

THE POSSIBILITIES OF RECONSTRUCTING THE COMPOSITION OF VEGETATION COMMUNITIES ON THE BASIS OF CONJUGATED PALYNOLOGICAL, PHYTOLITH AND CARPOLOGICAL ANALYSES FOR LOWER COURSE AREA OF THE KOLYMA RIVER

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The results of investigation of the phytofossil complexes (spore-and-pollen spectra, phytoliths and seeds) from surface samples characterizing different plant associations from the area of the Kolyma lower course are presented. The peculiarities of fossilization of vegetative micro remnants in various ecotopes of the permafrost zone have been revealed. The formation regularities of the examined complexes and the possibility of combined application of palynological, phytolith and carpological methods for paleoecological reconstructions of the Upper Quaternary deposits in the region have been defined.

Kolyma lower course, recent vegetation, phytolith analysis, palynological analysis, carpological analysis

INTRODUCTION

In view of reconstruction of the vegetation and climate of the Quaternary Period of the north-east of Asia, paleobotanical methods play the leading role. The use of the palynological method is of primary importance, because spores and pollen in the deposits of this age occur everywhere. In interpreting the results of the spore-and-pollen analysis of the deposits of the 'ice complex', a large amount of transported pollen in the spectra, poor preservation or inability of the pollen of some genii to be preserved in the fossil state should be taken into account [Kaplina et al., 1978; Giterman, 1985; Lopatina and Zanina, 2006], as well as re-deposition of palynological remnants considering the sedimentation character in the region. Due to the low temperatures of the active layer and rather low microbial activity, the carpological remnants in the region with the near-surface permafrost are usually well-preserved, which allows identification of plants up to the species level and thus more detailed characterization of the environmental conditions [Maximovich et al., 2007]. The advantage of the carpological method consists also in the fact that carpoids are as a rule autochthonous and provide information about the structure of local communities. Phytoliths are microscopic silicic formations formed in plants in the process of their biological activity. During intracellular deposition of earth silicon, formations emerge repeating the shape of a plant cell and having specific morphology. Practically all their signs (shape, size, color, etc.) carry certain information. Just like spores and pollen, phytoliths are common in Quaternary deposits, but, as opposed to palynological remnants, they are not volatile, so, they

characterize the local elements of plant associations. Phytolith analysis is widely used in studying the history of soil and landscape development [Rovner, 1971; Piperno, 1988; Golyeva, 2001; Kiseleva, 2006]. This method has been used for the first time for the modern deposits of NE Yakutia.

Comparative analysis of subrecent complexes of spores, pollen, phytoliths and seeds is of great paleoecological and taphonomic importance, as it allows the researchers to determine the causes of their similarities and differences at the genus and family levels and to compare them with the producing vegetation. To test compatibility of the considered approaches, data referring to plant remnants are studied from the surface samples including modern vegetation growing on the collection site. The results of palynological, phytolith and carpological analyses complement each other and reflect characteristics of the vegetation which differ by their degree of generalization.

Complex studies of different types of deposits, aimed at reconstructing the vegetation cover of the Late Pleistocene of Beringia [Lopatina and Zanina, 2005, 2006; Zanina et al., 2011, 2013], necessitated implementation of such work for the territory of NE Yakutia. The composition of the spore-pollen spectra of modern deposits of the Kolyma River is provided in the papers by G.M. Savvinova [1980], R.E. Giterman [1985], A.C. Vasil'chuk [2002], O.G. Zanina, D.A. Lopatina et al. [2013, 2014]. A.C. Vasil'chuk considered the specific features of the taphonomy of spores and pollen in the region's deposits.

The objective of the study was to establish the degree of compliance of the complexes of spores, pol-

len, phytoliths and carpoids from the upper mineral horizons of the modern soils in the area of the lower courses of the Kolyma River with the composition of the vegetation forming them. Special attention was paid to determining the composition of the floristic complex transforming into a subrecent state and identifying the objective criteria for reconstructing the vegetation cover based on the composition of phytofossils for the region under study.

MATERIALS AND METHODS OF STUDIES

The area of studies was located in the lower courses of the Kolyma River (68° N, 161° E) (Fig. 1). In this region, the zone of thin larch forests *Larix cajanderi* Mayr starts. The suffruticose tier in them is represented primarily by *Betula exilis* Sukacz., *Salix glauca* L., *Rosa acicularis* Lindl., the subshrubs are

Vaccinium uliginosum L., *Arctous erythrocarpa* Small., *A. alpina* (L.) Niedenzu. The grass cover consists of different varieties of gramineous plants, with *Bistorta vivipara* (L.) Gray, *Antennaria dioica* (L.) Gaertn., *Artemisia arctica* Less., *Potentilla stipularis* L., etc., also present [Kozhevnikov, 1981]. Steppe vegetation is well-developed on the well-warmed steep slopes of southern exposition, represented by different variations of motley grass communities, with participating *Carex pediformis* C.A. Mey., *Calamagrostis purpurascens* R. Br., *Bromopsis pumPELLIANA* (Scribn.) Holub., *Festuca lenensis* Drob., *F. auriculata* Drob., *Poa versicolor* Bess., *Silene linearifolia* Otth, *S. repens* Patrin, *Astragalus alpinus* L., *Artemisia dracunculus* L., *Draba cinerea* Adams, *Thymus serpyllum* L., etc. [Yurtsev, 1981].

