

Paleobotanical Analysis of Materials from Fossil Gopher Burrows and Upper Pleistocene Host Deposits, the Kolyma River Lower Reaches

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Abstract—The comparative analysis of palynomorphs and plant megafossils (fruits, seeds, twigs, leaves) in the Upper Pleistocene host sediments and materials filling in fossil burrows of gophers, their coprolites included, at the Duvannyi Yar, Stanchikovskii Yar and Zelenyi Mys sites of the Kolyma Lowland is carried out. Genera *Salix*, *Lychnis*, *Silene*, *Draba*, *Potentilla*, *Larix*, and families Poaceae, Polygonaceae, Cyperaceae, Compositae, and Leguminosae are determined among palynological remains and megafossils. Factors responsible for qualitative and quantitative differences in taxonomic compositions of palynological and megafossil assemblages are biological peculiarities of plants, different character of fossilization of palynomorphs and large plant remains, geographic conditions, different genesis of assemblages (allochthonous for microfossils and autochthonous for megafossils), and inadequately known morphology of certain spore and pollen taxa. The comprehensive paleobotanical analysis leads to the conclusion that the study region was occupied in the Late Pleistocene by plant communities of humid to somewhat dryer tundra with separate areas of pioneering and steppe vegetation.

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Key words: Upper Pleistocene, Karga beds, Kolyma River, glacial complex, burrows of fossil rodents, paleobotanical analysis.

INTRODUCTION

In most Upper Pleistocene sections of the Kolyma River lower reaches, there are exposed peculiar silty deposits (cryopedoliths) with abundant thick ice veins. Content of ice in the glacial complex deposits is usually 40 to 60%, being sometimes as high as 80–90%. Numerous mounds in the Late Pleistocene plain of north Yakutia, which are composed of the above deposits, have local name “Edoma.” According to the regional stratigraphic scheme (*Resolutions of the Interdepartmental...*, 1987), the Edoma deposits correspond to the Upper Pleistocene. The Oyagos, Molotkovo, and Muskhain horizons of the Edoma Superhorizon are correlative in general with the Zyryanka, Karga, and Sartan horizons of Siberia. Presence of fossil burrow in permafrost of the study region is mentioned in works by Kaplina et al., (1978), Tomirdiario and Chernen’kii (1987), Gubin and Khasanov (1996), and Boeskorov and Belolyubskii (2000). The in situ burrows of rodents (lemmings, gophers, mice) are suitable and informative objects for studying formation conditions of the glacial complex. These ancient refuges represent specific burials of organic remains (plants, animals, insects), soil, and other materials brought in from the Earth surface,

which were components of biogeocoenosis in the burrow sites.

In this work, we describe plant remains (spores, pollen, fruits, seeds, twigs, and leaves) from Upper Pleistocene host deposits and sedimentary fill of gopher burrows, their coprolites included, which are studied at the Duvannyi Yar, Stanchikovskii Yar, and Zelenyi Mys sites of the Kolyma Lowland. The studied sections are situated between 68° and 69° N within the belt of present-day thin forests (a subzone of north taiga), where pioneering and steppe vegetation populates the riverbank scarps and alluvial benches (Fig. 1). The burrows studied occur about 40 m below surface in deposits of the Karga (Molotkovo) time (50–26 ka old), which did not thaw after being frozen. Radiocarbon dates obtained for plant remains from three burrows are as follows: 31800 ± 310 years (Beta 157195), burrow P-1075, Duvannyi Yar site; 32800 ± 1400 years (IEMEZH 1178), burrow P-923, Zelenyi Mys site; 27700 ± 300 years (GIN 10874) burrow P-1010, Stanchikovskii Yar site. In permafrost of the Duvannyi Yar site, burrows P-1311 and P-1321 are at the level of burrow P-1075 38–40 m below the surface (Figs. 2–4).

Concurrent ages of samples from burrows and host deposits are granted by the sampling procedure used.

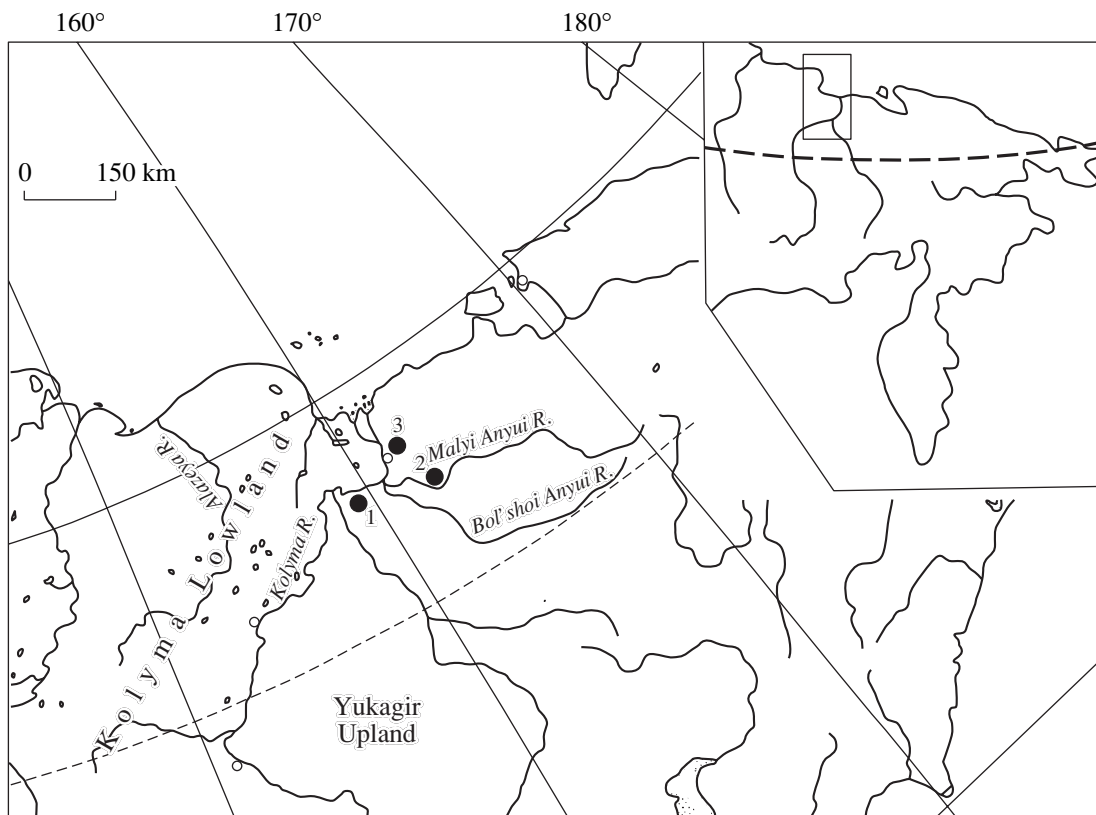


Fig. 1. The Duvannyi Yar (1), Zelenyi Mys (2), and Stanchikovskii Yar (3) sites of gophers' burrows studied in this work.

