a 500 µm 191 meshed sieve to remove large masking organic and mineral particles. The next day a drop of suspension mixed with a drop of glycerine was 192added on a glass slide. The samples were counted under light 193microscope at magnifications 100-400×. On the average, five slides 194 were examined for each sample. If possible a minimum of 150 TA 195shells were counted for each sample. We stopped counting if no shells 196 were found in the first two slides. 197

The TA identification followed Chardez (1967), Ogden and Hedley (1980), Ogden (1983), Ellison and Ogden (1987), Gel'tser et al. (1985, 200 1995). For ecological interpretation of TA assemblages we followed Q1 201 Chardez (1965), former arctic studies (Beyens et al., 1990, 1995; Dallimore 202 et al., 2000, Andreev et al., 2004a; Bobrov et al., 2004), as well as our own 203 field observations. TA analysis described here was done in the laboratory 204 of the Soil Science Faculty at Moscow State University.

The TILIA, TILIAGRAPH, and TGView computer programs were used 205 for calculation of taxa percentages and graphing the data (Grimm, 206 1993, 2004). The sum of all TA taxa counted in each sample was taken 207 as 100%. Photographs were done with the light microscope Axioskop 208

Zeiss 40 and a digital camera (integ). Scanning electron microscope 209

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212

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observations were done using the microscope Jeol GSM 6060A.

### 4. Results

### 4.1. Description of the general profile

The studied sequences were subdivided into several units (A to D, 213 Fig. 2) according to geochronological and sedimentological data. 214 Results of sediment analyses, which are used for the interpretation of 215 TA records, are presented in Table 1. The lowest unit A consists of 216 yellowish-grey, weakly bedded fine-grained sand without visible 217 plant remains (lower part of MaK-1). A transition layer of about one 218 meter thickness, which contains numerous in situ grass roots, covers 219 the organic-free sands. The sand is considered as fluvial deposit, and 220 the transition layer reflects shallow facies conditions of a flood plain. 221 The subsequent unit B (upper part of MaK-1, MaK-2 and MaK-3) 222 consists of an alternation of four cryoturbated peaty horizons and of 223 weakly laminated, dark-grey silty to fine sandy interbeds. The peaty 224 horizons mostly consist of brown coloured moss peat. The sandy 225 interbeds contain numerous plant remains like grass roots and twig 226 fragments. The sediments of unit B are most probably formed by 227 alternating processes of alluviation in the flood plain. Both units 228 contain separate ice wedges and are additionally penetrated by ice 229 wedges coming from the overlying unit C. The transition to unit C is 230 gradual without a sharp boundary. Unit C represents the Ice Complex 231 deposits with their typical huge ice wedges reaching from about 25 m 232 a.s.l. down below the present sea level. Unit C is composed of many 233 palaeosol layers with peat inclusions and numerous twig fragments. 234 This unit is subdivided into two subunits. The lower horizon of about 0 235 to 2 m a.s.l. consists of cryoturbated peat soils with silty to fine sandy 236 interbeds (MaK-12). The main part of unit C is formed by several 237 weakly developed palaeosol horizons and silty to fine sandy interbeds 238 with in situ grass roots and fragments of shrub twigs (MaK-5 to MaK-9 239 and Mak-13 to MaK-19). In places, unit C is covered by a 2 m thick 240 sequence of peat soils representing the filling of small thermokarst 241 ponds, which have developed on the surface of the Ice Complex 242 formation (Yedoma). They were often observed as peat spots 243 irregularly distributed on the Yedoma surface. These uppermost 244 deposits (MaK-10) were assigned to the Holocene (unit D). Addition- 245 ally unit D includes deposits of thermo-erosional valleys (sub-profile 246 MaK-11) and of a thermokarst depression, 8 km west of the Nuchcha 247 Dziele River mouth (sub-profile MaK-14). 248

### 4.2. TA analysis of fossil samples

In total, 59 samples from Late Quaternary deposits were studied. 250 TA were found in 40 samples of unit B, C and D. A total of 97 species, 251 varieties, and morphological forms of TA (Table 2) belonging to 252 different ecological groups were identified (Table 3). The sand 253 deposits of unit A did not contain visible plant remains and organic 254 material at all. No TA shells could be found in these sediments. The 255 number of taxa found per sample varied from 1 to 32. The number of 256 TA shells counted in one sample varied from 1 to 356. In the fossil TA 257 diagram (Fig. 3) the samples were ordered following the age-height 258 model. According to the chrono-stratigraphic information for Siberia 259 and results of the radiocarbon AMS-dating the diagram was divided 260 into three zones – Kargin Interstadial (MIS 3, Middle Weichselian), 261 Sartan Stadial (MIS 2, Late Weichselian), and Holocene (MIS 1) (Kind, 262 1974; Hubberten et al., 2004; Svendsen et al., 2004).

*Kargin Interstadial* sediments dated to between 44,310 and 26,400  $_{264}$  <sup>14</sup>C yr BP. In sediments dated to 44,310–40,000 <sup>14</sup>C yr BP the highest  $_{265}$ 

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### t4.1 Table 4

List of studied samples containing testate amoebae shells and palaeoecological interpretation of testate amoebae assemblages (correlated ages were estimated according to ageheight correlations of Schirrmeister et al., in press)