The samples were collected under vegetation associations typical of the region in different cenoses: both zonal – pre-tundra thin forests (larch forests),

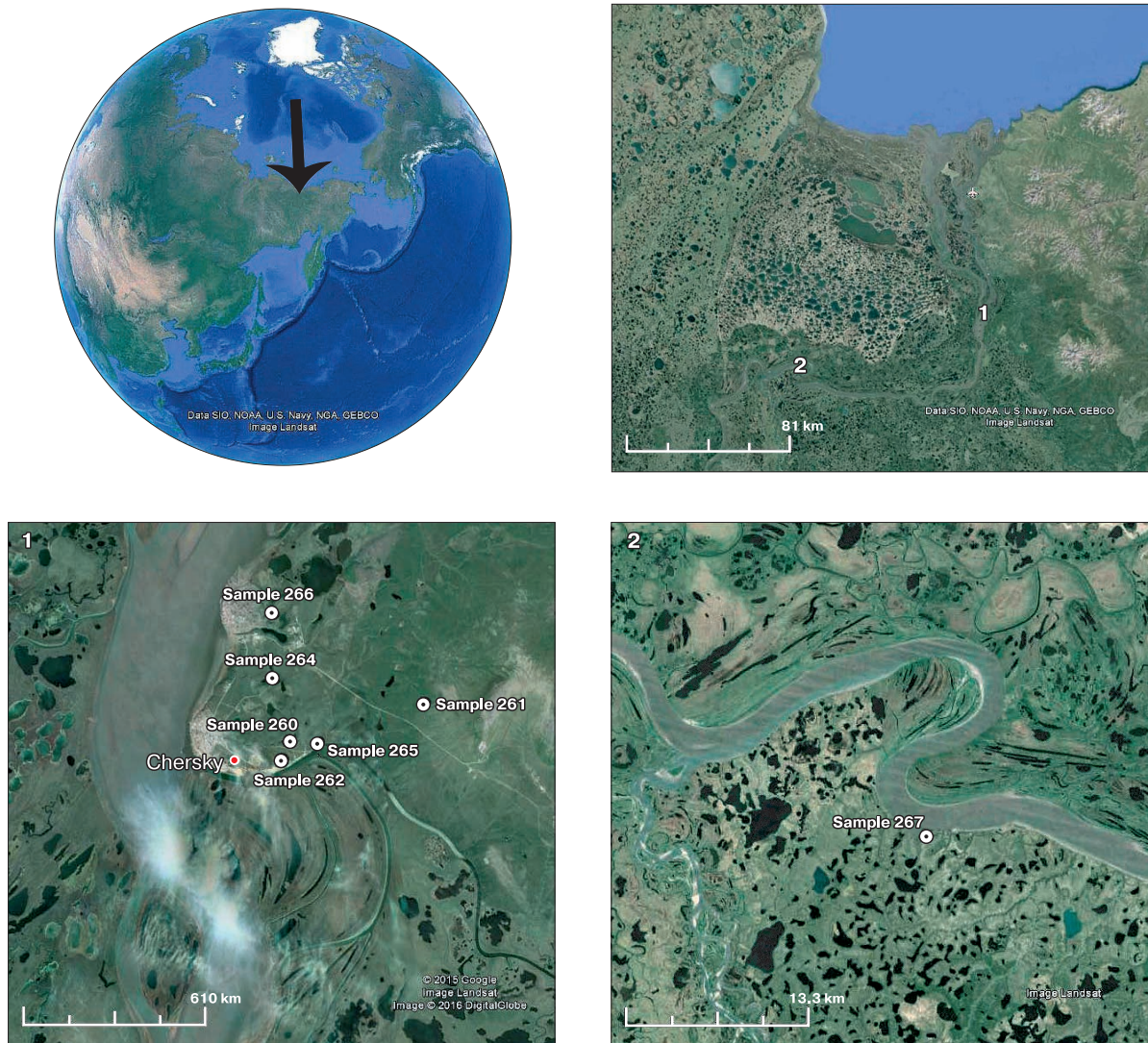


Fig. 1. The map of the key sampling areas 1 and 2.