As is shown earlier (Gubin et al., 2003; Zanina, 2005), burrow chambers have been formerly situated 60–80 cm below surface of that time, and samples of host deposits have been collected respectively 60–80 cm above the burrow's level.

The burrows studied are left by arctic gophers *Citellus (Urocitellus) parri* Richardson, 1825, who populated dry well-drained areas of riverbank or ravine scarps, benches and slopes of southern exposition.

Being of a simple configuration (one- or two-chambered refuges without system of tunnels), the burrows corked up by compact aleurite of uniform composition contain well-preserved biological material. These features suggest a quick transition into fossil state after a short period of occupation by animal. Sublimation ice present in chambers is lacking organic and mineral impurity thus implying a low humidity of deposits that hosted burrows and then turned into permafrost. Seeds

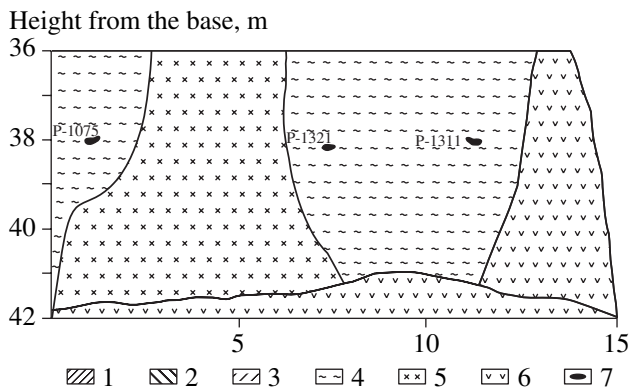


Fig. 2. Sketch of the Duvannyi Yar exposure with fossil burrows: (1) recent soil; (2) paleosol; (3) covering layer; (4) aleurite; (5) ice vein; (6) talus; (7) fossil burrow.

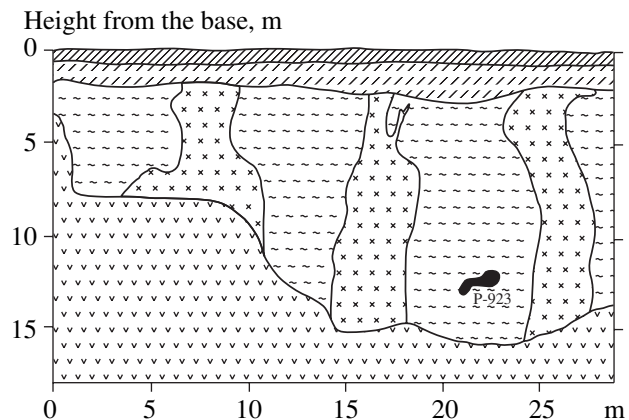


Fig. 3. Sketch of the Zelenyi Mys exposure with fossil burrow (symbols as in Fig. 2).

of higher plants from burrows showed their vital capacity after 30 ka of burial and germinated in laboratory; consequently, it was sufficiently cold at the chamber floor during summer periods, and burrows quickly entered permafrost after burial (Yashina et al., 2002; Gubin et al., 2003). The way of burial and subsequent residence of fossil burrows in permafrost secured perfect preservation of organic material for a long time, which is suitable therefore for paleoreconstructions.

INVESTIGATION HISTORY

Spores and pollen from the Duvannyi Yar reference section of Upper Pleistocene deposits have been studied in detail by Giterman (Kaplina et al., 1978; Giterman, 1985) who presented characterization of palynological assemblages at four horizons of the section (basal aleurites, peat bed, glacial complex, and upper covering bed) and in two alases inset into glacial complex. N.G. Ivanova (Sher, 1971) was first to study palynology of the Stanchikovskii Yar section, and Giterman continued her investigation based on materials collected by Alekseev (Alekseev and Giterman, 1972; Giterman, 1977, 1985). Kaplina et al. (1980) established that exposed at this site are remnants of watershed plain (Edoma complex) and an intervening alas section. When studied the latter, N.O. Rybakova distinguished palynological assemblages corresponding to Zyryanka and Sartan cold arid epochs and to Karga and Holocene epochs of warming. Vasil'chuk (1992) who studied palynology of glacial complex at the Zelenyi Mys site established rhythmic changes in abundance of regional and local components of palynological spectra, which are correlative with formation rhythms of syngenetic frozen deposits. According to dating results obtained for organic remains in host deposits and for repeatedly formed ice veins, the rhythms have been correlated with the Heinrich events, the periods of climatic fluctuations 5 to 10 ka long, which are recognized in marine sediments and core sections of glaciers (Vasil'chuk, 2003).

Paleovegetation of the study region used to be reconstructed based on results of palynological analysis. This approach promising because of a mass abundance of spores and pollen in deposits has some disadvantages nevertheless. These are the pollen transportation for a long distance, unsatisfactory preservation of many palynological taxa, which are hardly identifiable at the species and even generic levels, and decomposition of some pollen genera during fossilization. Reconstructions performed recently in the region based on plant megafossils (fruits, seeds, twigs, leaves) from burrows of animals (Khasanov, 1999; Gubin et al., 2001, 2003; Maksimovich et al., 2003) have some advantages. Plant remains from burrows are well preserved, and their species can be determined in fossil seeds and fragments of vegetative organs. In addition, we can exclude in this case an effect of allochthonous

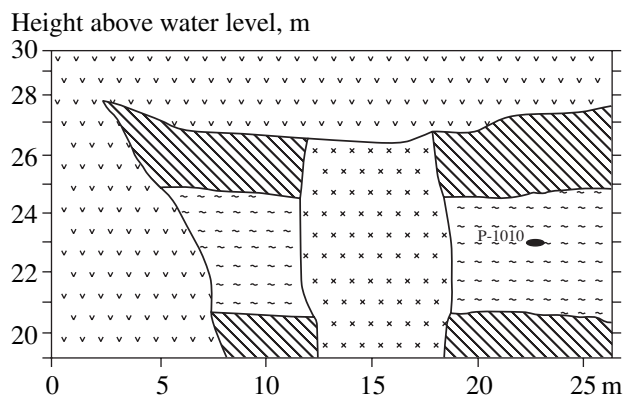


Fig. 4. Sketch of the Stanchikovskii Yar exposure with fossil burrow (symbols as in Fig. 2).

palynological components, because rodents stored food reserves near burrows.