		,,,,,		
t4.2 t4.3	Sample ID, height, m a.s.l.	Type of sediment	Age, <sup>14</sup> C yr BP correlated ages	TA assemblages with palaeoecological interpretation
t4.4	Unit B	l		
t4.5	Peat-sana-comp	iex aeposits		
t4.6	MaK-1- 14, 5.7	Peaty palaeosol, cryoturbated, peat inclusion	40,800	32 species and varieties. Highest species diversity (10 hydrobiotic <i>Difflugia</i> taxa) within studies samples including modern ones. Presence of sphagnobiotic <i>Heleopera</i> , <i>Nebela</i> and <i>Argynnia</i> sp. indicates boggy habitat conditions with permanent or temporal open water bodies. Numerous ostracod shells also indicate the existence of aquatic habitats. The climate was rather warm and wet
t4.7	MaK-1- 13, 5.5	Silty interlayer	40,600	13 taxa. Presence of <i>Trigonopyxis arcula</i> , characteristic for bogs with low water table (Woodland et al., 1998; Tolonen et al., 1992) reflects soil with well-developed humus litter.
t4.8	MaK-1- 12, 5.3	Peaty palaeosol	40,410+1230/ -1070	15 species and varieties. Mainly eurybiotic <i>Centropyxis aerophila</i> and <i>C. sylvatica</i> . Sphagnobiotic <i>Trigonopyxis arcula</i> , <i>Heleopera petricola</i> , <i>Argynnia sp</i> . f. A ( <i>minor</i> ) and calceophilic <i>Centropyxis</i> taxa indicating meso-oligotrophic peatland conditions.
t4.9	MaK-2-3, 7.4	Peaty palaeosol, cryoturbated, peat inclusion	41,600	17 species, varieties and forms including hydrophilic <i>Difflugia</i> , sphagnobiotic species from <i>Heleopera</i> and <i>Argynnia</i> . 2 species from the hydrophilic <i>Arcella discoides</i> v. <i>scutelliformis</i> . First find of <i>Paraguadrulla irregularis</i> in Late Pleistocene sediments. Increasing soil moisture.
t4.10	MaK-2-4, 7.8	Fine sand silt, plant remains	41,900	15 taxa. Sphagnobiotic/hydrophilic <i>Heleopera petricola</i> v. <i>amethystea</i> and hydrophilic <i>Difflugia</i> sp. 1 and sp. 2, indicating increasing moisture.
t4.11	MaK-2-5, 8.1	Palaeosol	42,100	12 species, varieties and forms from soil-eurybiotic <i>Centropyxis</i> , <i>Cyclopyxis</i> , <i>Plagiopyxis</i> , and <i>Phryganella</i> , partly represented by smaller forms ( <i>minor</i> , <i>minuta</i> , <i>minima</i> ). Soil environment.
t4.12	MaK-2-6, 8.3	Peaty palaeosol, peat inclusion	42,260+1860/ -1510	8 taxa. Mostly soil and eurybiotic species, like <i>Centropyxis aerophila</i> , <i>Cyclopyxis eurystoma</i> v. <i>parvula</i> . Single find of <i>Centropyxis plagiostoma</i> . Sphagnophilic <i>Heleopera petricola</i> and <i>H. sphagni</i> indicating peatland development. Hydrophilic taxa are absent. Sediment formation under more dry conditions, than in the previous sample.
t4.13	MaK-2-8, 9.2	Fine sand to silt	43,000	15 taxa including calceophilic <i>C. plagiostoma</i> and <i>Cyclopyxis kahli</i> , sphagnophilic <i>Heleopera petricola</i> and <i>Argynnia sp.</i> , hydrophilic <i>Difflugia globulus</i> . Rather wet meso-oligotrophic peatland conditions.
t4.14	MaK-2-9, 9.8	Peaty palaeosol, peat inclusion	44,310+1260/ -1090	24 taxa including genera <i>Centropyxis</i> (50%), <i>Arcella</i> , <i>Cyclopyxis</i> , <i>Heleopera</i> , <i>Nebela</i> , <i>Difflugia</i> , <i>Pseudodifflugia</i> , and <i>Phryganella</i> . Aquatic <i>Centropyxis aculeata</i> and <i>C. cassis</i> as well as hydrophilic Difflugia (D. globulus, D. lucida, D. penardi) are indicating wet habitat conditions. Calceophilic <i>Centropyxis plagiostoma</i> and <i>Cyclopyxis kahli</i> suggests pH close to neutral. Sphagnobiotic <i>Arcella</i> and <i>Nebela</i> species suggest an oligotrophic environment typical for bogs with a high water table.
t4.15	MaK-3-5, 6.9	Palaeosol, fine- sand silt, small, discontinuous peat inclusion	43,700	12 taxa. Dominated by eurybiotic and soil taxa (including <i>Plagiopyxis</i> ). Species diversity decreased only half of previous level. No hydrophilic species. Rather dry soil conditions.
t4.16	MaK-3-7, 7.0	Palaeosol, fine- sand silt, small, discontinuous peat inclusion	43,510+1010/ -900	17 taxa (mostly <i>Centropyxis</i> and <i>Cyclopyxis</i> taxa). Hydrophilic <i>Difflugia globulus</i> and sphagnobiotic <i>Heleopera petricola</i> v, <i>humicola</i> reflecting more humid conditions compared to MaK-3-5.
t4.17	MaK-3-10, 8.4	Palaeosol	43,550	13 taxa. Predominantly soil and eurybiotic species from <i>Centropyxis</i> , <i>Cyclopyxis</i> , <i>Plagiopyxis</i> , and <i>Phryganella</i> mostly represented by smaller forms like <i>minor</i> , <i>minuta</i> , <i>minima</i> . High decrease of species diversity and disappearance of numerous genera (in detail hydro- and sphagnobiotic taxa). Sedimentation under soil conditions.
t4.18	MaK-3-14, 10.3	Peaty palaeosol, peat inclusions	43,620+1700/ -1400	3 taxa. Soil-eurybiotic <i>Centropyxis aerophila</i> , <i>C. constricta</i> v. <i>minima</i> , <i>C. plagiostoma</i> f. <i>minor</i> . Unfavourable conditions for TA, probably too dry.
t4.19	MaK-3-16, 12.4	Peaty palaeosol, peat inclusions	32,700	10 soil-eurybiotic taxa from <i>Centropyxis</i> , <i>Cyclopyxis</i> , and <i>Phryganella</i> . <i>Centropyxis</i> and <i>Cyclopyxis</i> taxa mostly represented by f. minor, minuta, minima reflecting dry soil conditions.
t4.20	max-5-17, 15.2 Teaty paracosol, peat inclusions		-950	sphagnobiotic <i>Argynnia sp.</i> indicates wetter habitat conditions.
t4.21	Unit C			
t4.22	Ice Complex sedi	ments		
t4.23	Profile 1	Delegend most induction	24 000 - 170/	
t4.24	MaK-5-3, 14.3	Palaeosol, peat inclusion	- 160	21 taxa. Presence of sphagnobiotic (rigonopyxis arcula and 1. minuta, inhabitants of a coarse-numus litter, as well as soil taxa Plagiopyxis callida, P. minuta, and P. penardi.
04.20	Mak-0-3, 13.0	reaty palacosol, peat inclusion	22,000	Phryganella. Presence of sphagnobiotic Nebela parvula reflects short flooding. Absence of calceophilic taxa indicates acidic pH of soil solution.
t4.26	MaK-9-3, 20.9	Fine-sand silt	18,000	16 taxa of soil-eurybiotic <i>Centropyxis</i> , <i>Cyclopyxis</i> , <i>Plagiopyxis</i> , and <i>Phryganella</i> . Dominance of calceophilic <i>C. plagiostoma</i> (43.5%) point to nearly neutral pH soil solution.
t4.27	MaK-9-4, 21.4	Fine-sand silt	17,600	15 taxa. Species composition similar to that in MaK 9-3, but soil-living <i>Plagiopyxis</i> is replaced by hydrophilic <i>Difflugia globulus</i> and <i>D. lucida</i> . Presence of hydro-sphagnobiotic <i>Argynnia sp.</i> indicating increasing habitat moisture.
t4.28	MaK-9-5, 21.9	Fine-sand silt	16,510±60	17 taxa from the soil-eurybiotic group, mainly (63.5%) represented by small sized forms. Soil formation under unfavourable conditions – lower temperatures and decreasing moisture.
t4.29	Unit D <sub>2</sub>			
t4.30	Holocene cover			
t4.31	MaK-10-5, 24.3	Cryoturbated palaeosol, peat inclusion	9480±40	17 species and varieties reflecting meso-oligotrophic peatland conditions. Arcella arenaria v. compressa, Argynnia sp., and Phryganella hemisphaerica are indicating active processes of paludification
t4.32	MaK-10-7, 24.9	Peaty palaeosol, peat inclusion	9500	13 taxa reflecting soil formation under dry conditions.
t4.33	MaK-10-8, 25.2	Cryoturbated palaeosol, peat inclusion	9510±45	7 taxa reflecting the same environmental conditions like in MaK 10-7.
t4.34	MaK-10-11, 26.0	Palaeosol, peat inclusion	2785±30	4 taxa. Centropyxis cassis and Heleopera sphagni indicating peatland habitat conditions.

