===== **ECOLOGY** =====

Testaceans (Protozoa: Testacea) in Quaternary Permafrost Sediments of Bykovsky Peninsula, Arctic Yakutia

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Abstract—The results of the first protozoological study in terms of paleoecology of long-term sediments and buried soils formed in the cryolite zone of northeastern Siberia are discussed. The data on testaceans (Protozoa: Testacea) inhabiting various sites of Bykovsky Peninsula, Laptev Sea coast near estuary of Lena, within the last 53 000 years (Late Pleistocene and Holocene) are presented.

INTRODUCTION

Testaceans (Protozoa: Testacea) is a group of free-living protozoans with an organic shell coated with exogenous mineral material, plant detritus (xenosomes), or endogenous material—siliceous (calcium phosphate in some species) plates (idiosomas).

Integrity of the shells in peats and specific ecological preferendums in various species favored development of rhizopod analysis (Harnisch, 1927, 1948; Grospietsch, 1953; Schönborn, 1962; Meisterfeld, 1977; Tolonen, 1986) as a method for reconstructing climatic changes and environmental conditions. The earliest findings of this kind apply to Triassic period (Schönborn *et al.*, 1999). Testaceans being initially aquatic organisms rearrange their zoocenotic structure in response to the groundwater level, humidity, pH, concentration of biophilic elements, and the condition of organic matter. Various ecological groups are recognized among testaceans: hygrophilous, hydrophilic, xerophilous, acidophilic, calciophilic, sphagnophilic, and pedobiont organisms. Their density in the lacustrine and boggy sediments ranges from hundreds to tens thousands of specimens per cm³. Species diversity of testaceans inhabiting oligotrophic bogs can amount to tens species and intraspecific forms.

Significance of rhizopod analysis in paleoecology is due to the fact that, in contrast to most other larger and mobile organisms, protozoan testaceans are essentially attached organisms and reflect ecological properties of the studied sample in their community structure and shell morphology (Gilyarov, 1976). Upon redeposition, the testacean shells are easily destroyed; hence, testaceans are the rare paleocenotic organisms indicating ecological properties of the studied sample. One of the key notions of taphonomy—paleocenosis—is fully applicable to rhizopods (Yanin, 1983).

In Russia, the attention to rhizopod analysis in paleoecology was attracted by a publication of Gilyarov (1955). However, although almost 50 years passed after this publication, paleoecological studies based on rhizopod analysis remain singular in Russia (Bobrov, 1995; Bobrov and Minaeva, 2000).

Arctic East Siberia attracts the attention of researchers for a long time; now its present and late Quaternary flora and fauna are studied in detail (Yurtsev, 1966, 1981; Sher, 1997a, b; Andreev *et al.*, 2002). At the same time, the data on soil protozoans of this region are entirely absent.

Investigation of the present rhizopod flora in high latitudes of Arctic and Antarctic regions was primed in late 19th–early 20th centuries (Ehrenberg, 1870; Scourfield, 1897; Penard, 1903; Sandon, 1924) and continued after a long break in the second half of 20th century (Bonnet, 1965; Schönborn, 1966; Beyens *et al.*, 1986a–c, 1991, 1992, 2000; Smith, 1987; Opravilova, 1989; Balik, 1994). The regions of investigation and habitats included mosses, lichens, soils, and small ponds in East and West Greenland, northwestern Spitsbergen, and Brabant Island. Two publications in early 20th century by Awerintzew and Levander were based on the material collected in the region of Murmansk and Vaigach Island (Beyens *et al.*, 2000). The data on rhizopod population in the moss and aquatic biotopes at the shores and islands of the Barents and Kara Seas (Naryan–Mar, Dickson Island, Severnaya Zemlya, and Franz Joseph Land) indicate that testaceans are rare in this region of the Arctic Ocean—just 45 species, varieties, and forms in 37 samples (Beyens *et al.*, 2000).

Testacean fauna of Spitsbergen was, probably, studied best. Balik (1994 determined 48 species, varieties, and forms of testaceans in 21 samples of soils, mosses, and lichens from this island. Depending on the habitat, the number of species varied from 0 to 18. No rhizopods were observed in ca. 20% habitats (soil without

vegetation). In the total, 126 testacean taxa have been revealed in this well explored region of Spitsbergen for over a century of studies.

The last publication on rhizopod fauna in the northeastern Greenland deserves special attention (Trappeniers *et al.*, 2002). It presents quantitative evaluation of the relationship between the main ecological indices of the habitats (pH, organic matter, and humidity) and the composition of testacean communities; in addition, the communities specific for the soils under five plant species—*Salix, Cassiope, Vaccinium*, and *Astragrostis*—have been revealed.

Revision of the data on the present fauna of testaceans in high Arctic altitudes suggests the following conclusions: decrease in monthly summer temperature decreases the density of rhizopod population; the more severe is the climate, the lower is species diversity of testaceans; and some testacean species decrease their shells in response to decreased temperature.

In paleoecology, rhizopod analysis is mainly used to study the evolution of oligotrophic bogs in the boreal regions. By way of exception, Baeyns and Chardez (1987) reconstructed the changes in aquatic conditions for the last thousand years in a column of boggy sediments in Spitsbergen. Fourteen species and varieties of rhizopods have been found in 24 peat samples.

The natural conditions of Late Pleistocene and Holocene in Arctic East Siberia were reconstructed by various animal groups (Sher, 1997a, b). However, no such reconstruction have been done by the composition of free-living protozoans in the absence of studies on the Pleistocene and Holocene protist fauna and, particularly, testacean fauna.

The goal of this work was to analyze Late Pleistocene and Holocene communities of testaceans in the sediments and soils of Bykovsky Peninsula and to estimate the potential of rhizopod analysis for paleoreconstruction of the ecological and bioclimatic properties of terrestrial biotopes in high Arctic altitudes.

REGION OF STUDIES, MATERIALS, AND METHODS

The region of studies covers the eastern shore of Bykovsky Peninsula to the northeast of Tiksi settlement (71°40′–71°80′ N; 129°–129°30′ E). The main region—Mamontovy Khayata—is a 40 m coastal cliff stretched for about 2 km along the shore. It includes the sediments of Upper Pleistocene "ice complex"—highly icy thin silted sand and loam with peaty soil bands including large wedge ice. In the thermokarst depressions, the sediments of the ice complex are covered with the lacustrine sediments and peat of the Holocene age. All studied sediments were syngenetically frozen (i.e., from the side of the permafrost lying near the surface) and were subject to various degrees of cryogenic soil formation. The structure of the sediments and their age are described in detail by Schirrmeister *et al.*, 2002b).

Long winter (8 months) with −34 to −32°C in January and short summer with about 9°C in July are specific for the present climate. The annual precipitation is from 200 to 300 mm. The soils are mostly tundra gley and boggy gley with permafrost below 30–40 cm (*Atlas Arktiki*, 1985). Moss subshrub tundra with rare grass vegetation predominate in the plant cover. The main plant species include *Betula exilis, Dryas punctata, Salix pulchra, Cassiope tetragona, Oxyria digyna, Alopecurus alpinus, Poa arctica, Carex ensifolia, C. rotundifolia, Eriophorum medium, Aulacomnium turgidum, Hylocomium alaskanum, Drepanocladus iniciatus, Calliergon sarmentosum, Alectoria ochroleuca, Cetraria cuculliata*, and *C. hiascus* (*Atlas Arktiki*, 1985).

The samples for rhizopod analysis were collected within the field seasons 1998–2000 by the German–Russian expedition and provided for rhizopod analysis by the A. Wegener Institute for Polar and Marine Research (Potsdam, Germany). Detailed descriptions of the samples with radiocarbon dating are available in a series of publications (Siegert *et al.*, 1999, 2002; Sher *et al.*, 2000; Schirrmeister *et al.*, 2001).

The samples as aqueous suspension were passed through a sieve with 0.5 mm cell and centrifuged. Glycerol was added to a drop of suspension on a slide. The samples were completely inspected under light microscope at magnifications ×200 and ×400. On the average, five samples were inspected. We also used electron microscopes Jeol and Zeiss (Laboratory of Electron Microscopy, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, and Institut für Zoo- und Wildtierforschung, Berlin).