The comparative palynological analysis of sediments filling in and hosting burrows, as well as analysis of rodents coprolites, are of special interest. Dinesman and Metel'tseva (1967) used this approach to study paleosols and coprolites of gophers from Holocene deposits in Buryatia, while Panova et al. (1988) reported on experience to study palynological spectra of buried alluvium and fossilized coprolites of lemmings and voles in the Ob River lower reaches, where they presumably correspond in age to the Zyryanka Horizon. Our paleobotanical research in the Kolyma Lowland is based on parallel investigation of palynomorphs and large plant remains. The results obtained by two methods are complementary, giving general characteristics of vegetation at different levels. The autochthonous plant remains from burrows of small mammals enable reconstruction of local vegetation within a broader floral zone, plant communities of which are encoded in palynological spectra. The comparative analysis of palynological and plant megafossil assemblages, their taxa in common and distinctions in composition at the levels of genera and families are of paleoecological and taphonomic significance. Correctness of results obtained by two approaches can be tested, if megafossils from burrows are studied simultaneously with spores and pollen occurring in deposits filling in and hosting the burrows and in coprolites of small mammals.

INVESTIGATION PROCEDURE

Large plant remains separated from the studied fossil burrows are represented by fruits, seeds, leaves, stems, and rootlets. Most abundant components of megafossil assemblages are fruits and seeds. Since they are as abundant in average as 600 to 800 thousand specimens per a burrow, the relative occurrence frequency of individual taxa is determined in the following mode (Table 1): (+) single or rare, less than 10 specimens;

(++) frequent, 10–50 specimens; (+++) abundant, more than 50 specimens. In burrows P-1010, P-1311, and P-1321 (nested chambers), there is detected the nest substrate (stems of Gramineae and Cyperaceae, twigs and leaves of shrubby taxa, remains of mosses), and components of substrates are quantified in the same mode as carpological remains.

Spores and pollen are macerated from samples applying the procedure suggested by V.P. Grichuk and widely used in practice of many palynological laboratories (*Pollen Analysis*, 1950; *Paleopalynology*, 1966). Microfossils are identified and counted under microscope LOMO MICMED 2 under magnification of 400 to 600 times. According to gradation suggested by Romanovskaya and Kruchinina (1977), the samples studied are well (more than 200 grains per a slide) or moderately (100 to 200 grains per a slide) saturated with spores and pollen. In each slide, we counted 200–250 palynomorphs and then examined the rest of macerated material in order to detect the taxa missed. The calculated percentages characterize proportions of arboreal and fruticose taxa in this pollen group as a whole and occurrence frequency of families or genera and species, if they are identifiable, in the groups of herbaceous and fruticose pollen. Percentages of sporiferous plants are calculated relative to the total amount of spores. For any group consisting of less than 50 grains, percentages of taxa have not been calculated.

RESULTS AND DISCUSSION

Taxonomic composition, occurrence frequency and ecological characteristics of plant megafossils from the burrows studied are presented in Table 1 (taxa are determined by S.V. Maksimovich, IPBPSS RAS). Pollen of herbs is dominant in all palynological spectra; spores are at the second place, pollen of shrubs and trees at the third one. An exception is spectrum in sediments from burrow P-923, in which arboreal pollen is more abundant than spores.

General points to be mentioned based on quantitative and qualitative characters of palynological spectra (Table 2) are as follows.

(1) Spectra in deposits hosting burrows P-1075 and P-1311 at the Duvannyi Yar site are close in composition, being dominated by herbaceous pollen (Gramineae are dominants in this group) and by green mosses among sporiferous taxa. Host sediments of burrow P-1010, the Stanchikovskii Yar site, yielded a comparable spectrum though with greater percentages of shrub taxa (*Salix*, *Alnus*, *Betula nana*).

(2) A considerable proportion of arboreal and shrub pollen is established in sediments from burrows P-1311 (Duvannyi Yar site) and P-923 (Zelenyi Mys site). In spectra of sediments from burrows P-1075 and P-1311, the Duvannyi Yar site, the group of herbaceous taxa is dominated by *Artemisia* and Caryophyllaceae. Sediments from burrow P-1010, the Stanchikovskii Yar

site, are close in composition of spectrum to host deposits, being distinct in low content of arboreal and shrub pollen that occurs as single grains.

(3) *Artemisia* and Caryophyllaceae are dominant in spectra of coprolite samples P-1311, P-1321 (Duvannyi Yar site), and P-1010 (Stanchikovskii Yar site). Spectrum of coprolite sample P-923 (Zelenyi Mys site) dominated in distinction by pollen of Gramineae is lacking Caryophyllaceae and contains single grains of *Artemisia* pollen.

The low content of arboreal and shrub pollen in spectra of coprolites probably means that these plants ceased to bloom by the moment, when animals fed, and pollen, which appeared in their digestive tracts, likely corresponded in composition to components precipitated on eaten plants. Mosses had probably a little significance in ration of animals despite a considerable abundance of relevant spores in spectra of coprolites. Gophers used them to make the nest substrate or caught them occasionally when collected food with impurity of spores. The opinion of Panova et al. (1988) that there are fortuitous components in spectra of coprolites seems to be correct. In distinction from spectra in deposits filling in and surrounding burrows, spectra of coprolites are dominated by pollen of plants, which were in blossom at the time of feeding, and besides pollen of certain plants could be decomposed in digestive tracts under influence of ferments. It is therefore incompletely correct to figure out the consorting connections between plants and animals based on palynological spectra of coprolites, because flowering periods in tundra are very short and animals may consume plants with allochthonous pollen accumulated on leaves. Thus, the ecological analysis of large plant remains from fossil burrows is the only correct method of studying the gophers' diet. Nevertheless, palynological spectra of coprolites are suitable for getting insight into composition of vegetation in a small area, which is less generalized than that recorded in spectra of sediments in and outside burrows.