(continued on next page)

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t4.35	Table 4 (continued)							
t4.36	Sample ID, Type of sediment height, m a.s.l.		Age, <sup>14</sup> C yr BP correlated ages	TA assemblages with palaeoecological interpretation				
	Unit C							
t4.37	Profile 2							
t4.38	MaK-12-1, 0.5	Peaty palaeosol, peat inclusions	27,220+310/ -300	19 species and intraspecific taxa. Mostly soil-eurybiontic species. Hydrophilic <i>Difflugia globulus</i> and <i>D. pristis</i> c.f., and single find of sphagnobiotic <i>Argynnia sp.</i> reflect rather wet conditions. <i>Centropyxis plagiostoma</i> represented by different morphological types point to meso-oligotrophic water regime of				
t4.39	MaK-12-2, 0.75	Peaty palaeosol, peat inclusions	27,000	the habitat. Numerous diatom shells also reflect wet habitat conditions. 19 taxa. Species composition is similar to MaK 12-1, but hydrophilic <i>Difflugia</i> are replaced by aquatic and sphagnobiotic <i>Arcella</i> . Numerous diatom and ostracod shells support the assumption of moist bog conditions.				
t4.40	MaK-12-4, 1.0	Peaty palaeosol, peat inclusions	26,800	23 taxa. Sphagnobiotic Arcella, Nebela and Difflugia indicate meso-oligotrophic peatland conditions. Dominance of Centropyxis taxa and especially C. plagiostoma confirms this interpretation.				
t4.41	MaK-12-5, 1.25	Cryo-turbated palaeosol, peat inclusion	26,400	15 taxa. Species composition resembles that in MaK 12-4. Meso-oligotrophic peatland conditions.				
t4.42	MaK-13-7, 4.3	Fine-sand silt	24,150±120	4 <i>Centropyxis</i> taxa. Presence of morphological f. <i>major</i> of calceophilic <i>Centropyxis</i> plagiostoma previously found under higher moisture conditions (Bobrov et al., 2004) point to wet soil				
t4.43	MaK-17-3, 11.5	Peaty palaeosol	18,920±70	8 species and varieties from <i>Centropyxis</i> and <i>Cyclopyxis</i> represented by f. <i>minor</i> , <i>minuta</i> , <i>minima</i> , <i>microstoma</i> , which probably indicate unfavourable climatic conditions, e.g. lower temperatures (Smith, 1988) and/or climate deterioration accompanying with dehumidification (Bobrov et al., 1999), resulting in a reduction of shell size. Presence of <i>Cyclopyxis eurystoma</i> v. <i>parvula</i> (small sized variety)				
t4.44	MaK-19-4, 15.6	Palaeosol, organic rich spots	16,000	also confirms unfavourable habitat conditions. 2 taxa. Soil-eurybiotic <i>Centropyxis aerophila</i> v. <i>minor</i> and <i>C. sylvatica</i> v. <i>minor</i> indicates a period of unfavourable environmental conditions.				
+4.45	Unit D							
t4.40 +4.46	Denosits in them	mokarst depressions						
t4.40 t4.47	MaK-14-4, 1.4	Alas deposit, interbed-ding, peaty layers	1480±20	9 taxa. Dominance of <i>Difflugia globulus</i> (25%) indicating marshy environmental conditions. Absence of calceophilic taxa reflecting slightly acidic pH				
t4.48	MaK-14-5, 1.7	Alas deposit, sand-peat interbedding		14 taxa including some hydrobiotic ( <i>Difflugia cratera, D. globulus, D. minuta</i> ) and hydro-sphagnobiotic ( <i>Cyclopyxis arcelloides</i> ). Wet <i>Sphagnum</i> -peatland environment, probably with periodically open water bodies. Numerous diatom and ostracod shells confirm the existence of open water bodies. Soil taxa				
t4.49	MaK-14-6, 2.0	Alas deposit, sand-peat interbedding		Plagiopyxis callida and P. penardi suggest seasonal changes in water table. 17 taxa. Species composition indicates meso-oligotrophic peatland conditions. Presence of soil species Plagiopyxis penardi and xerophilic moss-soil inhabitant Bullinularia indica, as well as ostracod shells, indicate fluctuations in the seasonal water regime, interchange with a period of water supply and drying. Similar combination of hydrophilic and xerophilic species is rather chracteristic for sediments in the device of the seasonal water regime.				
t4.50	MaK-14-8, 2.6	Alas deposit, peaty soil	3720±30	Single find of aquatic <i>Difflugia cratera</i> reflect a lacustrine stage of sedimentation.				
+4.51	Unit D.							
+4.59	Thermo-erosion	al valley denosits						
t4.52	MaK_11_642	Laminated silty fine sand	2075+30	Single find of soil-eurybiotic (velonyxis eurystoma v. narvula				
t4.55 t4.54	MaK-11-7, 4.9	Peaty palaeosol, peat inclusions	2073130	9 taxa including hydro-sphagnophilic <i>Centropyxis platystoma</i> , <i>Cyclopyxis arcelloides</i> , and <i>Pseudodiffugia gracilis</i> indicating an active stage of paludification				
t4.55	MaK-11-9, 5.5	Peat inclusion		22 taxa. Aquatic Difflugia globulus, D. minuta, D. oblonga, D. sp., hydro-sphagnobiotic Centropyxis platystoma, and sphagnobiotic Nebela collaris indicate wet peatland stage with near-surface water				
t4.56	MaK-11-10, 5.8	Fine sand to silt		table. Numerous diatom shells confirm the existence of very wet habitats. 18 taxa including <i>Centropyxis cassis, Heleopera petricola, Pseudodifflugia gracilis</i> characteristic for drier habitat conditions than in MaK 11-9. Youngest find of sphagnobiotic <i>Argynnia sp.</i> , previously found only in Ice Complex sediments in the Laptev Sea region.				
t4.57	MaK-11-11, 6.0	Soil transition layer		17 soil-eurybiotic, sphagnobiotic taxa (like <i>Nebela collaris, N. penardiana</i> ), and hydrophilic (like <i>Difflugia globulus, D. penardi</i> and <i>D.</i> sp.) indicate wetter conditions than in MaK 11-10. Numerous diatom shells and tardigrada eggs confirm this interpretation.				
±4.59	Modern surface	samples						
t4.58 t4.59	MaK-AA-1	Modern vegetation on dry Yedoma top	Recent	22 taxa, mostly soil-eurybiotic. Presence of few hygro- and hydrophilic taxa (like Arcella artocrea, A. arenaria y. compressa. Centropysis cassis) may reflect seasonal fluctuations in the hydrological regime				
t4.60	MaK-AA-2	Large temporary polygon 22 cm deep						
t4.61	MaK-AA-2.1	pond on Yedoma top Litter	Recent	10 taxa. Hydrophilic Difflugia globulus and Arcella arenaria v. compressa indicate wet habitats in the				
+4.02		Upper humus herizer	Pacant	local environment.				
t4.62 t4.63	MaK-AA-2.2 MaK-AA-3	Large pond (<50 cm deep) on the	Recent	10 taxa. Litter indicating and nydropnilic taxa absent. 10 taxa. Dominance (29%) of sphagnobiotic <i>Nebela tincta</i> reflects marshy habitats.				
t4.64	MaK-AA-4	Modern soil with litter	Recent	18 taxa. Hydrophilic and sphagnobiotic Difflugia difficilis, Nebela biggibosa, N. lageniformis, and N. tincta confirm wet habitat conditions.				
t4.65	MaK-G-2	Thermokarst mound on the slope of a thermo-erosional vallev	Recent	Poorly preserved amoebae shells. 3 soil-eurybiotic taxa.				
t4.66	MaK-G-5	Very moist bottom of a thermokarst depression	Recent	Single find of Centropyxis sylvatica.				
t4.67	MaK-G-11	Peaty detritus from beach	Recent	Single hydrophilic Difflugia globulus and hygrophilic Centropyxis platystoma.				

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amounts in TA sums (150–356 shells per sample) and taxa diversity 266 267 (15-32 taxa per sample) for the whole studied units are noted, especially for hydrophilic Difflugia taxa (10). Dominant taxa are soil 268 269eurybiotic and moss-living Centropyxis. During the period between ca 40,000 and 33,000 <sup>14</sup>C yr BP TA shells were absent in the studied 270samples. After 32,700 <sup>14</sup>C yr BP TA abundance and diversity slowly 271increases to 150 shells per sample and 20 taxa per sample and remain 272stable until the end of the interstadial. Dominant taxa are still soil-273274living TA and hydrophilic taxa are rarely found.