METHODOLOGICAL PROBLEMS OF RHIZOPOD ANALYSIS OF THE SAMPLES FROM ICE COMPLEXES

Usually, ice complex sediments are polygenetic formations. They were formed, on the one hand, *in situ* and, on the other hand, as a result of elution and redeposition. This fundamentally distinguishes the sediments of ice complexes from peats. The main problem for analysis of such sediments is correctness of the paleoreconstructions. Analysis of single or insignificant number of the samples allows us to describe specific habitats only. Increased number of the studied samples gives us grounds to judge habitat types specific for a given landscape within a given time period and, hence, gives us an insight into the past climatic properties of the region.

The second important problem is comparative analysis of the present and paleocommunities of testaceans. Unfortunately, there are no descriptions of the present protist fauna at the studied territories; the available published data refer to the regions with a warmer climate and are qualitative. This makes the comparative analysis impossible for the moment.

It is important that testaceans cannot be redeposited due to fragility of their shells. In practice, we always deal with paleocenosis rather than taphocenosis. This largely provides for correctness and significance of the conclusions of ecological descriptions of habitats.

Here we magnified the system of ecological groups of testaceans, mainly, due to low density of rhizopods in some samples as well as to the specific goal—to reveal possible correlations between rhizopod composition and environmental indices, presumably, interpretable as a consequence of climatic peculiarities. When we examine a set of samples referring to different time intervals and reveal different biodiversity in them, an interpretation of the data is based on several assumptions. First, the diversity of habitats depends on the climate. Second, the diversity of habitats increases with the diversity of rhizopod species. Enlarged group of hydrophilic and sphagnophilic species is a marker of waterlogging resulting from climatic warming and generally increased moistening at a given territory. The more severe is climate at given territories, the lower is the diversity of the habitats and, conversely, the milder is the climate, the higher is the diversity.

The true (obligatorily) soil species are not numerous in the tundra zone (Beyens *et al.*, 2001). However, apart from the soil species, only euribionts can occur in the soil conditions inferred from the sample descriptions. Hence, the presence of euribionts alone in a sample increases the probability that this sample was taken from a paleosoil rather than from boggy or ice complex deposits. Otherwise, species from other ecological groups should be found. That is why we combined the soil and euribiont species in a single ecological group.

RESULTS

In the total, we studied 96 samples from the present soils as well as Late Pleistocene and Holocene deposits representing the period of last 53 000 years. No testaceans were found in 48 samples; while 10 samples included remains of destroyed shells or singular shells. In 38 samples, we found 86 species, varieties, and forms of testaceans (Table 1) falling into different ecological groups (Fig. 1a). The number of species in a sample varied from 2 to 28 (Fig. 1b). In general, species diversity of rhizopods in the Holocene samples is higher than in the Pleistocene ones. The highest species diversity is specific for the samples from the Late Holocene habitats—up to 28 species and intraspecific taxa; however, species diversity in some Pleistocene samples is also quite high—up to 15 species. Considering that the species diversity is a result of both ecological conditions and climate, one can propose that the hydrothermal conditions of the habitats with paleocenosis of high species diversity was the most favorable and the climatic conditions were not extreme.

Late Pleistocene Samples

B-S7, outcropping Bykovsky-Severnyi, 6.7 km to the south of Bykovsky Cape, the lower part of the ice complex section, ice-rich clay sand (53020+2670/–2000 years ago). This is the earliest finding of rhizopods in the Pleistocene samples. The species diversity is comparable to the population of the present soils—15 species, varieties, and forms falling into seven genera, mostly, of the euritopic–soil group (*Centropyxis, Cyclopyxis,* and *Plagiopyxis* genera). The presence of hydrophilic species *Plagiopyxis callida* and *Difflugia pristis* indicate hydromorphic pattern of the habitat.

Mkh-K1-5, boggy soil (45 300+1200/–1050 years ago). Thirteen species and intraspecific forms have been revealed. Two-thirds of the dominant group is composed of euribiont and soil species of *Centropyxis* genus. Three marker species can be mentioned: aquatic-moss species *Difflugia lucida*; raw humic hydromorphic species *Argynnia* sp.; and calciophilic *Centropyxis plagiostoma.* Sphagnophilic species are absent. The raw humic pattern of the organic matter is also indicated by the presence of *Schoenbornia humicola* shells (typical for such conditions) as well as pedobionts of *Plagiopyxis* genus. A soil species *Cyclopyxis puteus* common in fluvial and sandy soils (Decloitre, 1977) has been found in the high altitude Arctic habitats for the first time. Species diversity and the pattern of marker species point to subacid or near-neutral environmental pH and hydromorphic pattern of the hydrological conditions of the soil. The thermal conditions are relatively favorable—the species presently occurring mostly in the forest zone are widely presented.

Mkh-HB2-4, peat with sandy particles (>44980 years ago). The species diversity is low, the paleocenosis includes only six species. The hydrophilic species (*Arcella arenaria* v. *compressa*) and *Centropyxis platystoma*) indicate close watertable and mesotrophic nutrition. The mesotrophic nutrition is also confirmed by finding of calciophilic *Centropyxis plagiostoma* presented by two forms, *major* and *minor*.

Mkh-KB2-2, cryoturbated soil with inclusions of shrub remains (44 280+1320/–1130 years ago). Fifteen species and intraspecific rhizopod taxa were revealed mostly falling into soil and euribionts species of *Centropyxis* genus. The calciophilic *Centropyxis plagiostoma* includes two size groups previously revealed in the forest soils with mull humus (Foissner and Korganova, 1995). Three soil species of *Plagiopyxis* genus were revealed in the rhizopod community. The presence of *Schoenbornia humicola* is a marker of raw humic condition of the organic matter, while finding a hydrophilic species *Difflugia globulosa* points to an increased moistening of the habitat. Similar to the *K1-5* sample, *Argynnia* sp. has been found. The sample includes the shells of *Centropyxis laevigata*, a species not previously found in the habitats to the north of 70° (Beyens *et al.*, 1986a, b, c, 1991; Smith, 1987; Balik, 1994) but widespread in the moss samples of West

Table 1. Species composition of testaceans from Holocene and Pleistocene permafrost sediments of Bykovsky Peninsula

Species	Occurrence in samples, %		Ecological description
	Pleistocene	Holocene	
Arcella arenaria Greef	5.3	21.1	M
A. arenaria v. *compressa* Chardez	21.1	21.1	M
A. rotundata v. *aplanata* Deflandre	0.0	5.3	WM
A. sp.	0.0	5.3	
Centropyxis aculeata (Ehrenberg) Stein	5.3	0.0	W
C. aerophila Deflandre	26.3	89.5	M
C. aerophila v. *sphagnicola* Deflandre	0.0	5.3	SpM
C. aerophila v. *grandis* Stepanek	0.0	15.8	W
C. aerophila v. *minuta* Chardez	10.5	5.3	WMS
C. cassis (Wallich) Deflandre	47.4	84.2	SBM
C. cassis v. *grandis* Chibisova	0.0	5.3	W
C. constricta (Ehrenberg) Penard	47.4	68.4	WS
C. constricta v. *minima* Decloitre	47.4	47.4	W
C. ecornis (Ehrenberg) Leidy	0.0	21.1	W
C. elongata (Penard) Thomas	0.0	36.8	MS
C. gibba Deflandre	0.0	15.8	BM
C. kolkwitzi Schönborn f. A (*grandis*)	5.3	0.0	W
C. laevigata Penard c.f.	10.5	0.0	WBMS
C. orbicularis Deflandre	42.1	42.1	WSpM
C. plagiostoma Bonnet, Thomas	26.3	78.9	S
C. plagiostoma f. A (*major*)	63.2	52.6	S
C. *plagiostoma* f. B (*minor*)	47.4	21.1	S
C. platystoma (Penard) Deflandre	10.5	47.4	SWM
C. sylvatica (Deflandre) Thomas	47.4	63.2	WSpM
C. sylvatica v. *microstoma* Bonnet	5.3	0.0	S
C. sylvatica v. *minor* Bonnet, Thomas	36.8	26.3	SpS
C. sylvatica f. A (*major*)	0.0	5.3	
C. sp. 1	0.0	10.5	
C. sp. 2	0.0	52.6	
Cyclopyxis eurystoma Deflandre	21.1	15.8	WSp
C. eurystoma v. *parvula* Bonnet, Thomas	31.6	63.2	S
C. kahli Deflandre	21.1	36.8	WM
C. puteus Thomas	5.3	0.0	S
Plagiopyxis bathystoma Bonnet	0.0	10.5	
P. callida Penard	15.8	0.0	WSpMS
P. callida f. *grandis* Thomas	5.3	0.0	BMS
P. declivis Thomas	26.3	0.0	SpS
P. minuta v. *oblonga* Bonnet	5.3	0.0	S
P. penardi Thomas	5.3	5.3	WS
P. sp.	5.3	0.0	
Heleopera petricola Leidy	10.5	10.5	WSp
Argynnia sp.	15.8	0.0	
Nebela bigibbosa Penard	0.0	15.8	WBM
N. lageniformis Penard	0.0	10.5	SpM

Table 1. (Contd.)