COMPARATIVE ANALYSIS OF MICRO- AND MACROFLORAS: METHODICAL ASPECTS

When comparing compositions of micro- and macroflora (Table 3), one can see that number of families determined based on spores and pollen is usually greater than amount of families identifiable among plant megafossils. This is primarily a consequence of fossil palynomorphs' preservation in mass. The greatest number of families is established in spectra characterizing sediments from burrows. Families Betulaceae (arboreal and fruticose group), Valerianaceae, Ericaceae, Gentianaceae, Labiatae, and Umbelliferae (herbs and fruticose taxa) are identified in the pollen only. Sporiferous plants Polypodiaceae, Sphagnaceae, Equisetaceae, Lycopodiaceae, Sellaginaceae, and Ophioglossaceae are identifiable exclusively by

Table 1. Large plant remains from Late Pleistocene burrows of gophers, the Duvannyi Yar, Zelenyi Mys, and Stanchikovskii Yar sites in the Kolyma Lowland

Taxa	Type of remains	Duvannyi Yar			Zelenyi Mys	Stanchikovskii Yar
		P-1075	P-1311	P-1321	P-923	P-1010
Pioneering plants of wet habitats						
<i>Arctophila fulva</i> (Trin.) Anderss.	seeds				+++	++
<i>Ranunculus repens</i> L.						
Pioneering plants of dry habitats						
<i>Chenopodium album</i> L.	seeds	+				
<i>Sisymbrium polymorphum</i> (Murr.) Roth.	seeds					++
<i>Draba</i> sp.	seeds	++			+++	
<i>Plantago canescens</i> Adams	seeds	++			+	++
<i>Taraxacum macilentum</i> Dahlst.	seeds	+				+
<i>Potentilla stipularis</i> L.	seeds	+				
Steppe plants						
<i>Allium strictum</i> Schrad.	seeds	+				
<i>Festuca lenescens</i> Drob.	seeds					++
<i>Lychnis sibirica</i> L.	seeds	+				
<i>Papaver</i> sp.	seeds				+	
<i>Poa attenuata</i> Trin.	seeds	+++			+	+++
<i>Poa botryoides</i> (Trin. ex Griseb.) Roshev	seeds	+++				+++
<i>Silene repens</i> Patrin	seeds				+	
<i>Silene stenophylla</i> Ledeb.	seeds	+++			+++	++
Mesopsychrophutes						
<i>Arctous alpina</i> L.	seeds				+	+
<i>Astragalus alpinus</i> L.	seeds		+			
<i>Bromopsis pumPELLIANA</i> (Scribn.) Holub	seeds				+	
<i>Sanguisorba officinalis</i> L.	seeds					++
<i>Larix cajanderi</i> Mayr	seeds				+	
Psychrophytes						
<i>Bistorta vivipara</i> (L.) S.F. Gray	seeds		++		+++	
<i>Carex bonanzensis</i> Britt.	fruits		++			
<i>Carex concolor</i> R. Br. (<i>C. stans</i> Drej.)	fruits				++	+
<i>Carex norvegica</i> Retz.	fruits	+				
<i>Carex vesicata</i> L.	fruits		++			
<i>Myosotis asiatica</i> Schischk. Et Serg.	seeds				+	
<i>Poa arctica</i> R.Br.	seeds					++
<i>Polemonium acutiflorum</i> Willd. ex Roem. et Schult.	seeds				+	
<i>Potentilla nivea</i> L.	seeds		+++	+++	+++	++
<i>Rumex arcticus</i> Trautv.	seeds	+			+	++
<i>Pedicularis kolymensis</i> A. Khokhr.	seeds					+
<i>Salix krylovii</i> E. Wolf						+
Psychrohalophytes						
<i>Puccinella hauptiana</i> V. Krecz.	seeds					++
Mosse						
<i>Aulacomnium palustre</i> var. <i>imbricatum</i> Hedw.	vegetative parts					+
<i>Polytrichum juniperum</i> Hedw.	vegetative parts					+
Remains of Gramineae and forbs			+++	+++		+++
<i>Carex</i> sp.	cloves			+	+	
<i>Salix</i> sp.	pod, leaves, twigs			+++	+++	

Note: Classification of vascular plants after Cherepanov (1995); mosses after Savich-Lyubitskaya and Smirnova (1970).

Table 2. Spore and pollen taxa from late Pleistocene burrows of gophers, the Duvannyi Yar, Zelenyi Mys, and Stanchikovskii Yar sites in the Kolyma Lowland