Sartan Stadial sediments are dated to 24,600-16,000 <sup>14</sup>C yr BP. At 275the beginning of this zone TA abundance slightly increases (almost 276200 shells per sample) while TA diversity remained constant (20 taxa 277per sample). Dominant taxa are from soil eurybiotic genera Centro-278pyxis and Plagiopyxis. Hydrophilic taxa are absent until ca 17,600<sup>14</sup>C yr 279BP. In one sample (ca 18,000 <sup>14</sup>C yr BP) the number of calceophilic 280 Centropyxis plagiostoma group sharply increases (up to 43.5%). 281 Sediments accumulated during the Sartan Stadial are generally 282 characterized by the absence of hydrobiont taxa. 283

Holocene sediments are dated to between 9510 and 500 <sup>14</sup>C yr BP. 284In the lowermost two samples dated to ca 9000 <sup>14</sup>C yr BP TA 285abundance is very low (50 shells), but increases up to 200 at 7400 <sup>14</sup>C 286 yr BP. After that a sedimentary hiatus is noted between ca 7400 and 287288 3720 <sup>14</sup>C yr BP (Schirrmeister et al., in press). Within the TA palaeocoenoses the number of hygro-hydrophilic and sphagnophilic 289 taxa strongly increase (up to 40%) towards present times. However, 290dominant taxa are belonging to the soil- and moss living Centropyxis 291 292genus.

#### 293 4.3. TA analysis of modern surface samples

294 No TA shells were found in two modern samples. One sample 295(MaK-G-1) was taken from the beach of a marine terrace where 296 frequent flooding and poor or no available organic substrate makes it an unfavourable habitat for TA. The other sample (MaK-G-8) was 297taken from a thermokarst depression with sparse vegetation and very 298 dry soil which also makes it impossible for TA communities to 299establish and survive, because TA require a certain minimum amount 300 of water for their activity. In total 40 species, subspecies, and forms 301 were identified in the other eight surface samples. The results are 302 compiled in a diagram (Fig. 4). Sample AA-1 was taken from the 303 surface vegetation of a Yedoma hill. In this sample we counted the 304 305 highest number of TA shells (259). Taxa diversity was the highest (25). too. We also counted a high number of shells in sample AA-3, which 306 was taken from a large pond (<50 cm depth) on the floor of a thermo-307 erosional valley. Sphagnophilic and moss taxa dominate this TA 308 spectrum. In the other six surface samples, taken from different 309 310 habitats, TA abundance was rather low (<100 shells per sample). The TA communities of modern habitats include representatives of all 311 ecological groups found in the fossil samples. Main differences of the 312 studied surface samples from the fossil ones are (1) significantly 313 smaller number of sphagno-, hygro- and hydrobiont taxa from genera 314 315Arcella, Bullinularia, Trigonopyxis, Heleopera, Nebela, Argynnia, Difflu-316 gia; (2) rare finds of soil-living taxa from genus *Plagiopyxis*; (3) frequent finds of Sphagnum-moss taxa from genera Valkanovia, 317 Assulina, Euglypha and Trinema in modern TA communities. Simila-318 rities are in dominant taxa from soil-living genera Centropyxis. 319

### 320 5. Interpretation and discussion

The TA assemblages and their palaeoecological interpretations, as well as radiocarbon and correlated ages are presented according to the sample height in Table 4. The sand deposits of unit A do not contain any TA shells. This is most likely caused by the fluvial origin of these sediments. TA communities could not develop in this environment and/or TA shells were mechanically damaged and destroyed by the fluvial processes. This unit is also almost free of pollen and plant macro fossils (Schirrmeister et al., in press). Running water tends to 328 remove lightweight sediment fractions, including TA shells, pollen, 329 and plant macrofossils. 330

TA assemblages of the Kargin Interstadial zone (unit B) reflect 331 environments with well drained soils. High abundance and diversity 332 of TA in these samples indicate favourable environmental conditions 333 and possibly also a diversity of microhabitats allowing species with 334 diverse ecological requirements to develop. Especially the high taxa 335 diversity of hydrophilic genus Difflugia indicates the existence of 336 small, shallow water bodies in either low-centred ice wedge polygons 337 or in small thermokarst depressions that could warm during the 338 summer season prior ca 40,000 <sup>14</sup>C yr BP. This conclusion is supported 339 by the high contents of green algae colonies of Botryococcus and Pe- 340 diastrum recorded in the microscopic analysis of these sediments as 341 well as by the plant macrofossil record, demonstrating that wetland 342 plants such as sedges and cotton grass dominated the macrofossil 343 assemblages (Schirrmeister et al., in press). Dominant TA taxa include 344 the soil eurybiotic Centropyxis and among them frequent moss-living 345 taxa such as Heleopera petricola, H. sphagni, and Argynnia species. Ar- 346 cella species and Centropyxis aerophila reflecting wet moss-tundra 347 habitats, rather similar to the modern vegetation in the study area. 348 Based on the TA data, the climate at ca 40,000 <sup>14</sup>C yr BP can be 349 described as moderately warm and humid. In the sample dated to 350 43,600 <sup>14</sup>C yr BP the abundance of TA is strongly decreased suggesting 351 a change to colder and drier habitat conditions. The variations of 352 habitat conditions reconstructed by TA assemblages demonstrate 353 slight environmental changes during the Kargin Interstadial. After ca 354 40,000 <sup>14</sup>C yr BP TA taxa completely disappeared suggesting 355 unfavourable environmental conditions induced by repeated flooding 356 and soil erosion caused by fluvial activity, respectively. The drastic 357 decrease in hydrophilic taxa persisting until ca 32,700 <sup>14</sup>C yr BP may 358 also be interpreted as an indication of a general climatic deterioration. 359 From ca 32,700 <sup>14</sup>C yr BP to 27,220 <sup>14</sup>C yr BP low TA shell concentration 360 indicate a cooling period and the transition to the Sartan Stadial 361 interval. Soil eurybiotic taxa dominate the TA assemblages, but 362 sphagnobiotic taxa from genera Centropyxis and Argynnia are also 363 frequent. This together with the abundance of calceophilic Centropyxis 364 plagiostoma indicates the presence of meso-oligotrophic peatland 365 conditions. The deposits of this peat-sand alternating complex (unit B) 366 demonstrate the highest variations in the organic carbon contents. 367 TOC contents vary from 0.2% to 15.3% and the C/N ratios of the studied 368 sediments vary from 1.2 to 24.9 (Table 1). Environmental conditions 369 must have changed drastically during the formation of unit B 370 sequence. Sediment accumulation occurred in swampy and water- 371 logged areas, most likely situated in the floodplain environments near 372 the river channel. Periods of soil formation with stable surface 373 conditions were interrupted by periods or short events of increased 374 sediment accumulation pointing to unstable surface conditions. Thus, 375 changes of water level, bog and soil stages can be reconstructed for the 376 period of the Kargin Interstadial by the TA analysis.