Species	Occurrence in samples, %		Ecological description
	Pleistocene	Holocene	
N. parvula Cash	0.0	105	SpM
N. tincta (Leidy) Awerintzew	0.0	5.3	SpM
Schoenbornia humicola (Schönborn) Decloitre	21.1	0.0	S
Difflugia ampululla Playfair	0.0	5.3	W
D. angulostoma Gauthier-Lievre and Thomas	0.0	15.8	W
D. brevicola Cash	0.0	10.5	W
D. decloitrei Godeanu	5.3	15.8	W
D. difficilis Thomas	0.0	10.5	W
D. globularis Wallich	0.0	15.8	W
D. globulosa Dujardin	0.0	52.6	W
D. globulus (Ehrenberg) Hopkinson	10.5	63.2	WSp
D. lacustris (Penard)	0.0	10.5	W
D. litophila Penard	0.0	5.3	W
D. lucida Penard	5.3	0.0	WSp
D. mica Frenzel	0.0	15.8	W
D. minuta Rampi	0.0	21.1	Sp
D. oblonga Ehrenberg	0.0	21.1	W
D. oblonga v. *longilollis* Gassowsky	0.0	5.3	W
D. oblonga f. A (160 μm)	0.0	10.5	W
D. molesta Penard	0.0	5.3	W
D. penardi Hopkinson	0.0	5.3	W
D. pristis Penard	5.3	5.3	W
D. pulex Penard	0.0	15.8	W
Lagenodifflugia sp.	0.0	5.3	
Phryganella acropodia (Hertwig et Lesser) Hopkinson	10.5	10.5	WMS
Ph. acropodia v. *australica* Playfair c.f.	0.0	31.6	W
Assulina muscorum Greef	0.0	10.5	M
Valkanovia delicatula (Valkanov)	0.0	15.8	M
Cyphoderia sp.	0.0	5.3	W
Euglypha anadonta Bonnet	0.0	10.5	S
E. ciliata (Ehrenberg) Wailes	0.0	5.3	WSpM
E. ciliata f. *glabra* Wailes	5.3	5.3	WSpMS
E. compressa Carter	0.0	10.5	SpM
E. laevis (Ehrenberg) Perty	0.0	15.8	SWBM
E. strigosa (Ehrenberg) Leidy	0.0	10.5	SpM
E. tuberculata Dujardin	0.0	10.5	WBM
E. sp.	5.3	15.8	
Corythion dubium Taranek	0.0	10.5	WSpM
Trinema complanatum Penard	0.0	10.5	SpMS
T. enchelys (Ehrenberg) Leidy	0.0	10.5	WSpM
T. lineare Penard	5.3	15.8	WSpMS
Pseudodifflugia gracilis Schlumberger	5.3	0.0	W
Total	41	72	Total in samples – 86

Note: M, green mosses; Sp, sphagnums; W, water; S, soil; B, bog; ecological description after Chardez (1965).
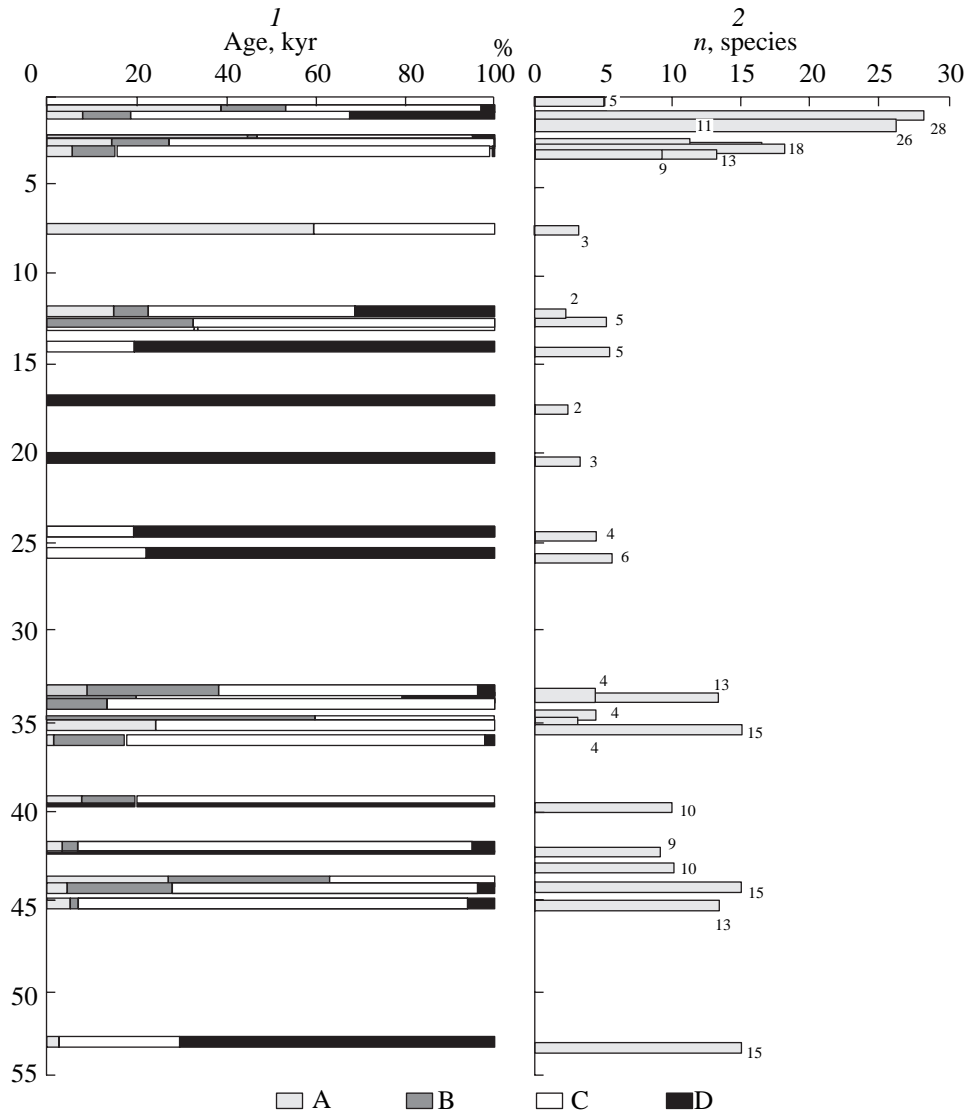
Fig. 1. Ecological groups (*1*) and number of species, varieties, and forms (*2*) in the Pleistocene and Holocene habitats; A, hygro- and hydrophilic species; B, sphagnophilic species; C, calciophilic species *Centropyxis plagiostoma* (three size groups of the species); D, euribionts and soil species; 2, number of testacean species in the Holocene and Late Pleistocene samples of ice complex of Bykovsky Peninsula.

Greenland at 66–67° N (Beyens, 1992). The differences in the ecological conditions for the testacean populations between *K1-5* and *KB2-2* are not very pronounced. The habitats have similar hydrological conditions.

Mkh-HB2-10, peat with sand particles (>41 830 years ago). The rhizopod community is presented by nine species. The habitat features high moistening—in addition to the euribionts species, a hydrophilic *Difflugia decloitrei* as well as hygrophilous *Argynnia* sp. occur. A lot of diatoms as well as ostracodes confirm the proposed hydromorphic pattern of the habitat. Eudominant *Cyclopyxis kahli* has never been found in high Arctic latitudes previously (Beyens *et al.*, 1986a, b, c, 1991, 1992; Smith, 1987; Balik, 1994). This indirectly indi-

cates warmer conditions as compared to the present time.