Taxa	Duvannyi Yar							Zelenyi Mys		Stanchikovskii Yar		
	P-1075		P-1311			P-1321		P-923		P-1010		
	HD	BD	HD	BD	C	BD	C	BD	C	HD	BD	C
Arboreal and fruticose plants	3.4	7.4	14.8	21.6	3.8	5.9	3	30.2	5.9	25	7.5	5.2
<i>Pinu pumila</i> Regel.	–	–	–	–	–	–	–	9.9	–	–	–	–
<i>Pinus</i> s/g <i>Haploxyylon</i>	+	+	–	24.4	+	–	+	42.2	–	9.8	+	–
<i>Pinu</i> s/g <i>Diploxyylon</i>	–	–	–	–	–	–	–	2.8	–	–	–	–
<i>Larix</i> sp.	–	+	–	8.9	+	–	–	7	–	–	–	–
<i>Salix</i> sp.	–	+	+	6.7	–	+	+	15.5	–	17.7	+	+
<i>Alnaster fruticosus</i> Ledeb.	–	–	+	4.4	–	+	+	1.4	+	3.9	–	+
<i>Alnaster</i> sp.	+	+	+	17.9	+	+	–	11.3	+	25.5	+	+
<i>Betula</i> sect. <i>Albae</i>	–	–	–	11.1	–	–	–	–	–	3.9	–	–
<i>Betula nana</i> L.	+	+	+	22.2	+	+	+	9.9	+	35.3	+	+
<i>Betula exilis</i> Sukacz.	–	–	+	4.4	–	–	–	–	–	3.9	–	–
Herbaceous and fruticulose plants	71.1	80.5	47	50.5	71.1	62.9	69.4	46.8	65.2	46.6	74.1	62.7
Poaceae gen. indet.	96.6	56.6	82.4	35.1	13.3	82.7	4.4	79.1	94.7	82.1	91	45.9
<i>Lychnis</i> sp.	–	0.6	–	2.9	1.3	–	4.4	–	–	1	–	0.7
<i>Minuartia</i> sp.	–	–	1	–	–	–	2.2	–	–	–	–	–
<i>Silene</i> sp.	–	0.6	–	–	–	–	–	–	–	–	–	–
<i>Stellaria</i> sp.	–	–	–	8.5	4	3.1	7.4	–	–	–	–	5.4
Caryophyllaceae gen. indet.	0.7	32.4	1	11.4	18.7	3.1	47.1	0.9	–	3.2	–	31.7
<i>Artemisia</i> sp.	2	6.9	3.9	20	54	7.1	22.8	10.9	0.8	7.4	1.8	9
<i>Senecio</i> sp.	–	0.6	–	1	–	–	3.7	0.9	1.5	–	3	–
Compositae gen. indet.	–	–	3.9	4.8	–	0.8	3.7	4.6	–	2.1	–	–
Cyperaceae gen. indet.	–	1.7	2.9	7.6	–	–	–	–	–	3.2	2.4	0.7
<i>Valeriana capitata</i> L.	–	–	–	–	–	2.4	2.2	–	–	–	–	0.7
<i>Draba</i> sp.	–	0.6	–	–	–	–	–	1.8	0.8	–	–	–
<i>Oxyria</i> sp.	–	–	1	–	–	–	–	–	–	–	–	–
<i>Potentilla</i> sp.	–	–	–	1	3.3	–	0.7	–	2.2	–	0.6	3
<i>Polemonium</i> sp.	–	–	–	–	0.7	0.8	0.7	–	–	–	–	0.7
Polygonaceae gen. indet.	–	–	–	–	–	–	–	–	–	–	0.6	–
Ericaceae gen. indet.	–	–	–	1	–	–	–	1.8	–	–	–	–
Gentianaceae gen. indet.	–	–	–	–	–	–	–	–	–	–	–	0.7
Labiatae gen. indet.	–	–	–	–	–	–	–	–	–	–	–	1.5
Leguminosae gen. indet.	0.7	–	1	1.9	4	–	–	–	–	–	0.6	–
Ranunculaceae gen. indet.	–	–	2.9	2.9	0.7	–	0.7	–	–	1	–	–
Umbelliferae gen. indet.	–	–	–	1.9	–	–	–	–	–	–	–	–
Sporiferous plants	25.5	12.1	38.2	27.9	25.1	31.2	27.6	23	28.9	28.4	18.4	32.1
Bryales	96.2	+	76	55.2	90.5	46	72.3	42.7	88.1	39.6	+	82.3
<i>Asplenium</i> sp.	–	–	–	3.4	–	–	–	–	–	–	–	–
Polypodiaceae gen. indet.	–	+	12	15.6	5.7	42.9	20.5	9.3	3.4	29.3	+	11.8
<i>Sphagnum</i> sp.	1.9	+	4.8	3.4	1.9	6.3	1.8	11.1	5.1	17.2	+	1.5
<i>Equisetum</i> sp.	1.9	–	–	3.4	–	–	1.8	1.8	1.7	–	–	–
<i>Lycopodium alpinum</i> L.	–	–	2.4	–	–	1.6	–	1.8	1.7	3.5	–	–
<i>L. anceps</i> Wallr.	–	–	–	–	–	–	–	5.6	–	–	–	–
<i>L. pungens</i> La Pyl.	–	–	–	–	–	–	–	1.8	–	–	–	–
<i>Lycopodium</i> sp.	–	–	2.4	–	–	1.6	1.8	16.7	–	6.9	–	–
<i>Selaginella sibirica</i> (Milde) Hieron	–	+	2.4	15.6	1.9	1.6	1.8	–	–	3.5	–	2.9
<i>Selaginella</i> sp.	–	–	–	3.4	–	–	–	7.4	–	–	–	–
<i>Botrychium lunaria</i> Sw.	–	–	–	–	–	–	–	1.8	–	–	–	1.5

Note: Abbreviations: (HD) host deposits of burrows; (BD) burrow deposits; (C) coprolites.

Table 3. Amounts of species, genera and families in micro- and macrofloras from late Pleistocene burrows of gophers, the Duvannyi Yar, Zelenyi Mys, and Stanchikovskii Yar sites in the Kolyma Lowland

Taxa	Duvannyi Yar						Zelenyi Mys		Stanchikovskii Yar			
	P-1075		P-1311			P-1321		P-923		P-1010		
	HD	BD	HD	BD	C	BD	C	BD	C	HD	BD	C
Macroflora												
Families		10		4		3		14				13
Genera		11		4		3		16				17
Species		11		5		1		14				19
Microflora												
Families (in total)	13		19			15		15		20		
	8	11	13	16	12	11	15	15	9	12	11	15
Genera (in total)	13		17			16		14		15		
	6	12	9	13	11	10	16	13	9	9	8	12
Species (in total)	2		5			5		7		6		
	1	2	5	4	2	5	4	7	3	4	1	5
Taxa identified by two methods simultaneously												
Families	5		4			2		7		7		
Genera	3		1			2		4		2		
Determined in total												
Families	18		19			15		22		26		
Genera	21		20			17		26		31		

Note: Abbreviations as in Table 2.

palynological method. The only exclusion is group of green mosses whose remains found in the burrow P-1010 correspond to the class Bryales and cannot be determined more precisely. Herbaceous families Boraginaceae, Papaveraceae, Plantaginaceae, Liliaceae, Chenopodiaceae, and Scrophulariaceae are distinguished in macerates from carpolites and among vegetative remains. Amount of families identified by two methods simultaneously varied from two to seven in each series of samples. These are Salicaceae, Poaceae, Caryophyllaceae, Polygonaceae, Cyperaceae, Cruciferae, Compositae, Rosaceae, Leguminosae, and Pinaceae (the last family is found in Sample P-923). Pollen of Poaceae, Caryophyllaceae and Compositae is present in spectra of deposits hosting and filling in the burrows (Caryophyllaceae are missing however from the burrow material of the Stanichkovskii Yar site), frequently being dominant. Families Cruciferae and Rosaceae are encountered in spectra of burrow deposits and coprolites, while pollen of Pinaceae, Salicaceae, Polygonaceae, Cyperaceae and Leguminosae occurs in three types of spectra without regularity.