Prior to the transition to the Sartan Stadial TA abundance as well as 378 taxa diversity of soil- and moss-living taxa increased before 24,150 <sup>14</sup>C 379 yr BP reflecting recurring stable environmental conditions. The strong 380 decrease in TA abundance and diversity and the complete disappear- 381 ance of hydrophilic taxa reflect climate deterioration between 24,150 382 <sup>14</sup>C yr BP and 18,000 <sup>14</sup>C yr BP (Last Glacial Maximum/LGM). 383 Hubberten et al. (2004) found out that most of the Sartan Stadial 384 (24,000–15,000 <sup>14</sup>C yr BP) was characterized by the lowest levels of 385 xerophilic insects and a dominance of Arctic tundra taxa. They 386 inferred from palaeobotanical data that the LGM was marked by high 387 aridity and relatively low summer temperatures compared to the 388 previous Interstadial. TA assemblages are reflecting a period of rather 389 stable environmental conditions, less favourable than in unit B 390 sediments. Decreasing C/N ratios reflect relatively dry well aerated 391 conditions in the unfrozen active layer zone with enhanced decom- 392 position of the organic material. The decreasing TOC content and low 393

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### 12

#### Table 5

t5.1

Relative frequency (min, max, average) and standard deviation of five different forms and varieties of *Centropyxis plagiostoma* in Late Pleistocene (*n*=27) and Holocene (*n*=13; except surface samples) deposits

Таха	Pleistocene/Holocene min (%)	Max (%)	Average (%)	SD (%)
Centropyxis plagiostoma	0/0	45.50/14.10	13.31/2.76	12.43/4.12
C. plagiostoma f. major	0/0	10.00/0	1.04/0	2.13/0
C. plagiostoma f. minor	0/0	11.11/7.50	1.92/1.98	3.15/2.68
. plagiostoma v. oblonga	0/0	0/0.89	0/0	0/0
C. plagiostoma v. terricola	0/0	2.04/0.70	0.08/0	0.39/0

C/N ratios reflect the reduction of the number of nutrition rich habitats (mainly bogs). Many taxa, especially soil eurybiotic *Centropyxis* and *Cyclopyxis*, are represented by small sized forms and varieties (*minor, minuta, minima, microstoma*) probably indicating unfavourable climatic conditions, e.g. lower temperatures (Smith, 1988) and/or colder and drier climate (Bobrov et al., 1999), resulting in a reduction of shell size. The presence of *Cyclopyxis eurystoma* v. *par*- *vula*, small sized variety, reflects unfavourable habitat conditions 401 during this period, too. Pollen and macrofossil data indicate that open 402 tundra- and steppe-like associations dominated the area during the 403 Sartan Stadial (Andreev et al., 2002a,b; Kienast, 2002; Schirrmeister 404 et al., in press). It can be therefore assumed a very continental, winter- 405 cold and yearly dry climate for this period. After ca 16,000 <sup>14</sup>C yr BP, at 406 the end of the Late Pleistocene, a hiatus in the sediments is noted. 407



**Fig. 5.** Some characteristic testate amoebae taxa in surface samples, and Late Quaternary sediments from Cape Mamontov Klyk: 1 – *Nebela bigibbosa*, 2 – *Centropyxis aerophila*, 3 – *C. plagiostoma v. oblonga*, 4 – *C. plagiostoma*, 5 – *C. platystoma*, 6 – *C. sylvatica*.

408 Probably the result of a short period of warmer climate conditions
409 (Allerød) and permafrost thawing enabled the establishment favour410 able habitats and thus aquatic TA palaeocoenoses.

411 The increase of the calceophilic Centropyxis plagiostoma and Plagiopyxis group taxa reflect higher nutrient supply between 18,000 and 412 16,000 <sup>14</sup>C yr BP. The favourable habitat conditions for calceophilic TA 413 taxa are also confirmed by the pH measurements showing rather 414 alkaline values (Table 1). C. plagiostoma is present in more than 75% of 415 416 the samples, but it was found only in samples with relatively high TA abundance and high TA diversity. C. plagiostoma is a well-defined 417 418 stenobiotic species whose polymorphism was already mentioned in 419 permafrost deposits from the Bykovsky Peninsula (Bobrov et al., 420 2004). They distinguished between forms major, typica, and minor in 421 the samples. It was concluded that f. typica occurred more frequently in the Holocene habitats, which were wetter than the Pleistocene 422 ones. Whereas f. minor and major were more frequent in the 423 Pleistocene habitats, probably because of the greater diversity of 424ecological niches during the Late Pleistocene due to a greater biotope 425differentiation as compared with the Holocene. In our analysis we 426 distinguished between f. major, typica, and minor but also between 427 varieties terricola and oblonga (Tables 2 and 5). In this study C. 428 plagiostoma f. minor and f. typica were frequent in Holocene samples, 429 430 whereas f. major was exclusively found in Late Pleistocene (Kargin 431 Interstadial and Sartan Stadial) samples. We conclude that the forms typica and major correspond to the forms that Bobrov et al. (2004) 432 found on Bykovsky Peninsula. In contrast to this we found f. minor in 433 Holocene samples in higher abundances as they did on Bykovsky. It 434 435can be explained by an overall high abundance of small-sized TA forms in the whole MaK-sequences and may be interpreted as an adaptation 436 to the specific permafrost habitats around the study site of Cape 437Mamontov Klyk. 438

Slight increases in TOC (up to 8%) contents and C/N ratios (14) during 439 440 the Holocene sediments reflect a general shift in environmental conditions. Around 9500 <sup>14</sup>C yr BP environmental conditions were 441more favourable and TA communities established in the study area. The 442 relatively high amount of Alnus fruticosa, Betula sect. Nanae and Salix 443 pollen as well as plant macrofossils point to higher temperatures and 444 445 increasing humidity than before, too (shrub-tundra vegetation) (Andreev et al., 2004b; Schirrmeister et al., in press). Samples are characterized by 446 high TOC contents (up to 21.8%) and C/N ratios (around 13) indicating 447 favourable plant growth and nutrient supply for TA after the hiatus 448 between 9480±40 and 3720±30 <sup>14</sup>C yr BP, probably caused by thermo-449erosion. During the Late Holocene TA abundance slowly increased 450 towards modern values reflecting favourable conditions that allow TA 451 to spread and become abundant in all distinguished habitats. Especially 452 the number of hydrophilic taxa is increased until present times. 453454Schirrmeister et al. (2003) described that after 7700 <sup>14</sup>C yr BP the local soil environment at the Olenek Channel (Lena Delta) was much wetter 455than during the previous Late Glacial period indicated by the presence of 456hydrophilic and sphagnophilic taxa. A single find of aquatic Difflugia 457cratera shell may reflect a lacustrine stage of sedimentation. Only vascular 458459plant remains, belonging to Salix, Luzula and Juncus were identified 460 among the moss remains in the macrofossil record. These plants indicate continuously wet conditions in the study area (Schirrmeister et al., in 461 462 press).

TA taxa diversity is about 30% higher in the Kargin Interstadial 463 464 samples than in Holocene ones. This was also shown by Bobrov et al. (2004) from Ice Complex sediments from Bykovsky Peninsula, where the 465maximum diversity was recorded for the Kargin Interstadial (54,000-466 33,000 <sup>14</sup>C yr BP) too. The pronounced cold/dry periods during the last 467 45,000 <sup>14</sup>C yr BP are characterized by the lack of hydrophilic TA taxa. This 468 is consistent with Bobrov et al. (2004) study on Bykovsky Peninsula and 469finds of Schirrmeister et al. (2003) at the Olenek Channel. It can be 470assumed that the minimum temperature required for successful 471 reproduction is higher for TA taxa living in aquatic environments than 472473for those living in soils.

Beyens et al. (1992) found a higher number of TA taxa in soils with 474 a high content of organic matter. This can be explained by the 475 hypothesis that higher organic content results in more food resources 476 for the TA. However, Trappeniers et al. (2002) reported that the 477 observation of higher diversity together with a higher organic content 478 could not be consistently proved. Our study does not show direct 479 correlations either. The loss of an important soil TA *Phryganella* 480 *acropodia* already described in Beyens et al. (1990) for the Canadian 481 Arctic (Devon Island) could be observed in our study too, where only 482 in 19 of the 40 samples this taxa was found.