Mkh-KB3-1, peaty soil (39 320+600/–560 years ago). The community includes 10 species. The dominant complex is presented by euritopic and soil species— *Centropyxis sylvatica* and *C. plagiostoma.* The proper soil portion of the community is not numerous, neither species of *Plagiopyxis* genus nor *Schoenbornia humicola* are present. A polymorphous species *Centropyxis plagiostoma* is presented only by the largest form; coupled with finding of hydrophilic species of *Arcella* and *Difflugia* genera, this points to moist conditions and nutritional pattern similar to mesotrophic.

Mkh-KB8-3, cryoturbated peaty soil (35 050+390/– 370 years ago). Sporadic instances of three species. The

presence of an aquatic–moss species *Centropyxis platystoma* (Chardez, 1965) indicates moist conditions. Very low density of testaceans and low species diversity can result from low annual temperature. Relatively high density of ostracods describes the habitat as waterlogged. According to this index, this paleocenosis sharply differs from the other samples.

Mkh-KB4-2, loamy soil with the remains of branches (ca. 35 000 years ago). Considerable species diversity—15 species and intraspecific taxa. In contrast to the *Mkh-K1-5, Mkh-KB2-2,* and *Mkh-KB3-1* samples, the density of a raw humic species *Schoenbornia humicola* increases and *Euglypha ciliata* as well as *Trinema lineare* actively utilizing silicic acid in the soil moisture for the shell building appeared. There are neither pronounced hydrobionts nor sphagnophils. The soil rhizopods are presented by a polymorphous species *Centropyxis plagiostoma.* The presence of almost all subspecies of the euribiont species *Centropyxis sylvatica* is an important character related either to high heterogeneity of the microhabitats or sharp seasonal changes of ecological conditions. It is common knowledge that polymorphism is a part of adaptive strategy of rhizopod species (Schönborn, 1992; Bobrov, 1999). Apparently, accumulation of organic matter was accompanied by its active mineralization typical for the soil conditions with favorable thermal rate. The moistening conditions were also optimal, as indicated by finding a hydrophilic species *Centropyxis cassis* and *C. orbicularis.*

Mkh-KB8-4, clayey soil with peat inclusions and ligneous remains (34 800+340/–330 years ago). The rhizopod community is presented by 10 species and subspecies. By ecological properties, these are mostly euribionts and soil species. Finding *Centropyxis cassis, C. constricta*, and *Plagiopyxis callida* common in moist habitats suggests increased moistening.

Mkh-KB6-10, peaty clayey soil (ca. 34 000 years ago). Four species of *Centropyxis* genus have been revealed at very low density. Similar to other Pleistocene probes, calciophilic *C. plagiostoma* have been found in addition to the euribionts. No hydrophilic species have been revealed. Apparently, the sample represents a humus-accumulating horizon of the soil with rare grass vegetation.

Mkh-KB7-3, peaty material from a cryoturbated soil (33 450+260/–250 years ago). The rhizopod community is presented by 13 species and resembles the *Mkh-KB2-2* by the conditions. The aquatic conditions were more hydromorphic then while the habitat was more moist, as indicated by the presence of hydrophilic species of *Arcella* and *Difflugia* genera.

Mkh-KB7-2, loamy material of a cryoturbated soil (ca. 33 000 years ago). The pattern is largely similar to that of *Mkh-KB6-10;* however, there is an important distinction—moist conditions indicated by the presence of hygro- and sphagnophilic species *Heleopera petricola* and high density of diatoms.

Mkh-99 samples with radiocarbon age from 25 570+170/–160 to 13 920 ± 100 years ago feature rare occurrences of rhizopods and their low species diversity (from 2 to 6 species). The population is based on euribionts; singular pedobionts occur (*Plagiopyxis declivis*). Neither sphagnophilic nor hydrophilic species have been found in any of the inspected 25 samples. Importantly, considerable portion of the rhizopods is presented by *minor* forms—*Centropyxis aerophila* v. *minor*, *C. constricta* v. *minor, C. plagiostoma* f. B (*minor*), *C. sylvatica* v. *minor*. Decreased dimensions of the shelves with decreased temperature (Smith, 1988) and deficiency in soil moisture (Chardez and Leclercq, 1963; Heal, 1963; Bobrov *et al.*, 1999) can be considered as a result of adaptive strategy of rhizopods. The obtained data allow us to consider the studied habitats as very cold and xeromorphic.

Mkh-4.3-3, black peat (ca. 12 000 years ago). Singular instances euribiont *Centropyxis constricta* (*minor* form) and calciophilic *C. plagiostoma* (*minor* form). Highly dispersed organic matter and its black color indicate deep mineralization of the organic remains in conditions of a mesotrophic bog. These processes could destroy the shells of virtually whole paleocenosis of testaceans, which is common in the present mesotrophic bogs.

Mkh-4.3-4, brown peat (12 020 ± 205 years ago). Low species diversity (five species) can result from low temperature at the background of relatively high moisture content. High moisture markers include hygro- and sphagnophils *Centropyxis aculeata* and *Heleopera petricola.*

Holocene Samples

Mkh-99-1, loamy soil with peat inclusions (7520 ± 50 years ago). This is a moist habitat with single rhizopods species.

Mkh-6.2 samples (3000–2800 years ago) of peat bog with large wedge ice formed at the stage of overgrowth of thermokarst pond at the bottom of a large alas.

Mkh-6.2-1, loamy soil (2925 ± 30 years ago). No testaceans have been found.

Mkh-6.2.6, peat from the base of a peat bog (2885 ± 30 years ago). Eleven species and intraspecific taxa of rhizopods. The community has a high proportion (about 50%) of hygro- and hydrophilic species of *Centropyxis* and *Difflugia* genera. A hydromorphic habitat, pool.

Mkh-6.2-8, peat (2980 ± 35 years ago). Seventeen species and intraspecific taxa. No sphagnophils have been found; the proportion of calciophilic species *Centropyxis plagiostoma* is high. The hydrophils of *Difflugia* genus are diverse—six species. A representative of mesotrophic–eutrophic bogs—*Cyphoderia* sp.—has been found. Apparently, it is a mesotrophic habitat.

Mkh-6.2-11, peat. Eighteen species and intraspecific taxa of testaceans specific for mesotrophic hydromor-

phic habitat. The sample is rich in rhizopods. The previous marker species are present—*Centropyxis plagiostoma* and the group of hydrophilic species of *Difflugia* genus.

Mkh-6.2-12, peat (2740 ± 35 years ago). No testaceans have been found.

Mkh-6.2-14, peat. A lot of slightly decomposed plant remains, apparently, sedges. Thirteen species and intraspecific taxa represent the community specific for meso–oligotrophic stage of bogging. Various representatives of sphagnophils are present. The dominant complex includes *Difflugia globulosa* and *D. globulus.* The first species is specific for sphagnums and bogs of the 1 and 2 classes with temporary open water bodies (Meisterfeld, 1977).

Mkh-6.2-15, peat. Fifteen species and intraspecific taxa represent a community of hydromorphic biotopes. Considerable waterlogging is indicated by the presence of hydrophilic species of *Difflugia* genus.

Mkh-6.2-16, peat. Thirteen species and intraspecific taxa form a community quite close to the paleocenoses of samples Mkh-6.2-11 and Mkh-6.2-14 specific for hydromorphic biotopes.

Mkh-6.2-17 (3020 ± 70 years ago). No testaceans have been found.

Mkh-6.2-18, peat. Nine species and intraspecific taxa include euritopic and hydrophilic testaceans. The species are specific for meso–oligotrophic and oligotrophic conditions with subacid pH. The presence of typical hydrophils—*Difflugia globulus* and *D. globularis*—indicate hydromorphic stage of the community development.

Mkh-6.2-19, peat. The community of 13 species and intraspecific taxa is mostly represented by euritrophic species occurring both in soils and bottom lacustrine sediments. Specifically, *Centropyxis ecornis* has been found, a hydrophilic species preferring oligo–mesotrophic and mesotrophic conditions with nearneutral pH. This conclusion is confirmed by the presence of calciophilic species *Centropyxis plagiostoma* and *C. plagiostoma* f. A (*major*) as well as *Difflugia globulus*, a species specific for lacustrine and lacustrine-bog stages of paleocenosis development, in the dominant complex.

Mkh-1.6-1 samples were collected from a peat bog formed in a shallow thermokarst depression in a wide hollow above the ice complex. The peat bog contains new ice veins indicating recent shrinking of the pond.