and intrazonal – steppified and marshy cenoses (Table 1). The samples were taken in the field season of 2003; this was accompanied by the study of the floristic composition of the region's vegetation and of the sampling site. S.V. Maximovich and O.G. Zanina described the vegetation. The samples were taken from the depth of 0–2.5 cm on the site of 1 m² (a test sample was mixed from 20–30 samples). The test samples were sieved through a column of sieves with the mesh sizes ranging from 5 to 0.25 mm. The obtained organic fraction (seeds, fruits, twigs, leaves) were studied with binoculars MBS-9. The carpological remnants were identified by S.V. Maximovich. The test samples were prepared for palynological analysis based on the technique offered by V.P. Grichuk

[*Pollen Analysis, 1950; Paleopalynology, 1966*]. To isolate the components of the light biogenic fraction of the samples (phytoliths, detritus, and tissue and epidermis remnants), heavy liquid (KJ + CdJ) with the density of 2.1–2.2 g/cm was used. The names of modern plant species are given based on S.K. Cherepanov's index [1995].

The data of palynological, phytolith and carpological analyses are difficult to compare quantitatively, as the amount of spores, pollen and phytoliths produced by plants is greater by several orders of magnitude than that of fruits and seeds. In palynological analysis, the ratio of the components of the spore-pollen spectrum is used, with pollen and spores concentration in sediments considered, while in the

Table 1. Data on the surface sample collection sites, the lower course of the Kolyma River

No.	Geographic position	Vegetation	Coordinates		Height a.s.l., m
			N	E	
1	Sample 260 The right basic bank of the Panteleikha River	Fescue-petrophyte-motley grass steppe (projective coverage 60 %, in bare areas – siltstone rubble up to 80–90 %). <i>Festuca lenensis</i> Drobow, <i>Poa attenuata</i> Trin., <i>Carex pediformis</i> C.A. Mey., <i>Dracocephalum palmatum</i> Steph., <i>Thymus diversifolius</i> Klokov, <i>Veronica incana</i> L., <i>Eremogone tschukt-schorum</i> (Regel) Ikonn., <i>Dianthus versicolor</i> Fisch. ex Link, <i>Galium verum</i> L., <i>Pulsatilla multifida</i> (Pritz.) Juz., <i>Potentilla nivea</i> L.	68°44'23.0"	161°23'56.4"	11
2	Sample 265 The right basic bank of the Panteleikha River, opposite the inflow of the affluent of the Ambolikha River	Gramineous-petrophyte-motley grass steppe (projective coverage 50 %) on moving ground. The plants form cushions or small tussocks stabilizing the ground. <i>Dracocephalum palmatum</i> Steph., <i>Thymus diversifolius</i> Klokov, <i>Eremogone tschukt-schorum</i> (Regel) Ikonn., <i>Dianthus versicolor</i> Fisch. ex Link, <i>Festuca lenensis</i> Drobow, <i>Calamagrostis purpurascens</i> R. Br., <i>Pulsatilla multifida</i> (Pritz.) Juz., <i>Potentilla nivea</i> L.	68°44'35.0"	161°25'17.2"	10
3	Sample 266 An outcrop near the settlement of Zeleny Mys	The bottom of a drained lake with growing willow weed. <i>Chamaenerion angustifolium</i> (L.) Scop., <i>Tanacetum vulgare</i> L., <i>Erigeron acris</i> L., <i>Poa pratensis</i> L., <i>Hordeum jubatum</i> (L.) Nevski, <i>Salix glauca</i> L.	68°47'02.3"	161°24'22.2"	8
4	Sample 261 Settlement of Chersky, the western shore of Lake Shchuchye	Sphagnum bog. Growing on the bog hummocks are: <i>Betula exilis</i> Sukacz., <i>Oxycoccus microcarpus</i> Turcz. ex Rupr., <i>Ledum decumbens</i> (Ait.) Lodd. ex Steud., <i>Vaccinium uliginosum</i> L., <i>Chamaedaphne calyculata</i> (L.) Moench., <i>Rubus chamaemorus</i> L., <i>Carex gynocrates</i> Wormsk.	68°44'53.6"	161°23'46.1"	10
5	Sample 262 The right basic bank of the Panteleikha River	Yernik larch forest. <i>Larix cajanderi</i> Mayr, <i>Betula divaricata</i> Ledeb., <i>Salix glauca</i> L., <i>S. pulchra</i> Cham., <i>Ledum decumbens</i> (Ait.) Lodd. ex Steud., <i>Vaccinium uliginosum</i> L., <i>V. vitis-idaea</i> L., <i>Arctous alpina</i> (L.) Spreng., <i>Empetrum nigrum</i> L., <i>E. androgynum</i> V.N. Vassil., <i>Rosa acicularis</i> Lindl., <i>Arctagrostis latifolia</i> R. Br., <i>Equisetum arvense</i> L., <i>Aulacomnium turgidum</i> (Wahlenb.) Schwaegr., <i>Dicranum</i> sp., <i>Cladonia rangiferina</i> (L.) Harm., <i>Peltigera aphthosa</i> (L.) Willd.	68°44'24"	161°23'22"	11
6	Sample 264 Settlement of Chersky, the northeastern slope of Lake Shchuchye	Yernik larch forest. <i>Larix cajanderi</i> Mayr, <i>Betula divaricata</i> Ledeb., <i>Salix glauca</i> L., <i>Ledum decumbens</i> (Ait.) Lodd. ex Steud., <i>Vaccinium vitis-idaea</i> L., <i>Arctagrostis latifolia</i> R. Br., <i>Equisetum arvense</i> L., <i>Aulacomnium turgidum</i> (Wahlenb.) Schwaegr., <i>Dicranum</i> sp., <i>Peltigera aphthosa</i> (L.) Willd., <i>Cladonia sylvatica</i> (L.) Harm., <i>Cetraria cucullata</i> (Bellardi) Ach.	68°44'53.6"	161°23'46.1"	11
7	Sample 267 Duvanny Yar outcropping, the right basic bank of the Kolyma River	Yernik larch forest. <i>Larix cajanderi</i> Mayr, <i>Salix pulchra</i> Cham., <i>Betula exilis</i> Sukacz., <i>Vaccinium vitis-idaea</i> L., <i>V. uliginosum</i> L., <i>Ledum decumbens</i> (Ait.) Lodd. ex Steud., <i>Arctagrostis latifolia</i> R. Br., <i>Empetrum nigrum</i> L., <i>Rosa acicularis</i> Lindl., <i>Aulacomnium turgidum</i> , <i>A. palustre</i> , <i>Dicranum</i> sp., <i>Cladonia sylvatica</i> , <i>Cetraria cucullata</i> , <i>Peltigera aphthosa</i>	68°37'55.4"	159°05'34.4"	60