TA analyses show that different sedimentation processes and 484 different habitats result in different species composition. The genus 485 *Centropyxis* (Fig. 3) dominated in all types of sediments. Beyens 486 et al. (1992) has already drawn attention to the shift in faunistic 487 composition within the water-dwelling TA communities. In the arctic 488 water bodies the genus *Difflugia* is replaced by the genus *Centropyxis*. 489

Special interest is given to findings of rare TA species in Late 490 Pleistocene Ice Complex and Holocene sediments. Shells of Argynnia 491 sp. were found in 10 Late Pleistocene samples (9 in Kargin Interstadial 492 samples, 1 in Sartan Stadial sample) and in 2 Holocene samples. Today, 493 only two species of the 15 known species, A. dentistoma and A. vitrea 494 have cosmopolitan distribution (Ogden and Hedley, 1980). Other 495 species are restricted to specific regions in Canada, Eurasia, Australia 496 and the Antarctic (Deflandre, 1936; Meisterfeld, 1998). Almost all Ar- 497 gynnia species inhabit Sphagnum-bogs and acidic hummocks within 498 the forest zone. No species of this genus, except A. dentistoma, have 499 been found in the present-day Arctic biotopes (Beyens and Chardez, 500 1995). This fact provides an additional evidence of a unique soil 501 environment that existed in northeastern Siberia during the Kargin 502 Interstadial. It is also interesting to notice the findings of the 503 sphagnophilic Nebela bigibbosa (syn. Porosia bigibbosa; Fig. 5) in the 504 surface sample AA-4 (litter). Our study presents the most northern 505 find of this species for the Eurasian mainland. Todorov (2001) pointed 506 out that Nebela bigibbosa is not a typical inhabitant of Sphagnum- 507 mosses but is closely related to the litter soil layer. So far this species 508 was only identified in Late Pleistocene sediments from Bykovsky 509 Peninsula (Bobrov et al., 2004). Another rare species Paraquadrulla 510 irregularis, typical for mesotrophic peatlands (Opravilova and Hajek, 511 2006), was identified in fluvial sediment samples (MaK 2-3, Kargin 512 Interstadial). Until today the find of P. irregularis in Late Quaternary 513 sediments is unique. 514

A striking feature in the Pleistocene TA communities is the absence of 515 the filose genera *Trinema, Euglypha* and *Corythion*. These were frequently 516 found in the modern surface samples and are also known to be 517 sometimes dominant genera in Arctic habitats (e.g. Beyens et al., 1992; 518 Trappeniers et al., 2002). The absence of these taxa in the Late Pleistocene 519 samples could mainly be explained by taphonomical problems; composi- 520 tion difficulties and bad preservation could cause the absence of filose 521 genera in the studied Late Quaternary sediments. Further investigation in 522 this particular region and comparison of fossil samples with reliable 523 surface samples can probably answer this question. 524

Located at the Laptev Sea coast, the study area today is subject to 525 and effectively changed by strong coastal erosion. This study has 526 shown that complex relationships between TA and different environ- 527 mental factors can be detected. Climate change could be the main 528 cause of environmental change and thus habitat variations. In 529 permafrost landscapes thermokarst processes have also to be taken 530 into account when interpreting the TA changes through the time. 531

### 6. Conclusions

532

Our study represents one of the first attempts to use TA from 533 permafrost regions of Eurasia as indicators of environmental changes 534 at local and regional scales. During the last 45,000 <sup>14</sup>C yr the 535 composition of TA communities in permafrost sequences shifted 536 along with changes in habitat and climate conditions. The recorded TA 537

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fauna from the studied high arctic locality show highest abundances 538 539 and taxa diversity in fossil samples dated to 44,000–40,000 <sup>14</sup>C yr BP (during the Kargin Interstadial). Low TA abundances were recorded 540during the period between 24,000 and 18,000 <sup>14</sup>C yr BP (Sartan 541Stadial). Our study confirm that TA are valuable as complementary 542palaeoenvironmental proxies for the Arctic regions and can thus 543provide more detailed information for environmental changes in the 544study area and their causes. The low number of surface samples 545546analysed so far prevents from quantitative interpretations of the fossil samples. Further work will focus on detailed analysis of recent surface 547samples from the Arctic Siberia collected in summer 2007 to get 548reliable information of arctic micro-habitats and to quantify observed 549changes in the fossil TA records. 550

### **Q2**551 **7. Uncited references**

552 Bobrov, 1995

553 Schwamborn et al., 2002

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### 567 References

568 ACIA, 2004. Impacts of a Warming Arctic: Arctic Climate Impact Assessment. Cambridge 569 Univ. Press.

- Andreev, A.A., Siegert, Ch., Klimanov, V.A., Derevyagin, A.Yu., Shilova, G.N., 2002a, Late
   Pleistocene and Holocene vegetation and climate on the Taymyr Lowland, northern
   Siberia. Ouaternary Research 57, 138–150.
- Andreev, A.A., Schirrmeister, L., Siegert, Ch., Bobrov, A., Demske, D., Seiffert, M.,
  Hubberten, H.-W., 2002b. Paleoenvironmental changes in northeastern Siberia
  during the Quaternary evidence from pollen records of the Bykovsky Peninsula.
  Polar Research 70, 13–25.
- 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.,
   Kunitsky, V.V., 2004a. 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., Schwamborn, G., Ilyashuk, B.P., Ilyashuk, E.A., Bobrov, A.A.,
   Klimanov, V.A., Rachold, V., Hubberten, H.-W., 2004b. Holocene paleoenviron mental records from Nikolay Lake, Lena River Delta, Arctic Russia. Palaeogeography
   Palaeoclimatology Palaeoecology 209, 197–217.
- Q3586
   Andreev, A.A., Grosse, G., Schirrmeister, L., Kuznetsova, T.V., Kuzmina, S.A., Bobrov, A.A., 587

   587
   Tarasov, P.E., Novenko, E.Yu., Meyer, H., Derevyagin, A.Yu., Kienast, F., Bryantseva, A., Kunitsky, V.V., in press. Weichselian and Holocene palaeoenvironmental history of the Bol'shoy Lyakhovsky Island, New Siberian Archipelago, Arctic Siberia. Boreas. 590

   591
   Atlas Arktiki. 1985, GUGK, Moscow, (in Russian).
  - Beyens, L., Chardez, D., 1987. Evidence from testate amoebae for changes in some local hydrological conditions between c. 5000 BP and c. 3800 BP on Edgeøya (Svalbard).
     Polar Research 5, 165–169.
  - Beyens, L., Chardez, D., 1995. An annotated list of testate amoebae observed in the Arctic
     between the Longitudes 27° E and 168° W. Archiv für Protistenkunde 146, 219–233.
  - Beyens, L., Meisterfeld, R., 2001. Protozoa: testate Amoebae. 2001 In: Smol, J.P., Birks,
     H.J.B., Last, W.M. (Eds.), Tracking environmental changes using lake sediments,
     vol.3. Kluwer Academic Publishers, Dordrecht, The Netherlands.
  - 599 Beyens, L., Chardez, D., De Landtsheer, R., De Bock, P., Jaques, E., 1986. Testate amoebae populations from moss and lichen habitats in the Arctic. Polar Biology 5, 165–173.
  - Beyens, L., Chardez, D., De Landtsheer, R., De Bock, P., Jaques, E., 1990. Ecology of terrestrial testate amoebae assemblages from coastal lowlands on Devon Island (NWT, Canadian Arctic). Polar Biology 10, 431–440.
  - 604Beyens, L., Chardez, D., De Baere, D., De Bock, P., 1992. The testate amoebae from the605Søndre Strømfjord Region (West-Greenland): their biogeographic implications.606Archiv für Protistenkunde 142, 5–13.