Mkh-1.6.1-2 (1080 ± 35 years ago). This layer has the maximum species diversity—29 species and intraspecific forms. Euribiont *Centropyxis constricta* and calciophilic *C. plagiostoma* predominate. Numerous sphagnobiont species are present. The testacean community is more specific for afforested moss communities.

Mkh-1.6.1-3–Mkh-1.6.1-9 (1240 ± 60 and 1105 ± 35 years ago). No testaceans have been found.

Mkh-1.6.1-10 (1360 ± 35 years ago). The sample features high species diversity—28 species, varieties, and forms of testaceans. The raw humic sphagnophilic group with xerophilous species of *Valkanovia, Assulina, Corythion*, and *Nebela* genera is pronounced as well as the mesotrophic group (*Centropyxis plagiostoma* and the whole complex of *Centropyxis* genus) with hygrophilous species (*C. elongata, C. platystoma*, and *Difflugia decloitrei*). Apparently, such structure of the testacean population reflects variable aquatic conditions during the vegetation season—from waterlogging to temporary xeromorphic conditions.

Mkh-1.6.1-13, peat underlying the seasonally thawed layer. There is a lot of half-decomposed plant remains, mostly, mosses with minor content of flaky humic blobs. The layer is not considerably mineralized. Eighteen species and intraspecific taxa form a community with relatively high species diversity, including both sphagnophilic species of *Arcella, Valkanovia*, and *Nebela* genera and hydrophilic species of *Difflugia* genus. This is a typical testacean community for a habitat of oligotrophic bogs with low groundwater table.

Mkh-1.6.1-14, peat from seasonally thawed layer. Twelve species and intraspecific taxa represent a pronounced complex of hygro- and hydrophilic species. The first ones include species of *Arcella* and *Centropyxis* genera, while the second ones include five species of *Difflugia* genus. A similar species composition of rhizopods is specific for boggy habitats, possibly, with an open water face and more pronounced oligotrophic nutritional conditions as compared to most other studied samples (only a singular finding of calciophilic *Centropyxis plagiostoma*, a species specific for most studied samples).

Mkh-1.6.1-15, peat from a seasonally thawed layer. Sixteen species and intraspecific taxa represent population of the community from a hydromorphic habitat with more pronounced oligotrophic conditions as compared to most samples. Top species diversity of hydrophilic species of *Difflugia* genus was observed. Open water face is possible.

Mkh-1.7.2-4, sandy soil (spoon-shaped deposits formed over an ice complex ca. 1400 ± 60 years ago). There is a lot of slightly decomposed plant remains. Euribiont species predominate among the twenty-six species and intraspecific taxa. The presence of hydrophilic species of *Difflugia* genus and a calciophilic species *Centropyxis plagiostoma* suggests subacid pH of the boggy soil.

TKS-1, sediments of a small contemporary thermokarst lake. The testacean community features low density and low species diversity. A singular finding of a calciophilic species *Centropyxis plagiostoma* indicates subacid pH.
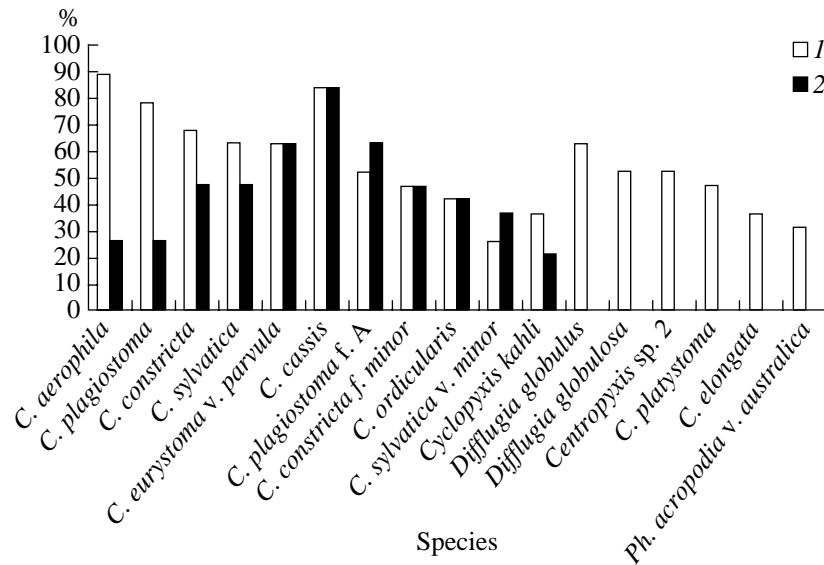
Fig. 2. Dominant complex of testaceans (occurrence > 30%) in Holocene and Late Pleistocene sediments of Bykovsky Peninsula; *1*, Holocene; *2*, Pleistocene.

Specific Structure of Testacean Population from Late Pleistocene and Holocene Permafrost Sediments

The structure of domination. Euribiont species predominate in the dominant complex (with frequency of occurrence above 30%) (Fig. 2) with prominent *Centropyxis aerophila*, a species common for most habitats in high latitudes (Beyens *et al.*, 1986). In addition to the usual Arctic species, inhabitants of soils of lower latitudes occur—*Centropyxis plagiostoma, C. platystoma*, and *Cyclopyxis kahli*. The characteristic predomination of considerable number of hygro- and hydrophilic species of *Centropyxis* and *Difflugia* genera is an important marker of enhanced hydromorphism of most studied habitats with high species diversity of testaceans.

The composition of dominants of the Late Pleistocene and Holocene rhizopod communities is quite similar. The common species of the dominant complex form a taxonomic core of testacean communities of permafrost in Bykovsky Peninsula. Most of them include euribionts (*Centropyxis aerophila, C. sylvatica*, and *Cyclopyxis eurystoma* v. *parvula*). There are marker species. A calciophilic *Centropyxis plagiostoma* indicates subacid pH of soil solutions in most habitats of Late Pleistocene and Holocene; aquatic–moss *Centropyxis cassis* present in over 80% samples indicates waterlogged conditions in most studied habitats. At the same time, this hydrophilic species was absent from the Mkh-99 samples of the period ca. 25 000—14 000 years ago.

Marker species. The sphagnophilic species of *Nebela* genus are present only in the samples of the Holocene peat bogs in a thermokarst depression (alas) starting ca. 3000 years ago. Other sphagnophils— *Assulina muscorum* and *Valkanovia elegans*—were noted in the samples from a peat bog (dated between

1360 ± 35 and 1080 ± 35 years ago) covering spoon-shaped sediments embedded in the ice complex of the southern region of Mamontovy Khayata cliff. The pattern of mineral nutrition in the bulk of the biotopes is closer to mesotrophic rather than to oligotrophic according to frequency of calciophilic *Centropyxis plagiostoma*. That is why the frequency of typical sphagnophils is low. The hygro- and hydrophilic species (*Arcella arenaria, Difflugia globulus, D. globulosa, D. minuta, D. oblonga, Centropyxis ecornis, C. elongata*, and *C. platystoma*) were mostly found in the Holocene samples; as was already mentioned, they often belong to the dominant complex; however, they are rare in the Pleistocene samples. Conversely, the species of the soil group—*Plagiopyxis declivis* and *Schoenbornia humicola*—have been found in the Pleistocene samples.

Ecological groups. The next step in the analysis of the rhizopod communities was their comparative evaluation in terms of ecological groups of testaceans (Fig. 1a). The main ecological groups of rhizopods were recognized including the species from different genera with similar ecological properties: (1) hygro- and hydrophilic species, (2) calciophilic species *Centropyxis plagiostoma* (three size groups of the species), (3) euribionts and soil species, and (4) sphagnophilic species. *Centropyxis plagiostoma* was given a particular emphasis in the analysis of testaceans community composition as the most frequent species specific for all studied permafrost sediments in general with considerable marker significance.