quantitative analysis of carpological remnants, their number in a certain volume of the soil is counted [Zyuganova, 2005]. Phytoliths were counted on fifteen rows of the preparation sized 24 × 24 mm. Phytoliths were divided into a number of groups by their morphotypes. In each group, phytoliths were studied in different planes to reveal the specific forms. Simultaneously, remnants of vegetative tissues, sponge spiculae and carcasses of diatoms were investigated. In this study, the fraction (%) of a taxon of palynological or carpological remnants in their total number was calculated.

THE MAIN FEATURES AND THE LOCAL SPECIFICS OF THE SUBRECENT COMPLEXES OF PHYTOLITHS, SPORE-POLLEN SPECTRA AND SEED BANKS

Zonal vegetation

Yermik larch forests. The samples were taken from three larch forests of the region close for their floristic composition: the right basic bank of the Panteleikha River, the north-eastern slope of Lake Shchuchye in the area of Chersky settlement and the right basic bank of the Kolyma River in the area of the well-known basic section Duvanny Yar (samples 262, 264, 267; see Table 1, Fig. 1). The district under study is an alluvial bench with some hills of the intrusive origin (Rodinka, Panteleikha etc.). Frequent rock outcroppings are characteristic of it. As a mother rock, silty loams with high ice content (siltstone) of the Upper Pleistocene yedoma formation (of the loess-ice complex) or products of their Holocene transformation, which overlap the eluvium-deluvium of solid primary rocks, appear.

For the spore-pollen spectra of larch forests, single occurrences of the larch pollen are characteristic, an insignificant amount of the willow is present, as well as the considerable amount of the pollen shrub birches *Betula* sect. *Nanae* (до 44 %), growing in the undergrowth of these forests. Transported pollen of trees and shrubs – *Pinus*, *Alnus*, *Duschekia* and *Betula* sect. *Albae* accounts for 20 % of the spectra. In the pollen of grasses and dwarf shrubs, the families of Poaceae and Ericaceae prevail, gramineous plants prevail over heath plants, whereas an opposite situation was observed on the sampling sites – heath plants were dominant there. There are single occurrences of the taxa of grasses not recorded among the vegetation in the sampling places: *Senecio*, *Stellaria*, Cyperaceae and Ranunculaceae. The qualitative and quantitative composition of the spore-pollen spectra from the surface samples of the larch forests is generally close to that provided by R.E. Giterman [1985]. However, in this study a large amount of green mosses (15 %) were recorded, with no data on the participation of transported taxa. Regional differences were not revealed.

In the seed banks of the larch forests, the seeds of *Larix* prevail, and the content of *Betula divaricata* Ledeb. and *Arctagrostis latifolia* R. Br. in them is constant (Fig. 2). The seeds of heaths, common in the area under study, are not always present in the samples obtained. The share of transported species is small, only the seeds of *Empetrum androgynum* V.N. Vassil. were found, growing at the distance of 50–100 m from the sites under study.