- Bobrov, A.A., 1995. Testate amoebae (Protozoa, Testacea) of Russia and Canada as 607 indicators of climatic changes in Holocene. In: Heikinheimo, P. (Ed.), Proceedings of 608 the SILMU (Finnish Research Programme on Climate Change) International 609 Conference on Past, present and Future Climate. Held in Helsinki, Finland. 610 Publications of the Academic of Finland, Helsinki, pp. 113–114. 611
- Bobrov, A., Charman, D., Warner, B., 1999. Ecology of testate amoebae (Protozoa: 612 Rhizopoda) from peatlands in Western Russia with special attention to niche 613 separation in closely related taxa. Protist 150, 125–136. 614
- Bobrov, A.A., Andreev, A.A., Schirrmeister, L., Siegert, Ch., 2004. Testate amoebae 615 (Protozoa: Testacealobosea and Testaceafilosea) as bioindicators in the Late 616 Quaternary deposits of the Bykovsky Peninsula, Laptev Sea, Russia. Palaeogeo- 617 graphy Palaeoclimatology Palaeoecology 209, 165–181. 618
- Chardez, D., 1965. Ecologie generale des Thecamoebiens (Rhizopoda, Testacea). Bulletin 619 de l'Institut Agronomigue et des Stations de Recherches Gembloux 3, 306–431. 620
- Chardez, D., 1967. Histoire naturelle des Protozoaires Thecamoebiens. Les Naturalistes 621 Belges. 622 CAVM Team 2003. Circumpelar Arctic Verentation Man. Scale 1:7500.000. Concernition 622
- CAVM Team. 2003. Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Conservation 623 of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, 624 Anchorage, Alaska. 625
- Charman, D.J., 2001. Biostratigraphic and palaeoenvironmental applications of testate 626 amoebae. Quaternary Science Reviews 20, 1753–1764. 627
- Dallimore, A., Schröder-Adams, C.J., Dallimore, S.R., 2000. Holocene environmental 628 history of thermokarst lakes on Richard Island, Northwest Territories, Canada: 629 thecamoebians as paleolimnological indicators. Journal of Paleolimnology 23, 630 261–283. 631
- Deflandre, G., 1936. Etude monographie sur le genre *Nebela* Leidy. Annales de 632 Protistologie 5, 201–322. 633
- Ellison, R.L., Ogden, C.G., 1987. A guide to the study and identification of fossil testate 634 amoebae in Quaternary lake sediments. International Revue der Gesamten 635 Hydrobiologie 72 (5), 639–652. 636
- Gel'tser, Yu G., Korganova, G.A., Alexeev, D.A., 1985. Pochvennye rakovinnye ameby i 637 metody ikh izuchenija (Soil testacean amoebae and their study techniques). 638 Izdatelstvo Moskovskogo Universiteta, Moscow, Russia. (in Russian). 639
- Gel'tser, Yu G., Korganova, G.A., Alexeev, D.A., 1995. Opredelitel pochvoobitaiyushchikh 640 rakovinnykh ameb (Practical guidebook for the identification of soil testaceans). 641 Izdatelstvo Moskovskogo Universiteta. (in Russian). 642
- Grimm, E.C., 1993. TILIA 2.0 Version b.4 (Computer Software). Illinois State Museum, 643 Research and Collections Center. Springfield. 644
- Grimm, E.C., 2004. TGView. Illinois State Museum, Research and Collections Center. 645 Springfield. 646
- Gilbert, D., Mitchell, E.A.D., Amblard, C., Bourdier, G., Francez, A.-J., 2003. Population 647 dynamics and food preference of the testate amoebae *Nebela tincta major*- 648 *bohemica-collaris* complex (Protozoa) in a *Sphagnum*-peatland. Acta Protozoologica 649 42, 99–104. 650
- Hubberten, H.-W., Andreev, A., Astakhov, V., Demidov, I., Dowdeswell, J.A., Henriksen, 651
   M., Hjort, C., Houmark-Nielsen, M., Jacobsson, M., Kuzmina, S., Larsen, E., Lunkka, P., 652
   Pekka, J., Lyså, A., Mangerud, J., Möller, P., Saarnisto, M., Schirrmeister, L., Sher, A.V., 653
   Siegert, C., Siegert, M.J., Svendsen, J.I., 2004. The periglacial climate and 654
   environment in northern Eurasia during the Last Glaciation. Quaternary Science 655
   Reviews 23, 1333–1357. 656
- Khotinskiy, N.A., 1984. Holocene climate change. In: Velichko, A.A. (Ed.), Late 657 Quaternary environments of the Soviet Union. University of Minnesota Press, 658 Mineapolis, pp. 305–309. 659
- Kienast, F., 2002. Die Rekonstruktion der spätquartären Vegetations- und Klimagesch- 660 hichte der Laptewsee-Region auf der Basis botanischer Großrestuntersuchungen. 661 Ph.D. thesis, Potsdam University, 122pp. 662
- Kienast, F., Schirrmeister, L., Siegert, C., Tarasov, P., 2005. Palaeobotanical evidence for 663 warm summers in the East Siberian Arctic during the last cold stage. Quaternary 664 Research, 63 (3), 283–300. 665
- Kienast, F., Tarasov, P., Schirrmeister, L., Grosse, G., Andreev, A., 2008. Continental 666 climate in the East Siberian Arctic during the Last Interglacial: implications from 667 palaeobotanical records. Global and Planetary Change 60 (3–4), 535–562. 668
- Kind, N.V., 1974. Geokhronologia pozdniego antropogena po izotopnym dannym 669 (Geochronology of Late Anthropogene based on isotope data). Nauka, Moscow. 670 (in Russian). 671
- Lamentowicz, M., Mitchell, E.A.D., 2005. The ecology of testate amoebae (Protists) in 672 Sphagnum in north-western Poland in relation to peatland ecology. Microbial 673 Ecology 50, 48–63. 674
- Lozhkin, Ä.V., Anderson, P.M., Matrosova, T.V., Minyuk, P.S., 2007. The pollen record from 675 El'gygytgyn Lake: implications for vegetation and climate histories of northern 676 Chukotka since the late middle Pleistocene. Journal of Paleolimnology 37, 135–153. 677
- McCarthy, F., Collins, E., McAndrews, J., Kerr, H., Scott, D., Medioli, F., 1995. A comparison 678 of postglacial arcellean ("Thekamoebian") and pollen succession in atlantic Canada, 679 illustrating the potential of arcelleans for paleoclimatic reconstruction. Journal 680 Paleontology 69, 980–993. 681
- Medioli, F., Scott, D., 1988. Lacustrine Thekamoebians (mainly Arcelleans) as potential 682 tools for paleolimnological interpretations. Palaeogeography, Palaeoclimatology, 683 Palaeoecology 62, 361–368. 684
- Meisterfeld, R., 1998. First records of testate amoebae (Protozoa: Rhizopoda) from 685 Mount Buffalo National Park, Victoria: preliminary notes. Victorian Naturalist 115 686 (5), 231–238. 687
- Meyer, H., Dereviagin, A. Yu, Siegert, C., Hubberten, H.-W., 2002. Paleoclimate studies on 688
   Bykovsky Peninsula, North Siberia, hydrogen and oxygen isotopes in ground ice. 689
   Polar Research 70, 37–51. 690
- Mitchell, E.A.D., Bragazza, L., Gerdol, R., 2004. Testate amoebae (Protista) communities 691 in *Hylocomium splendens* (Hedw.) B.S.G. (Bryophyta): relationships with altitude, 692 and moss elemental chemistry. Protist 155 (4), 423–436. 693