Amount of plant genera determined by palynological method in samples from the Duvannyi Yar site is greater than number of genera identifiable here in megafossils (Plate 3). In burrows of Zelenyi Mys and Stanchikovskii Yar sites, megafossil genera exceed by

two the number of genera determined in spores and pollen. Genera *Pinus*, *Alnaster*, *Betula*, *Minuartia*, *Stellaria*, *Senecio*, *Valeriana*, *Oxyria*, *Sphagnum*, *Equisetum*, *Lycopodium*, *Selaginella*, and *Botrychium* are determined by palynological method only; genera *Allium*, *Arctophila*, *Arctous*, *Bromopsis*, *Festuca*, *Pedicularis*, *Puccinella*, *Plantago*, *Poa*, *Rumex*, *Sanguisorba*, *Sisymbrium*, *Carex*, *Taraxacum*, *Chenopodium*, *Bistorta*, *Astragalus*, *Myosotis*, *Papaver*, *Ranunculus* (herbs), *Aulacomnium*, and *Polytrichum* (mosses) by analysis of megafossils. Number of genera identified simultaneously by two methods is from one to four in each series of samples; these are *Salix*, *Potentilla*, *Draba*, *Lychnis*, *Silene*, and *Larix*, the latter from Sample P-923. By palynological method, we discovered genera in common among micro- and megafossils. An exclusion is pollen of *Salix* present in the burrow's host deposits of the Stanchikovskii Yar site (17.7%) occurring as well in coprolites and burrow fill, though as single grains only.

Plant remains from burrows, where they are perfectly preserved, are identifiable as a rule at the generic and species levels. The poorly preserved pollen retaining indistinct morphological features characteristic of genera and species is classed only with families (Poaceae, Cyperaceae, Polygonaceae, Ericaceae, Gentianaceae, Leguminosae, Labiatae, Ranunculaceae,

Umbelliferae). Species identified among better preserved spores and pollen are *Alnaster fruticosus* Ledeb., *Betula nana* L., *B. exilis* Sukacz., *Valeriana capitata* L. (the only species of herbs determinable in palynological spectra), *Lycopodium alpinum* L., *L. anceps* Wallr., *L. pungens* La Pyl., *Selaginella sibirica* (Milde) Hieron, and *Botrychium lunaria* (L.) Sw.

Data on palynological and megafossil plant assemblages from five borrows buried in Upper Pleistocene deposits of the Kolyma Lowland reveal certain regularities in distribution of plant families and genera in deposits under consideration.

The spore-pollen spectra of tundra type characterize severe climate with intense circulation of cold air masses and short vegetation period of plants. Under these conditions, pollen productivity of many plants is low, and frequently concentration of pollen transported from remote sources is relatively high in palynological spectra (Vasil'chuk, 2002). In the studied spectra, pollen of anemophilous genera *Pinus*, *Betula*, and *Alnaster* likely belongs in part to this type. Kabailene (1976, 1983) attributed pollen of pine, birch, and alder, a relative of *Alnaster*, to the group of long-transported pollen. Development of dwarfed pine forest is inferable from palynological spectrum of sample P-923, the Zelenyi Mys site (a part of pine pollen belonging to subgenus *Haploxylon* is of this origin probably).

As for pollen of the other two genera determined in the group of arboreal and shrub taxa, we should note the following. Pollen *Larix* sp. is either missing from spectra, or occurs as single grains except for sediments from burrows P-1311 and P-923 (remains of larch wood were also found in the latter). Pollen of this genus hardly surviving fossilization cannot be carried for a long distance, and its presence in those burrows suggests existence of thin larch forests around. In palynological spectra of the Duvannyi Yar site, content of entomophilous genus *Salix* is low, lower than that of anemophilous genera, although abundant willow leaves have been found in burrow P-1321. In sediments filling in burrow at the Zelenyi Mys site and hosting burrow at the Stanchikovskii Yar, concentration of *Salix* pollen is higher (15.5 and 17.7% respectively), and in burrows we detected seeds, seed pods, and twigs of this genus. Analysis of recent and subrecent materials (Makhova, 1971; Smirnova, 1971) showed that concentration of *Salix* pollen in palynological spectra is considerably lower than actual percentage of this taxon in vegetation cover, although this pollen is more resistant to decomposing alkaline medium than pollen of alder and birch (Tyuremnov and Berezina, 1965). This is probably a consequence of its morphology (small grains often bounded together) and entomophily, because in opinion of Kozlyar (1985) insects collect the basic mass of pollen from entomophilous plants thus diminishing content of relevant taxa in fossil palynological spectra.

Kats and Fedorova (1983) believe that herbaceous pollen is of prime significance for paleogeographic

interpretations of palynological spectra produced by tundra vegetation. Occurrence of this pollen even in a small amount evidences without doubts that herbs were components of local vegetation. In tundra vegetation adapted to severe environments, pollen productivity of plants depends on conditions during their vegetation period and character of pollination. In response to unfavorable conditions, tundra plants can turn to vegetative reproduction and cause appearance of palynological spectra inconsistent with actual composition of vegetative cover. A long flowering period of anemophilous (up to five days) and entomophilous (up to eight and more days) plants is suitable for a homogeneous dispersal of pollen, while cleistogamy characteristic of some genera under unfavorable conditions and reducing pollen productivity leads to lower concentration of their pollen in deposits. The last feature is typical of some Cyperaceae, Gramineae and other genera (Tikhmenev, 1981; Vasil'chuk, 2005).

Prevalence of anemophilous Gramineae and significant content of *Artemisia* pollen also spread by wind are characteristic of herbaceous and fruticose groups in the studied palynological spectra (an exception is spectrum of coprolites from burrow P-1321, which is dominated by Caryophyllaceae). Pollen of high-productive Gramineae and *Artemisia*, which has smooth exine without sculpturing elements, is quickly dispersing in air for a long distance. Cyperaceae and several genera of Polygonaceae, which are identified in the studied samples, also belong to anemophilous plants.

The other genera and families recognizable in herbaceous pollen group correspond to entomophilous plants. Low concentrations of these taxa detected predominantly in coprolites and sediments from burrows do not reflect probably the actual role of respective plants in the vegetative cover, being determined by the pollen morphology and transport. Being often sculptured with tubercles, pollen of entomophilous herbaceous plants is either relatively large (*Valeriana*, some Compositae genera), or small, clustered into nubbins (Leguminosae). Even single found grains of entomophilous pollen signify that relevant plants were components of plant groupings. It should be noted as well that pollen of Rosaceae can be quickly destroyed during oxidation (Sangster and Dale, 1964; Vronskii and Fedorova, 1981). This pollen with very thin delicate exine occurs in the spectra studied as single grains in contrast to rather abundant remains of Rosaceae species *Potentilla nivea* L., which are found in burrows. Pollen of Liliaceae and Papaveraceae is also poorly retainable in fossil state. According to Kats and Fedorova (1983), pollen grains of some Umbelliferae, Boraginaceae, and Cruciferae growing in tundra are scarce and small, produced by 11% of flowers only.

It is clear from comparison of palynological spectra with megafossil plant assemblages that predominance of Gramineae in the former is consistent with abundance of these plant remains found in fossil burrows.