The hydrophilic species were found in all samples of the time interval 53 000–35 000 years ago; within the period 35 000–12 000 years ago it was found in the sample dated 33 450+260/–250 years ago as well as in all

Table 2. Kolmogorov-Smirnov test for significance of the size differences between three size forms of *Centropyxis plagiostoma* (*major*, *typica*, and *minor*)

Form	Sample volume	Mean, µm	Coefficient of variation	Significance of differences between the distributions, p
typica	30	74.9	9.2	<0.001
major	30	99.6	6.4	
major	30	99.6	6.4	<0.001
minor	30	55.1	8.0	
typica	30	74.9	9.2	<0.001
minor	30	55.1	8.0	

samples of the Holocene age. Temporal dynamics of the unfrequent group of sphagnophilic species is similar to that of the hydrophilic species; the differences apply to the samples dated >44980, 35050+390/–370, and 33450+269/–250 years ago. No sphagnophils have been found in these samples despite the presence of representatives of the hydrophilic group. The third group is presented by the polymorphous calciophilic species *Centropyxis plagiostoma* (three size groups of the species). This species has been found in over 80% samples (Fig. 3). It was absent from the samples with very low abundance of rhizopods and low species diversity. The fourth group combines the euribionts and soil species. They form a complex typical for humus-accumulating soil horizons and were found in the samples dated 53020+2670/–2000, 45300+1200/–1050, and 44280+1320/–1130 years ago. Their rare occasions were observed in the samples dated ca. 35000, 20000, and 12000 years ago. They were also present in three Holocene samples; however, it was chiefly *Plagiopyxis bathystoma*, a species typical for the initial stages of forest soils waterlogging in taiga (data not shown).

A part of euribiont species in the samples occurred as various dimensional forms—*typica, grandis, minor*, and *microstoma* (Table 1). In this regard, calciophilic and markedly stenobiontic species *Centropyxis plagiostoma* is particularly interesting. Polymorphism of this species from the upper layer of the mull soil in Dagestan elfin woodland was considered in detail in terms of taxonomy by Foissner and Korganova (1995). Three size classes were recognized for the species with large (103 µm), medium (80 µm), and small (57 µm) diameters, which are very close to the three forms *typica, major*, and *minor* found in the permafrost sediments (Table 2; Figs. 3f–h, 4). Morphometric analysis of *C. plagiostoma* in the samples of permafrost sediments from Bykovsky Peninsula with ecological conditions changing with time suggests adaptive significance of the dimensional polymorphism of the species.

The form *typica* is most frequent in the more moist Holocene habitats as compared to the Pleistocene ones; conversely, the *minor* and *major* forms are more com-mon in the Pleistocene biotopes (Fig. 4). This fact can be explained by diversity of econiches in Late Pleistocene resulting from a higher differentiation of the biotopes as compared to Holocene with predominating boggy soils (up to 79%).

Species with limited geographical distribution. A species of *Argynnia* Vuchetich, 1974 genus was found in three samples dated 45300+1200/–1050, 44280+1320/–1120, and >41830 years ago. Just one species of this genus including about 15 taxa, *A. dentistoma*, has wide cosmopolite distribution. *A. vitrea* also has wide (although considerably less wide) distribution (Ogden and Hedley, 1980), while the distribution of other species is limited to narrow geographical regions in the Canadian and Eurosiberian subregions of Holarctic as well as in the Australian and Antarctic regions (Deflandre, 1936; Meisterfeld, 1998). Almost all species of this genus occur in sphagnum bogs and acidic humus while their main range falls at the forest belt. Neither species of this genus except *A. dentistoma* has been found in the present Arctic biotopes (Beyens and Chardez, 1995). This fact additionally corroborates the proposed specific natural situation in the northeastern Siberia formed in Late Pleistocene. An additional confirmation can be provided by finding *Cyclopyxis puteus* in the sample dated ca. 45000 years ago, a species previously revealed at the northern boundary of its range in the soil of Devon Island (Canada), Spitzbergen (Beyens and Chardez, 1995), tundra soils of Bering Island, coniferous rainforests of British Columbia, and fir forests of southern taiga in Tver Region (unpublished data).

In terms of biogeography, sphagnophilic *Nebela bigibbosa* found in Spitzbergen at the beginning of the last century by Penard (1903) is of interest. In Bykovsky Peninsula, it was found in Late Holocene bog samples from the spoon-shaped complex sediments dated 1360 ± 35, 1240 ± 60, and 1080 ± 35 years ago.

DISCUSSION

Results of Undirected Correspondence Analysis. Ordination of the Studied Samples

We used correspondence analysis to compare the Late Pleistocene and Holocene habitats by composition of testaceans. Previously, we established that Axis1 and Axis2 show the effect of hydrological conditions and pH of the soil solutions, respectively, in ordination of the ecological factors for the population of oligotrophic bogs (Bobrov *et al.*, 1999). Stated differently, ordination of the Pleistocene and Holocene habitats (Fig. 5) primarily depends on the differences in the composition of ecomorphological groups of testaceans considerably influenced by the aquatic conditions and pH of the soil. The characteristic values (of a factor significance) in a four-dimensional ecological space of factors are as follows: Axis1, 0.43; Axis2, 0.28; Axis3, 0.26; and Axis4, 0.16. Factor significance is high for the first axis (hydrological conditions), while axes 2–4 show consid-
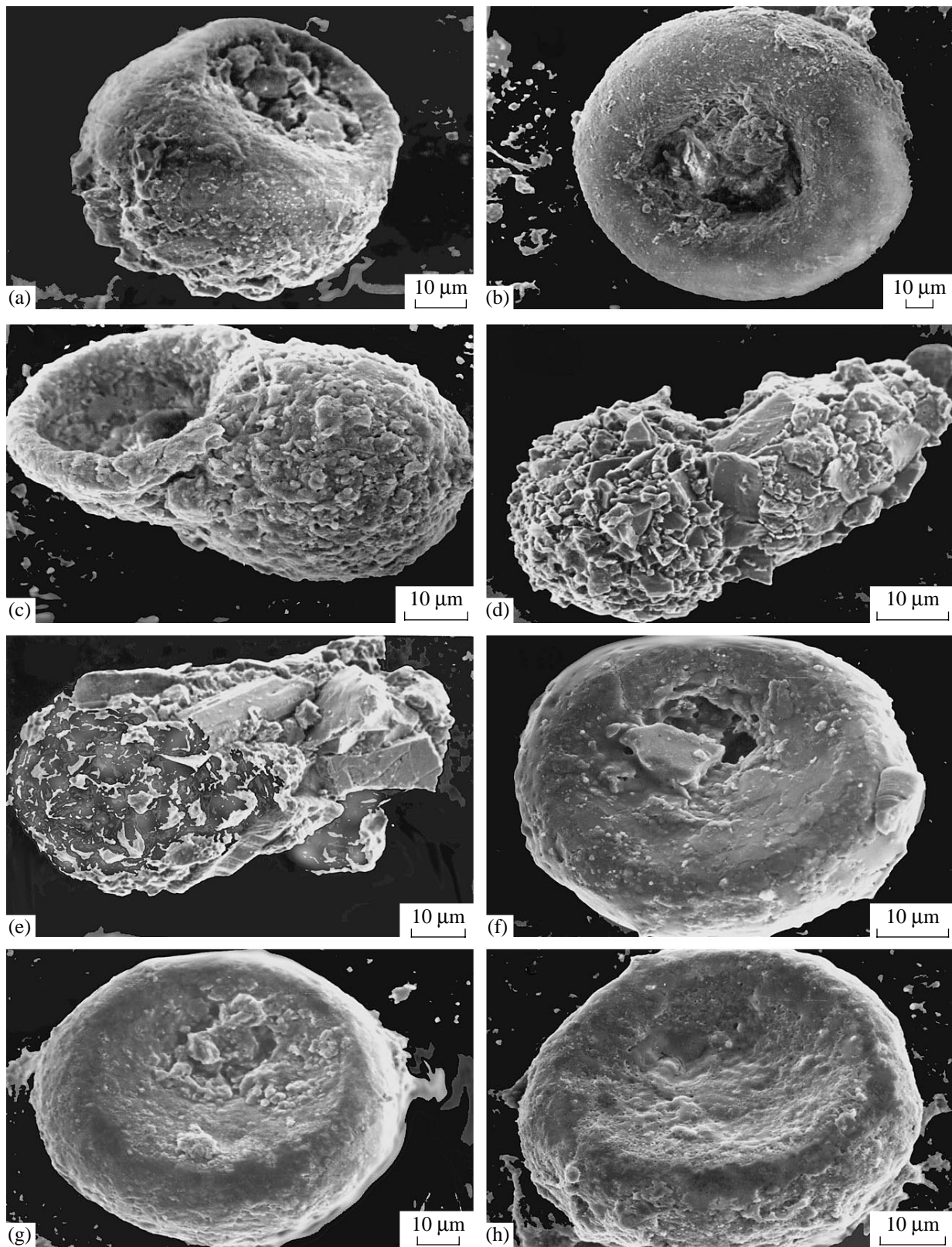
Fig. 3. Testaceans from the ice complex of Bykovsky Peninsula (Scanning electron microscopy picture); a, *Centropyxis sylvatica*, ×1000; b, *C. ecornis*, × 600; c, *C. platystoma*, × 1300; d, *Lagenodifflugia* sp., ×1200; e, *Difflugia oblonga*, ×500; f, *Centropyxis plagiostoma*, ×1300; g, *C. plagiostoma* f. A (*major*), ×1000; h, *C. plagiostoma* f. B (*minor*), ×1500.
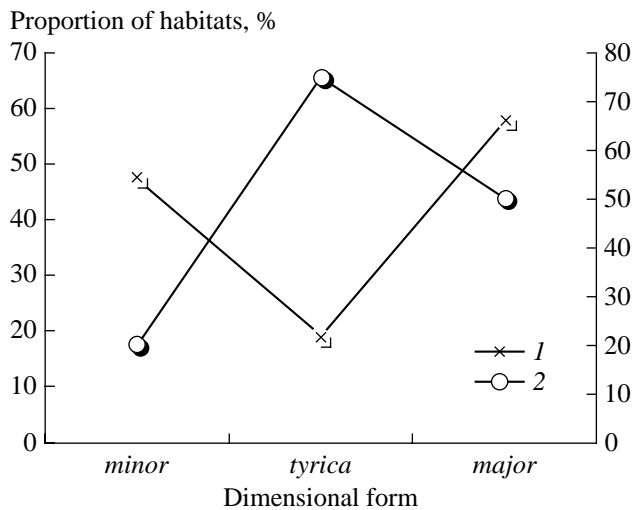
Proportion of habitats, %