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- Nadeau, M.J., Schleicher, M., Grootes, P.M., Erlenkeuser, H., Gottdang, A., Mous, D.J.W.,
   Sarntheim, J.M., Willkomm, H., 1997. The Leibniz-Labor facility at the Christian Albrecht-University, Kiel, Germany. Nuclear Instruments and Methods in Physics
   Research 123, 22–30.
- Nadeau, M.J., Grootes, P.M., Schleicher, M., Hasselberg, P., Rieck, A., Bitterling, M., 1998.
   Sample throughput and data quality at the Leibniz-Labor AMS facility. Radiocarbon 40, 239–245.
- Ogden, C.G., 1983. Observations on the systematics of the genus *Difflugia*. Britain
   (Rhizopoda, Protozoa). Bulletin of the British Museum (Natural History). Zoological
   Series, vol. 44 (1).
- Ogden, C.G., Hedley, R.H., 1980. An atlas of freshwater testate amoebae. British Museum
   (Natural History). Oxford Univ. Press, Oxford.
- Opravilova, V., Hajek, M., 2006. The variation of testacean assemblages (Rhizopoda) along the complete base-richness gradient in fens: a case study from the Western Carpathians. Acta Protozoologica 45, 191–204.
- Patterson, R., MacKinnon, K., Scott, D., Medioli, F., 1985. Arcelleans in small lakes of New
   Brunswick and Nova Scotia: modern distribution and Holocene Stratigraphic
   changes. Journal of Foramineral Research 15, 114–137.
- Schirrmeister, L., Siegert, Ch., Kuznetsova, T., Kuzmina, S., Andreev, A.A., Kienast, F.,
   Meyer, H., Bobrov, A.A., 2002a. Paleoenvironmental and palaeoclimatic records
   from permafrost deposits in the Arctic region of Northern Siberia. Quaternary
   International 89, 97–118.
- Schirrmeister, L., Siegert, C., Kunitzky, V.V., Grootes, P.M., Erlenkeuser, H., 2002b. Late
   Quaternary ice-rich permafrost sequences as a paleoenvironmental archive for the
   Laptev Sea region in northern Siberia. International Journal of Earth Sciences 91,
   154–167.
- Schirrmeister, L., Kunitsky, V.V., Grosse, G., Schwamborn, G., Andreev, A.A., Meyer, H.,
   Kuznetsova, T., Bobrov, A., Oezen, D., 2003. Late Quaternary history of the
   accumulation plain north of the Chekanovsky Ridge (Lena Delta, Russia) –, a
   multidisciplinary approach. Polar Geography 27 (4), 277–319.
- Schirrmeister, L., Grigoriev, M.N., Kutzbach, L., Wagner, D., Bolshiyanov, D.Y. (Eds.), 2004.
   Russian-German Cooperation "System Laptev Sea": The expedition "Lena-Anabar 2003". Reports on Polar and Marine Research, vol. 489.
- Q4727 Schirrmeister, L., Grosse, G., Kunitsky, V.V., Magens, M., Meyer, H., Derevyagin, A.Yu.,
   Kuznetsova, T., Andreev, A.A., Kienast, F., Grigoriev, M., Preusser, F., in press.
   Periglacial landscape evolution and environmental changes of Arctic lowland areas
   during the Late Quaternary (western Laptev Sea coast, Cape Mamontov Klyk). Polar
   Research.
  - Schwamborn, G., Rachold, V., Grigoriev, M.N., 2002. Late Quaternary sedimentation
     history of the Lena Delta. Quaternary International 89, 119–134.
  - Schnitchen, C., Magyari, E., Töthmérész, B., Grigroszky, I., Braun, M., 2003. Micropaleontological observations on a *Sphagnum* bog in East Carpathian region – testate amoebae (Rhizopoda: Testacea) and their potential use for reconstruction of microand macroclimatic changes. Hydrobiologia 506–509, 45–49.

778

- Schönborn, W., 1962. Die Ökologie der Testaceen in oligotrophen Seen, dargestellt am 738 Beispiel des Grossen Stechlinsees. Limnologica (Berlin), 1 (2), 11–182. 739
- Sher, A.V., Kuzmina, S.A., Kuznetsova, T.V., Sulerzhinsky, L.D., 2005. New insights into 740 the Weichselian environment and climate of the East Siberian Arctic, derived from 741 fossil insects, plants, and mammals. Quaternary Science Reviews 24, 533–569. 742
- Smith, H.G., 1988. Influence of temperature on test morphology of natural populations 743 of testate rhizopods in the maritime Antarctic. IX Protozoological Congress, Berlin. 744 p. 120. 745
- Smith, H.G., 1992. Distribution and ecology of the testate rhizopod fauna of the 746 continental Antarctic zone. Polar Biology 12, 173–176. 747
- Smith, H.G., 1996. Diversity of terrestrial Antarctic protozoa. Biodiversity and 748 Conservation 5, 1379–1394. 749
- Svendsen, J.I., Alexanderson, H., Astakhov, V.I., Demidov, I., Dowdeswell, J.A., Funder, S., 750
   Gataullin, V., Henriksen, M., Hjort, C., Houmark-Nielsen, M., Hubberten, H.W., 751
   Ingólfsson, Ó., Jacobsson, M., Kjær, K.H., Larsen, E., Lokrantz, H., Pekka Lunkka, J., 752
   Lysá, A., Mangerud, J., Matiouchkov, A., Murray, A., Möller, P., Niessen, F., Nikolskaya, 753
   O., Polyak, L., Saarnisto, M., Siegert, C., Siegert, M.J., Spielhagen, R.F., Stein, R., 2004. 754
   Late Quaternary ice sheet history of northern Eurasia. Quaternary Science Reviews 755
   23, 1229–1271.
- Todorov, M., 2001. Testate amoebae (Protozoa: Rhizopoda) in soil and litter of beech 757 forests (*Fagus sylvatica L.*) from Bulgaria. Acta Zoologica Bulgarica 53 (2), 19–37. 758
- Tolonen, K., 1986. Rhizopod analysis. In: Berglund, B.E. (Ed.), Handbook of Holocene 759

   Palaeoecology and Palaeohydrology. Wiley, Chichester, pp. 645–666.

   760

   Tolonen, K., Warner, B., Vasander, H., 1992. Ecology of Testaceans in mires in southern

   761
- Finland: I.Autecology. Archiv für Protistenkunde 142, 119–138.
- Trappeniers, K., Van Kerckvoorde, A., Chardez, D., Nijs, I., Beyens, L., 2002. Testate 763 amoebae assemblages from soils in the Zackenberg Area, Northeast Greenland. 764 Arctic, Antarctic, and Alpine Research 34 (1), 94–101. 765
- Velichko, A.A., 1984. Late Pleistocene spatial climatic reconstructions. In: Velichko, A.A. 766 (Ed.), Late Quaternary environments of the Soviet Union. University of Minnesota 767 Press, Mineapolis, pp. 261–285.
   Wilkinson, D.M., 1990. Glacial refugia in South Georgia? Protozoan evidence. 769
- Wilkinson, D.M., 1990. Glacial refugia in South Georgia? Protozoan evidence. 769 Quaternary Newsletter 62, 12–13. 770
- Wilkinson, D.M., 1994. A review of the biogeography of the protozoan genus Nebela in 771 the southern temperate and Antarctic zones. Area 26, 150–157. 772
- Woodland, W., Charman, D.J., Sims, P.C., 1998. Quantitative estimates of water tables and 773 soil moisture in Holocene peatlands from testate amoebae. Holocene 8 (3), 774 261–273. 775
- Yershov, E.D. (Ed.), 1989. Geokryologija SSSR (Geocryology of the USSR). Nedra, Moscow. 776

777

15