In the macerate from the surface samples of the larch forests, remnants of tissues (primarily mosses and heaths) and epidermis prevail. Characteristic of these samples is the low content of phytoliths, the composition of which is scanty. Phytoliths of gramineous plants and of the horsetail were found, as well as single occurrences of the sedge grass. It was found as a result of the studies that *Larix cajanderi* Mayr (one of the most common trees growing in the northeast of Russia) does not produce phytoliths. However, in the material of the surface samples, specific forms with margined pores, probably formed in the bark and cork of the larch, were found. In the dwarf shrubs of the Betulaceae families, including *Duschekia*, and Salicaceae, phytoliths were not revealed, either. However, structures characteristic of the cork of the Betulaceae are quite common in the samples. These are darkly colored (from dark brown to nearly black) remnants of tissues with five- or six-cant cells, which do not form regular rows.

Intrazonal vegetation

Steppe areas (stepoids). The areas studied are located on the right primary bank of the Panteleikha River (samples 260, 262; see Table 1, Fig. 1) in the regions of the fescue and gramineous-petrophyte motley grass steppe at the rock outcrops and are associated with steep slopes of the southern exposition well-warmed in the summer period.

In the spectra from intrazonal steppe-like areas within the larch forests, the pollen of *Pinus* s/g *Haploxylon* dominates (up to 80 %, Fig. 2, A), which seems to be related to the dwarf Siberian pine, the individual plants of which occur at the distance of 200–500 m, and the brush is found at the distance of 1–2 km from the areas under study. The pollen of grasses and small shrubs which constitute the majority of the areas' vegetation, occupies a subordinated position in the spectra. The pollen of only grasses and of the pink family were identified; the other families could not be identified by the palynological method. Thus, these spectra do not reflect the qualitative and quantitative composition of the vegetation producing them. R.E. Giterman [1985] provided data on the prevalence of the pollen of the dwarf Siberian pine in the surface samples from the steppe regions with larch forests.

In the banks of seeds from steppe areas, practically all the species growing in the collection areas