Fig. 4. Proportion between dimensional forms of a polymorphous species *Centropyxis plagiostoma* Late Pleistocene and Holocene permafrost samples of Bykovsky Peninsula; *1*, Holocene; *2*, Pleistocene.
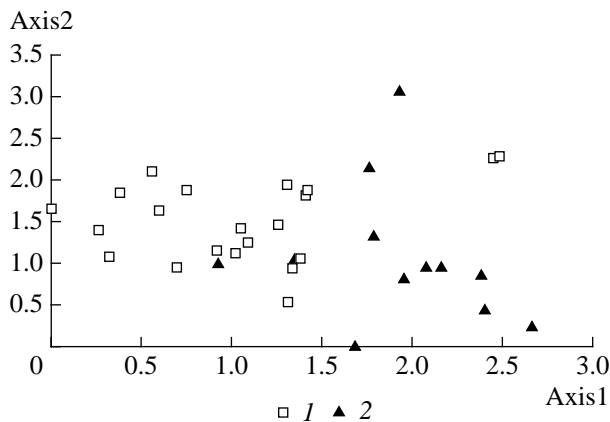
Fig. 5. Results of undirected correspondence analysis of Late Pleistocene and Holocene samples of Bykovsky Peninsula; *1*, Pleistocene; *2*, Holocene.

erably less pronounced gradients of data difference. The effect of pH was less pronounced for the Pleistocene samples; all the samples fall within a relatively narrow interval of the gradient—from 0.5 to 2.1. In the case of the Holocene samples, this effect was more pronounced—from 0 to 3.1. Apparently, this is due to the presence of considerable amount of peat samples with acidic pH among the Holocene samples. Undirected correspondence analysis demonstrated considerable difference between the Pleistocene and Holocene samples. The presence of the transition zone can be due to similar ecological conditions in a number of habitats—soil and bog ones.

Apparently, such ordination will yield somewhat different pattern for various habitats with aquatic conditions always being among the key factors. For

instance, the most significant factors for testaceans in the soils of monodominant vegetation groups in northeastern Greenland included organic matter, pH, thickness of the active layer, and humidity of the soil (Trappeniers *et al.*, 2002).

Cluster Analysis of the Samples

Comparison of testacean communities by cluster analysis implemented in TILIA software package confirms the difference between rhizopod communities of Late Pleistocene and Holocene (Fig. 6). All species with the same or similar distribution in the samples of various age were sorted into the following groups:

Arcella arenaria v. *compressa* complex—*A. arenaria* v. *compressa, A. rotundata* v. *aplanata*, and *A.* sp.;

Plagiopyxis callida sensu lato—*P. callida* and *P. callida* f. *grandis*;

Centropyxis sylvatica v. *microstoma* + *C. sylvatica* v. *minuta*;

Cyclopyxis eurystoma + *C. eurystoma* v. *parvula*;

Difflugia brevicola complex—*D. brevicola, D. ampululla, D. angulostoma, D. decloitrei, D. lacustris, D. litophila, D. mica, D. molesta, D. penardi, D. pristis, D. pulex, D. oblonga, D. oblonga* v. *longicollis*, and *D. oblonga* f. A (160 μm);

Centropyxis aerophila complex—*C. aerophila, C. aerophila* v. *grandis, C. aerophila* v. *sphagnicola, C. cassis, C. cassis* v. *grandis, C. constricta, C. ecornis, C. elongata, C. gibba, C. kolkwitzi* v. A (*grandis*), *C. orbicularis, C. plagiostoma* sensu lato *C. platystoma, C. sylvatica, C. sylvatica* f. A, *C.* sp.1, and *C.* sp.2;

Difflugia globulus complex—*D. difficilis, D. globularis, D. globulosa*, and *D. minuta*;

Nebela bigibbosa complex—*N. bigibbosa, N. lageniformis, N. parvula*, and *N. tincta*; and

Assulina muscorum complex—*A. muscorum, Valkanovia delicatula, Euglypha anadonta, E. ciliata, E. compressa, E. laevis, E. strigosa, E.* sp., *Corythion dubium, Trinema complanatum, T. enchelys*, and *Pseudodifflugia gracilis*.

Four main zones were recognized corresponding to specific composition of testaceans.

Zone D (53000–35000 years ago) features predomination of the soil and euribiont species of *Centropyxis, Cyclopyxis*, and *Plagiopyxis* genera.

Zone C (35000–12000 years ago) can be described by decreased species diversity of rhizopods. Singular hygrophilous species—*Heleopera petricola, Centropyxis aculeata, Euglypha tuberculata*, and *Difflugia globulus*—appeared in the upper and middle regions of the zone.