Like palynological spectra, plant assemblages from burrows contain noticeable amount of Cyperaceae and Polygonaceae, and these plants definitely existed in vegetative cover despite low abundance of their pollen in the spectra. Large plant remains of *Artemisia* whose pollen is present in all the spectra, frequently in remarkable concentration, have not been found in burrows. As plants of this genus produce a large amount of pollen, it probably was concentrated on the other plants consumed by animals or used to floor the nest. Seeds and pods of Caryophyllaceae whose pollen prevails in spectra characterizing sediments and coprolites from burrows P-1010 and P-1075 are abundant or frequent in these burrows among plant megafossils. In burrows P-1321 and P-1311, pollen of this family is also rather abundant, and relevant plants apparently existed in vegetative cover, although their large remain have not been encountered here. Abundant *Silene* remains are found instead in burrow P-923, although content of Caryophyllaceae pollen is less than 1% in sediments from this burrow, while in coprolites it is completely absent. Genera of other entomophilous families (Labiatae, Umbelliferae, Leguminosae, Gentianaceae, Ranunculaceae, Polemoniaceae, Ericaceae) whose pollen usually occurs as single grains in palynological spectra were components of vegetation because their representatives are identified among megafossils from burrows. These are species *Arctous alpina* L. (Ericaceae), *Astragalus alpinus* L., and *Polemonium acutiflorum* Willd. ex Roem. et Schult.

Pollen of most herbaceous genera present among megafossils from burrows is missing from palynological spectra. This is likely a consequence of entomophily and vegetative reproduction typical of many herbs (in particular, genera *Sanguisorba*, *Taraxacum*, *Allium*, and others are entomophilous). In addition, pollen of Liliaceae, Papaveraceae, and Rosaceae is hardly surviving fossilization, and pollen morphology of several genera is inadequately studied so far. Interpreting proportions of taxa in carpolites from fossil burrows, one should take into account conclusion of Khasanov (1999) who showed that their content in floral assemblages depends on forage selectivity of animals and on ripening dates of fruits (for instance, Gramineae ripen later than Cyperaceae and some other herbs). Consequently, percentages of particular taxa in carpolites do not reflect most likely the real content of corresponding plant genera within the forage area. However, assemblages of plant genera occurring in present-day burrows appear to be representative enough for getting an insight into general character of vegetation in habitat areas of rodents (Maksimovich et al., 2003; Zanina, 2005).

As is mentioned above, taxa of sporiferous plants are identified mostly by palynological method, and only remains of green mosses have been encountered among plant megafossils from burrow of the Stanchikovskii Yar site. Spores of Aspleniaceae, lycopods, and *Selaginella sibirica* (Milde) Hieron are relatively large,

having sculptured exine with tubercles and processes, and cannot be transported for a long distance. In general, spores survive fossilization better than pollen, because their walls contain more sporopollenin and less cellulose than pollen walls (Havinga, 1964, 1967; Kondratene, 1976; Petros'yants et al., 1990). That is why we identified many sporiferous plants at the species level (Table 2) and can be sure that they were present in plant groupings of the study region despite absence of relevant megafossils.

Animals utilizing spores and pollen as food influence of course their abundance in sediments. For instance, Berezina and Tyuremnov (1973) showed that life activity of earthworms is baneful for pollen, because they consume it and destroy indirectly by alkalizing and aerating soil, creating besides comfortable conditions for development of microflora.

Thus, palynological spectra and plant megafossils studied in and around five fossil burrows in the Kolyma Lowland are close enough in sets of identified plant families, being less similar in terms of generic taxonomic composition. Qualitative and quantitative differences between separate assemblages are explainable by several reasons. These are (1) biological peculiarities of plants (chemical composition of spore and pollen walls determining different extent of their preservation and unequal capability of plants to produce spores and pollen, which are different in specific weight and can be transported for different distances); (2) different character of fossilization of microscopic and large plant remains; (3) different genesis of microflora (allochthonous) and plant megafossils (autochthonous); (4) inadequately known morphology of separate spore and pollen taxa.

RECONSTRUCTION OF VEGETATION AND CLIMATE

Based on plant remains from burrows (P-1010, P-1075, and P-923 included) in Upper Pleistocene deposits of the Kolyma Lowland, Gubin et al. (2003) arrived at the conclusion that landscape of humid to dryer tundra with marshes, which existed here at that time, included areas of pioneering and steppe vegetation. Khasanov (1999) who reconstructed paleolandscapes based on plant remains from burrow P-923 suggested that surrounding vegetation corresponded to a thin larch forest or to plant communities of larch woodland. According to palynological data, *Salix*, *Alnaster*, and *Betula nana* were here the characteristic components of shrubby level that was underdeveloped or formed in places. Considering herbs remains of two ecologic groupings found in the burrow, Khasanov suggested that humid areas of mesophytic vegetation with meadow elements alternated here with dryer areas of steppe-like vegetation.

Giterman (1975, 1985) used the term tundra-steppe to characterize vegetation of the Karga time in lower

reaches of the Kolyma River, which were populated mostly by Gramineae and *Artemisia* but included motley-grass areas with diverse ecologic groupings of herbaceous plants. In opinion of Yurtsev (1972), the term tundra-steppe is conventional, inadequately characterizing tundra landscapes of the Late Pleistocene, because tundra-steppe communities occupied the intrazonal but not basic position in vegetative cover. Representatives of steppe vegetation penetrated in tundra zone along southern slopes and xerothermic biotopes. Proportion of grasses increased because of growing meadow areas and conversion of valley bogs into grazing land.