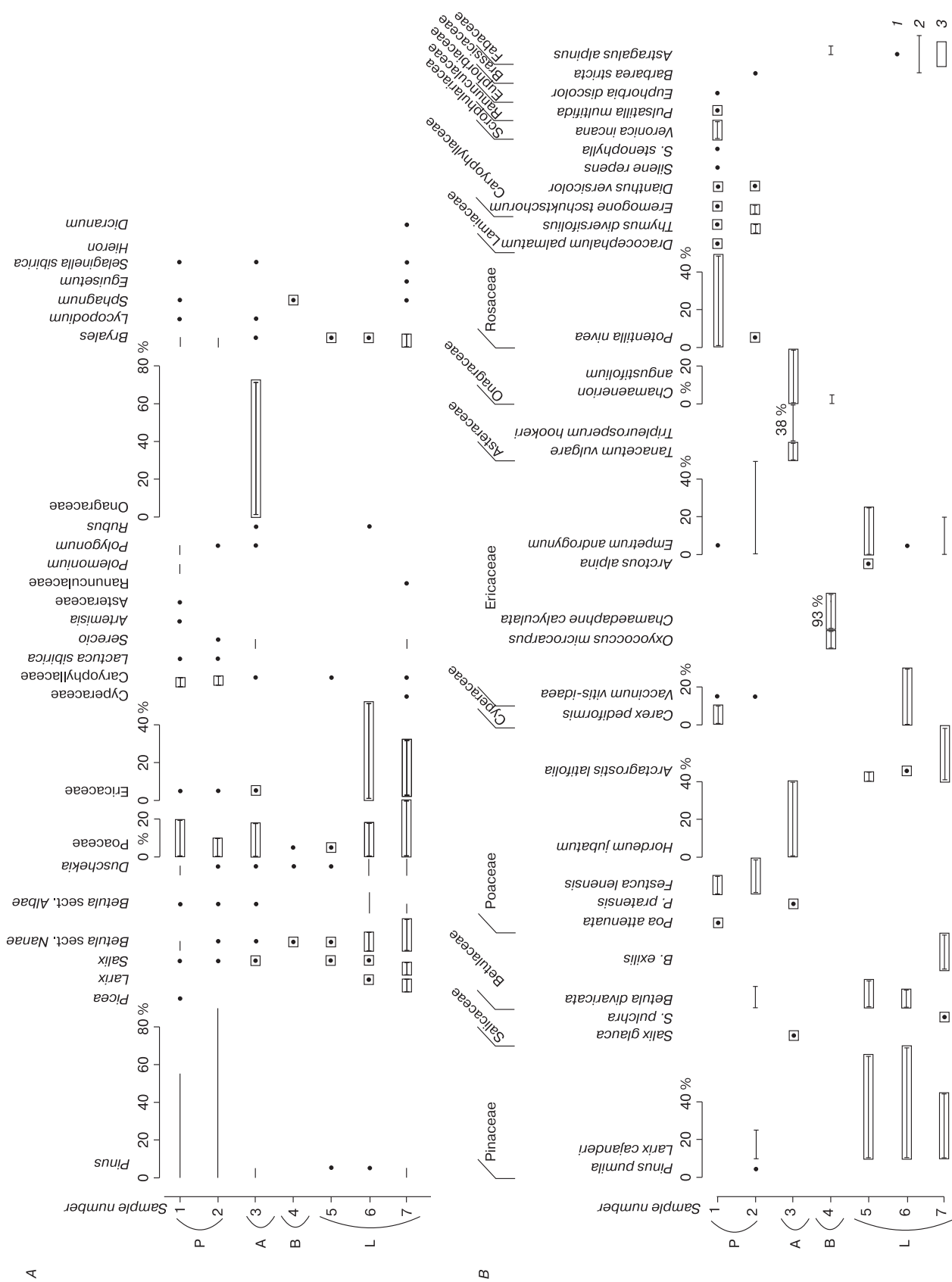


Fig. 2. The plant remains from the surface samples of the area of the lower courses of the Kolyma River: palynological (A) and carpological (B) remains.
 The content of vegetative remains: 1 – single occurrence (1–2 items); 2 – percentage (see the scale); 3 – taxa growing in the sampling area are enclosed in a frame. C – a steppe-like area, DL – the drained lake, B – bog, L – larch forest.

are present. However, just as in the spore-pollen spectra, transported components are recorded in the complexes of carpological remnants. In the bank of site 260, they occur singly, in the bank of site 265, the seeds of plants growing in the larch forests (*Empetrum androgynum* V.N. Vassil., *Larix cajanderi* Mayr and *Betula divaricata* Ledeb.) were identified in the amounts essentially exceeding the number of the seeds of plants recorded on the given site.

The surface samples from the steppe areas are characterized by the high content of phytoliths with various morphotypes (flexuous, flexuous-knitted, expressly dentate, trapezoidal, dumbbell-shaped, elongated shapes with morphologically varied edges, lanceolate (massive and aciculiform), characteristic of grasses (bluegrass and reed grass), sedge and bilobate grasses (see the Photo Table). Much detritus of monocotyledonous plants with air pores and lignified tissues of dwarf shrubs were identified. Remains of mosses occur rarely. Wood detritus and forms characteristic of coniferous plants are absent. The complex of phytoliths testifies to domination of grass groups growing on open landscapes with normal moisture content and reflects the composition of the vegetation on the collection site.

The bottom of a drained lake

Sample 266 (see Table 1, Fig. 1), taken near the Zeleny Mys settlement from the bottom of a drained lake, where willow weed grew, is characterized by the prevalence of the pollen of *Epilobium*, likely referring to the willow weed *Chamaenerion angustifolium* (L.) Hill., and by significant amount of gramineous plants and rather adequately reflects the composition of the local vegetation. All the plant species growing on the site under study, except *Erigeron acris* L., are available in the seed bank concerned. Transported seeds of *Tripleurospermum hookeri* Sch. Bip. have been recorded in significant amounts. The sample is characterized by a high proportion of various forms of phytoliths (smooth, dentate, expressly and poorly dentate, asymmetrical flexuose elongated, trapezoidal, rounded, oval, cylindrical and lanceolate forms). Elongated, lanceolate and trapezoidal forms prevail. Detritus of monocotyledonous plants with air pores and lignified tissues of dwarf shrubs were identified in large amounts. Remains of sedges and mosses occurred singly; remains of coniferous plants were not found. Thus, phytolith analysis quite adequately characterizes local grass communities.

Sphagnum bog

In the spore and pollen spectrum of the key site on the sphagnum bog of Lake Shchuchye near the settlement of Chersky (see Table 1, Fig. 1), the palynological remains occur only singly (*Sphagnum*, *Betula* sect. *Nanae* and Ericaceae). Only representatives of ericaceous plants were found. Tissues of mosses

prevail in the macerate (*Sphagnum*, *Dicranum*); epidermis of monocotyledonous plants and ericaceous plants with air pore complexes and lignified shrub tissues were found in large amounts. Phytoliths were mainly not available for diagnostics (smooth and cylindrical), but the oval and rounded shapes also occurred, characteristic of mosses. Phytoliths of sedges occurred singly; remains of coniferous plants were not found. The presence of amoeba shells and the variety of the types of diatomic algae, characteristic of the horizons with increased moisture content, is noticeable in the sample. Thus, phytolith analysis, unlike palynological and carpological analysis, reflects domination of mosses and of ericaceous plants with participation of sedges growing on this site.

THE RESULTS OF THE COMPARATIVE ANALYSIS OF SPORES, POLLEN, PHYTOLITHS, AND CARPOLOGICAL REMAINS FROM THE SURFACE SAMPLES TAKEN FROM THE LOWER COURSE AREAS OF THE KOLYMA RIVER

When comparing the composition of the local vegetation with subrecent spectra, we discovered that the transported pollen of trees and shrubs constituted a large portion of the spectra (*Pinus* s/g *Haploxylon*, *Betula* sect. *Albae*, *Duschekia*, *Alnus*). When analyzing the tundra spectra, A.C. Vasilchuk [2005] identified the following components in them: long-distance components transported from the producing plant to the distance of more than 500 km), regional (transported to the distance from 750 m to 200–500 km, depending on the landscape) and local components, reflecting participation of the plants growing in the area under study of the radius reaching 750 m. A.C. Vasilchuk leaves room for identification of sub-local and subregional pollen and spores, which may be referred to both regional and local components.