Zone B (12000–3000 years ago) features predomination of various hydrophilic species of *Difflugia* genus. Species of *Centropyxis* genus are widespread, most of them are hygrophilous—*C. gibba, C. elongata,*
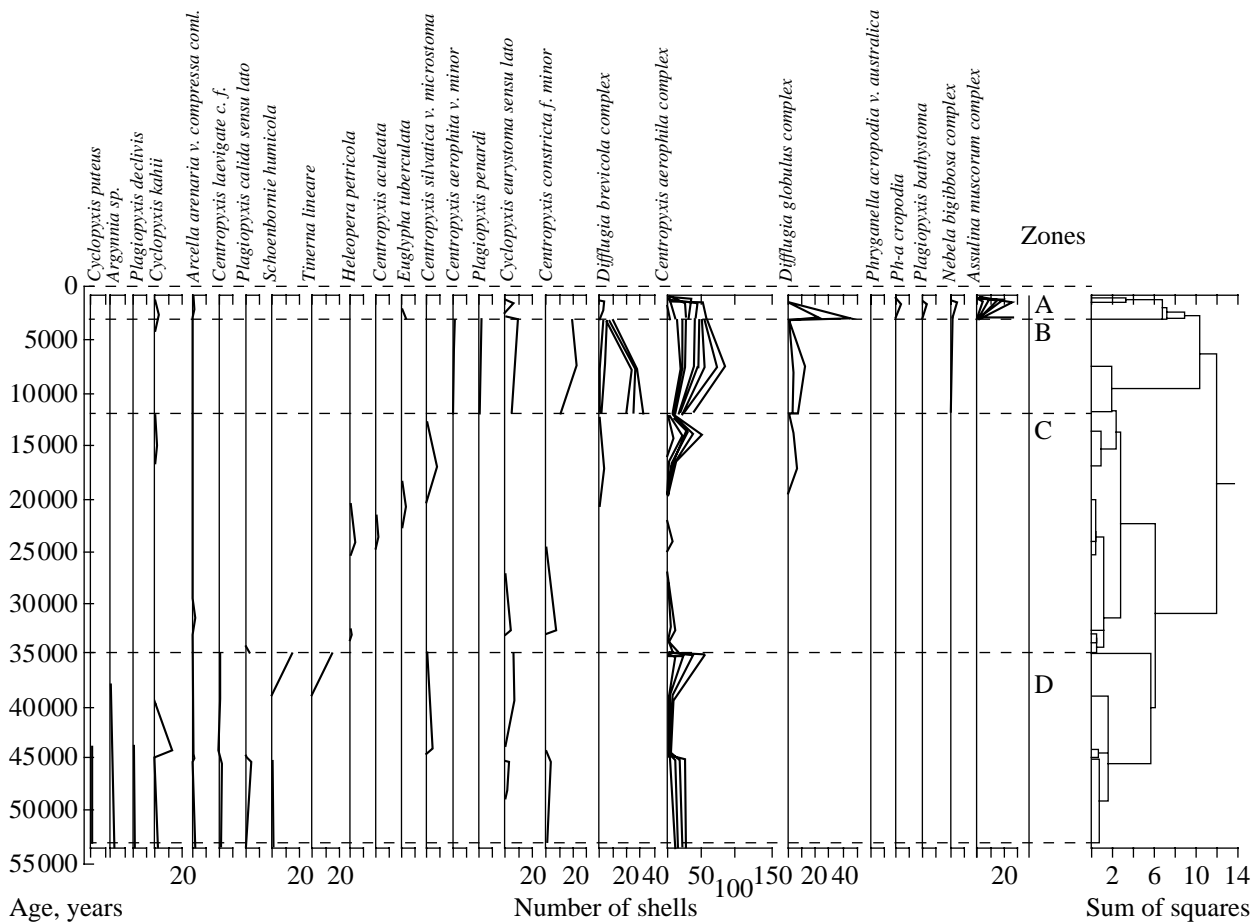
Fig. 6. Diagram of testacean distribution in the Late Pleistocene and Holocene samples of various age of Bykovsky Peninsula.

and *C. platystoma.* The complex of rhizopods of this zone is specific for moist habitats.

Zone A (3000 years ago–present time) can be described by a complex of hydro- and sphagnophilic species of *Nebela, Assulina, Valkanovia, Euglypha*, and *Difflugia* genera. A fraction of this species, for instance, *Corythion dubium*, inhabits raw humic litters as well and indicates xerophilous conditions.

Reconstruction of Paleoecological Conditions

Rhizopods in 42% Pleistocene samples are typical for hydromorphic habitats (bogs and waterlogged soils). Most samples where rhizopods were found are presented by automorphic soils. The Holocene samples where testaceans were found are represented by boggy and waterlogged soils in 79% cases.

The changes in the rhizopod community within 53 000 years were not as significant as one could expect on the basis of their long-term absence in the samples—testaceans have not been found in the samples dated 53 200–45 300, 39 320–35 500, 33 500–25 570, 24 470–20 600, and 12 000–10 000 years ago. These changes are mostly related to rare species as well as the dominant

complexes of testaceans in Pleistocene and Holocene. A group of species (Fig. 2) can be recognized by the frequency being over 30% within Pleistocene and Holocene. Particularity of rhizopod composition in permafrost sediments of Bykovsky Peninsula is predomination of species with narrow ecological plasticity, which indirectly indicates relative stability of testacean population resulting from similar ecological conditions. Specificity of these conditions is recorded in changed proportion of the ecological groups of rhizopods. The presence of uniform dominant complexes in most samples allows us to propose similar hydrothermal conditions in the sediments and soils within these periods. Despite the periods with unfavorable conditions, restored testaceans communities with a taxonomic core of similar species composition is observed in the samples.

Testacean communities specific for meso–oligotrophic and, to a lesser extent, oligotrophic conditions with subacid pH and low density of protists, apparently, occupied the habitats in the coldest climatic conditions. Mass development of species of *Centropyxis* and *Difflugia* is most likely due to permanent availability of calcium-rich material. This can be due to petrographic

properties of the rocks in the drift region (Siegert *et al.*, 2002).

The difference in paleoclimatic conditions in Pleistocene and Holocene are clearly demonstrated by rhizopod analysis. The group of hydrophilic species of *Difflugia* genus is considerably wider presented in the Holocene samples. Most found species of this genus are obligate hydrobionts. The frequency and species diversity of rhizopods in most Holocene samples allow us to propose moist and relatively warm conditions. The humidity seem to be lower in the Pleistocene samples, although high frequency of single hydrophilic species at particular horizons also point to moist microclimatic conditions. These include the samples dated 53020+2670/–2000, 45300+1200/–1050, 44280+1320/–1130, and >41830 years ago. In addition, the differences in species diversity of the communities allow us to recognize warmer and colder periods, particularly, in Pleistocene. This is also confirmed by polymorphism of certain testaceans species. For instance, the samples with low species diversity of testaceans fall on the period ca. from 33000 years ago to the beginning of Holocene. According to rhizopod analysis, this period can be described as particularly cold.

CONCLUSION

The probe dated 53020+2670/–2000 years ago contains testaceans specific for mineral boggy soils. The euribiont and soil species predominate—15 species and subspecies. The proportion of the calciophilic species *Centropyxis plagiostoma* is considerable—27.1%. According to pollen records, gramineous and sedgy vegetation prevails within this period (Schirrmeister *et al.*, 2002a).

During the period ca. 45000–43000 years ago, representatives of genera *Arcella, Centropyxis, Cyclopyxis, Plagiopyxis*, and *Argynnia* were widespread; at present, they mostly occur in sphagnum mosses and acidic soils with increased humidity in the forests of taiga zone. The presence of calciophilic *Cyclopyxis plagiostoma* points to mesotrophic pattern of nutrition. The thermal conditions are relatively favorable.

During the period ca. 39000–35000 years ago, the species composition of rhizopod communities became considerably poorer. Over a half samples lack hygro- and hydrophilic species. Apparently, the soils featured more extreme dry conditions within this period as compared to the preceding one. Both the species diversity increases and the structure of rhizopod ecological complex becomes more complex at the end of this period. Later testaceans virtually disappear until Late Pleistocene.

No testaceans have been found in most samples of the period ca. 25000–12000 years ago. The samples where they were found feature low species diversity—from 2 to 6 species of the ecological complex of euri- and pedobionts. Most species are presented by subspecies and *minor* forms. This fact can be explained by extremely dry and cold conditions. Just one peat sample dated to the beginning of Allerod warming (ca. 12000 years ago) includes representatives of all ecological groups. In general, this is an unfavorable period for the population of this group of free-living protists. The data on entomofauna of this period (Sartan time) demonstrated very cold landscapes soon replaced with true tundra–steppe during the first half of the Sartan (24000–19000 years ago) (Kuz'mina, 2001).

Late Pleistocene features low species diversity of testaceans most of which are presented by euribionts. The late Holocene phase (3000 years ago—present time) of development of testaceans communities features the presence of all main ecological groups of testaceans, the highest species diversity, the presence of raw humic sphagnophilic group with both xerophilous species of *Valkanovia, Assulina, Corythion*, and *Nebela* genera and hygrophilous species of *Centropyxis* and *Difflugia* genera. The mesotrophic complex of rhizopods is also pronounced. Apparently, such complex structure of rhizopod population reflects specific ecological conditions—contrast alternation of various humidity conditions within the vegetation season.

Results of rhizopod analysis are largely similar to the paleoreconstruction from pollen records (Andreev *et al.*, 2002). Apparently, the differences are largely due to different preservation of paleocenoses as well as other taphonomic reasons. As previously demonstrated by Schirrmeister *et al.* (2002a), another factor of disagreement in climatic reconstructions based on different groups of plants and animals is their different sensitivity to ecological environmental factors. In addition, one should consider specific ecology of species, such as changes in a species ecology from the central to marginal regions of its range, etc. Nevertheless, only a complex investigation of paleoecosystems can form a complete picture of ecological conditions of former periods. Rhizopod analysis holds a particular place among these methods; it describes local habitats, a set of which forms a unique mosaic of paleolandscape.

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