Summarizing earlier and new paleobotanical data obtained for the studied sites, we believe that landscapes around the burrows corresponded to humid and dryer tundra with local areas populated by dwarf-birch thickets, steppe and pioneering vegetation. Judging from plant megafossils occurring in burrows, psychrophilic *Potentilla nivea* L. and *Bistorta vivipara* (L.) S.F. Gray were most widespread species of vegetation. *Carex vesicata* L., *C. bonanzensis* Britt., *Salix krylovii* E. Wolf, *Alnaster*, *Betula nana*, *B. exilis* Sukacz., and *Valeriana capitata* L. identified in palynological spectra presumably grew in moistened marshy areas above thawing ice veins. Vegetation of moistened tundra meadows included *Poa arctica* R. Br., *Rumex arcticus* Trautv., *Carex norvegica* Retz., *polemonium acutiflorum* Willd. ex Roem et Schult., *Miosotis asiatica* Schischk., *Sanguisorba officinalis* L., *Astragalus alpinus* L., and *Bromopsis pumpelliana* (Scribn.) Holub, while *Puccinella hauptiana* V. Krecz. grew on humid brackish soil. Exposed slopes were populated by *Arctous alpina* L. and *Selaginella sibirica* (Milde) Hieron. Diverse Gramineae (*Poa attenuata* Trin., *P. botryoides* (Trin. ex Griseb.) Roshev, *Festuca lenescens* Drob.) and Caryophyllaceae (*Lychnis sibirica* L., *Selene stenophylla* Ledeb., *S. repens* Patrin, *Paraver* sp., *Allium strictum* Schrad.) were widespread in steppe-like meadow areas. Wormwood having a deep-penetrating root system and producing relatively much pollen grew in abundance on drained slopes, as one can judge from its pollen frequent or numerous in palynological spectra. Areas of disturbed (synlithogenic) soil layer were habitats of pioneering vegetation. Existence of dry, poorly overgrown areas in landscapes is evident from palynological spectra containing spores of *Selaginella sibirica* and *Lycopodium alpinum* and from plant remains of *Draba*, *Sisymbrium polymorphum*, *Chenopodium album*, *Plantago conescens*, *Potentilla stipularis*, and *Taraxacum macilentum* found in burrows. Judging from analysis of plant megafossils, the considered ecotopes surrounded burrows P-1075 (Duvannyi Yar site) and P-1010 (Stanchikovskii Yar site). Pioneering species of wet habitats were represented by *Ranunculus repens* and *Arctophila fulva* whose remains are found respectively in burrows P-923 (Zelenyi Mys site) and P-1010 (Stanchikovskii Yar). It is difficult to interpret ecology of Gramineae, Cyperaceae, Caryophyl-

laceae, Compositae, Leguminosae, Ranunculaceae, Polygonaceae, Gentianaceae, Labiatae, Ericaceae, and some other families, which are represented by many pollen species of plants characteristic of diverse ecotopes. Nevertheless, their occurrence is compatible in general with the reconstruction presented above. Green mosses and to a lesser extent Aspleniaceae prevailed among sporiferous plants. Sphagnum bogs were not widespread. Larch forests of island type likely appeared in most favorable habitats inferable from palynological data on the Zelenyi Mys site and plant megafossils found here. An area of pine elfin wood probably existed as well at this site adjoining foothills of mountains, which fringe in the south the Kolyma valley. A considerable part in vegetation around burrow P-923 belonged to lycopods, in particular, to *Lycopodium alpinum* that grew on dry rubble slopes, to *Lycopodium pungens* that populated wet larch forests, brush thickets and dry slopes, and to *Lycopodium anceps* characteristic of coniferous forests.

The comprehensive paleobotanical analysis showed that tundra landscapes were typical of the study region as a whole, while tundra-steppe plant communities grew on southern slopes and in xerothermic ecotopes. Rather widespread areas with disturbed or underdeveloped soil layer were colonized by pioneering vegetation. The results obtained confirmed conclusion of Yurtsev (1972) who suggested that steppe plant groupings occupied intrazonal position. During the late Karga time, winters were freezing, with thin snow cover; warm and dry summers were short but lasted long enough for ripening of seeds. As a result, thin forests, trees and shrubs of floodplains were displaced northward relative to their present-day position. Areas of pine elfin wood became reduced up to complete elimination on southern slopes because of thin snow cover and low winter precipitation. Marshes occupied predominantly the relief depressions.

CONCLUSIONS

The analyzed materials from fossil rodents' burrows buried in the glacial complex of the Kolyma Lowland elucidated natural environments of the Late Pleistocene in the study area. Main results of this work are as follows.

(1) When studying the Upper Pleistocene deposits in the Kolyma River lower reaches, we carried out for the first time the comparative analysis of palynomorphs and plant megafossils in host sediments and materials filling in fossil burrows of gophers, their coprolites included. Taxonomic composition of palynological spectra in sediments from burrows is more diverse than in deposits hosting the burrows. Analyzing palynological remains in coprolites, we get insight into composition of the in situ vegetation that grew in habitat areas of animals. However, it is to some extent misleading to judge from palynological spectra in coprolites about plants the animals lived on, because the eaten plants

could contain the allochthonous pollen precipitated on leaves, on the one hand, and pollen of many genera could be destroyed under influence of ferments in digestive tracts of animals, on the other.

(2) Based on palynological data and analysis of megafossils, we determined the following taxa: *Salix*, *Lychnis*, *Silene*, *Draba*, *Potentilla*, *Larix*, Poaceae, Polygonaceae, Cyperaceae, Compositae, and Leguminosae. Amount of genera identified simultaneously by two methods is from one to four in each series of studied samples. Among micro- and megafossils from burrow sediments and coprolites, there are detected genera in common by palynological method (an exception is pollen of *Salix* occurring as well in deposits hosting the burrow of the Stanchikovskii Yar site). Genera *Pinus*, *Alnaster*, *Betula*, *Minuartia*, *Stellaria*, *Senecio*, *Valeriana*, *Oxyria*, families Valerianaceae, Ericaceae, Gentianaceae, Labiatae, Umbelliferae, and sporiferous taxa Polypodiaceae, Equisetum, Sphagnum, Lycopodium, Selaginella (green mosses excluded) are established in palynological spectra only. Herbaceous genera *Poa*, *Bromopsis*, *Festuca*, *Puccinella*, *Arctophila*, *Rumex*, *Plantago*, *Sisymbrium*, *Sanguisorba*, *Pedicularis*, *Arctous*, *Carex*, *Taraxacum*, *Allium*, *Chenopodium*, *Bistorta*, *Astragalus*, *Myosotis*, *Papaver*, *Ranunculus*, and mosses *Aulacomnium* and *Polytrichum* are detected solely in burrows. Factors responsible for qualitative and quantitative differences in taxonomic compositions of palynological and megafossil assemblages are (a) biological peculiarities of plants, (b) different character of fossilization of palynomorphs and megafossils, (c) different genesis of assemblages, and (d) inadequately known morphology of certain spore and pollen taxa.

(3) The comprehensive analysis of palynomorphs and plant megafossils from burrows in the Upper Pleistocene deposits of the Kolyma Lowland leads to the conclusion that the study region was occupied at that time by plant communities of humid to dryer tundra and tundra marshes with separate areas of dwarf birch thickets and pioneering steppe vegetation. Paleobotanical data on burrow of the Zelenyi Mys site suggest distribution of thin larch forests around.

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