The pollen of the pine, transported by the wind to significant distances, is a long-distance-transported and regional component of the studied spectra [Kabailene, 1976, 1983]. Normally, its proportion in the spectra varies from 1.5 to 10 %; however, in the spectra from steppoid areas with projective coverage of 50–60 %, this type of pollen dominates (up to 80 %). The pollen of *Pinus* s/g *Haploxylon* prevails, likely referring to the species *Pinus pumila* (Pall.) Regel, the small woods of which are located at the distance of 0.2–2 km from the sampling sites. The motley grass communities growing on steppe territories are not reflected in the spore-and pollen spectra, except Poaceae and rare Caryophyllaceae and Astera-ceae. Long-distance-transported and regional components in the spectra are: the pollen of long-stemmed birches of the *Albae* section, present in large numbers in the spectra of larch forests and tundra, *Duschekia*, the proportion of which in the spectra of larch forests reaches 20 %, as well as *Alnus*. The northern bound-

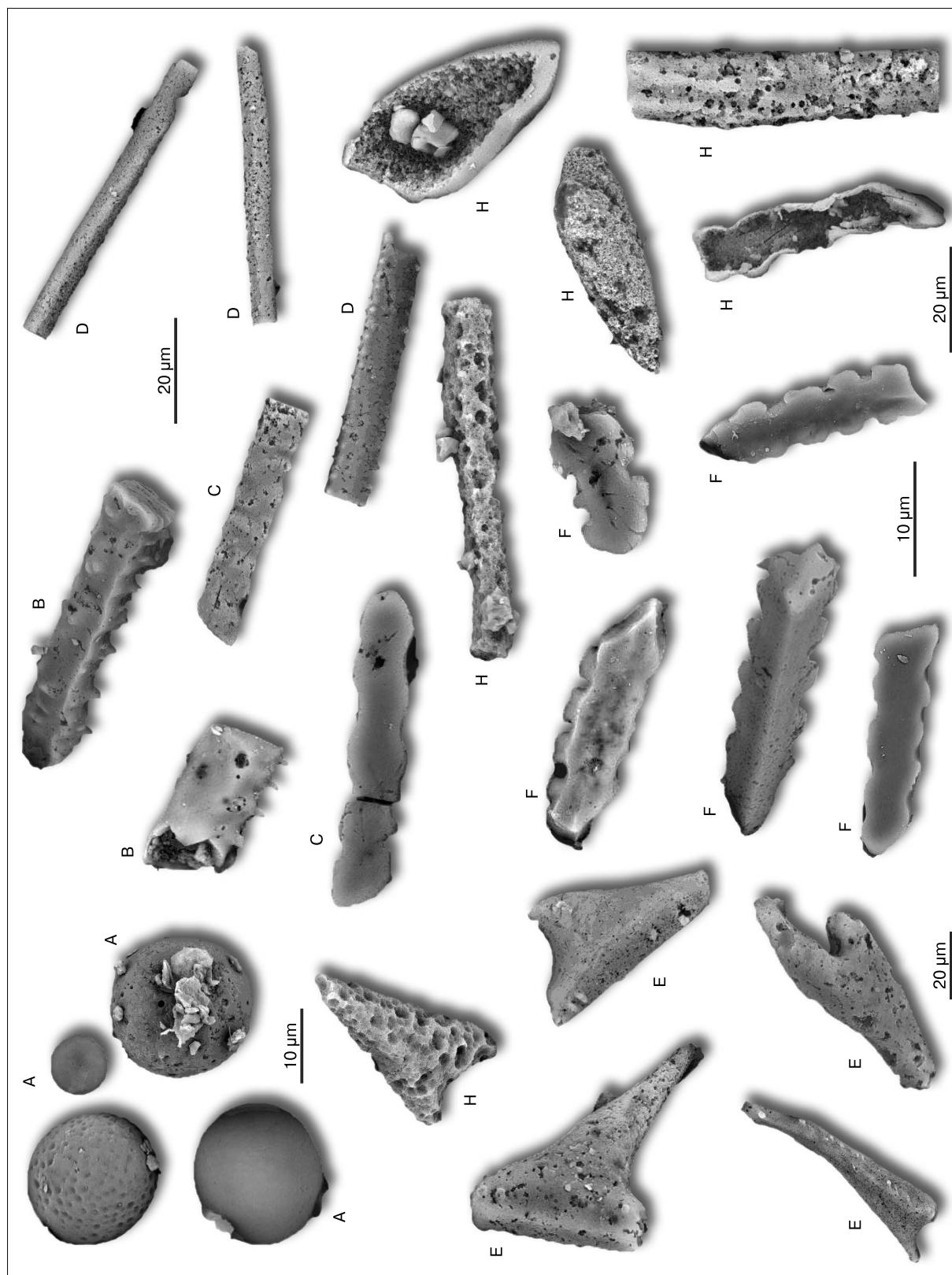


Photo table. Phytolith forms, isolated from the surface samples of the Kolyma River.

A – spherical phytoliths, B – elongated phytoliths, C – elongated forms with wavy edges, D – lanceol forms, E – trapezoidal forms, F – corroded phytoliths. The scale is provided for each morphological type.

ary of these species is at the distance of about 100 km from the studied territory, except the birches of *Albae* section, the northern boundary of which is much closer to the south. The subregional component is usually singly occurring pollen of some herbs, the representatives of the *Polemonium*, *Polygonum*, *Rubus*, *Valeriana* geni and of the Chenopodiaceae, Brassicaceae and Campanulaceae families.

A considerable proportion of transported pollen of trees and shrubs in the spectra is caused by the low palynological productivity of the plants of the region under study, likely resulting from severe climatic conditions [Tikhmenev, 1981, 1984].

Adjusting to adverse conditions, the tundra plants may switch to vegetative reproduction, and this distorts the picture of the vegetative cover reflected in the spore-and-pollen spectra, in which transported pollen plays a significant role [Dirksen, 2000]. N.Ya. Kats and R.V. Fedorova [1983] indicate that the pollen grains of a number of plants growing in the tundra, in particular, Brassicaceae, recorded among the local vegetation of the region, are small and rather rare. Cleistogamy (pollination in closed flowers), observed in several geni of anemophilous plants in a long period of low temperatures, contributes to reduction of palynological productivity and hence to lower concentration of pollen in the sediments. Transported taxa in the seed banks prevail in the open areas of steppoids – these are remains of the larch *Larix cajanderi* Mayr, the birch *Betula divaricata* Ledeb. and of the elfin Siberian pine wood *Pinus pumila* (Pall.) Regel (Fig. 2, B). In larch forests, the proportion of transported carpoids is usually low due to the closed nature of ecosystems.

The local component of the spore-and-pollen spectra carries specific information about the composition of the local phytocenoses. *Larix cajanderi* Mayr is the only species of trees in the studied region. The pollen of the larch in the larch forest samples occurs rarely, while an opposite picture is observed in the seed banks – its seeds prevail. The larch does not produce phytoliths; however, specific forms characteristic of the bark and cork of the larch have been identified in the surface samples from the larch forests. The shrub tier in the woods is represented primarily by willows, birches and the species of the Ericaceae family, which is reflected in the composition of the spectra. In the spectra, the noticeable amounts (about 30 %) of the pollen of *Betula* sect. *Nanae* are present, which seems to refer to the shrub-like birch species common in the modern flora of the region – *Betula divaricata* Ledeb. и *B. exilis* Sukacz and the pollen of the Ericaceae family (about 40 %). The pollen of the willow in the spectra from the larch forest occurs all the time but in small amounts (not more than 10 %). It was found from the recent and subrecent materials that the proportion of the willow pollen in the spectra

is much less than its actual participation in the vegetative cover [Makhova, 1971; Smirnova, 1971].

The seeds of the birch and the willow were identified in the samples and by the carpological method (up to 20 %). On the contrary, the phytolith analysis does not allow recording participation of these shrub forms in the vegetation. The shrub *Rosa acicularis* Lindl. can be found in the undergrowth of the larch forest; however, the remains of this species have not been recorded by any of the three above methods. The absence of pollen of this family in the spectra is likely to be caused by the fact that the pollen of the rose family has very fine and tender exine and becomes quickly disintegrated in the process of oxidation due to the low content of spore-pollenine [Sangster and Dale, 1964; Vronsky and Fedorova, 1981]. It cannot be excluded that birds and small mammals pick a large part of the juicy fruit of the rose family; therefore, their carpoids do not convert into a subrecent state.

While comparing the geo-botanical descriptions of the local vegetation with the subrecent spore-and-pollen and phytolith spectra and seed banks for each site, it is to be noted that comparison of the herbaceous and suffruticose plants identified in their composition is mainly made at the level of families. Due to poor preservation and the absence of genus-specific signs, the pollen of most plants in this group is often identified only to the degree of a family even in subrecent spectra. The presence of deformed pollen of grassy plants, predominantly gramineous plants and heaths, is to be noted, which seems to be due to severe climatic conditions affecting complete ripening of the pollen seeds and their preservation.

The phytoliths of herbs from the studied samples are mostly corroded (see the photo table, H), indicating either the shortage of minerals in the growth period of plants, either bad weather conditions in the period of vegetation. The degree of preservation of carpoids of grassy plants may be qualified as satisfactory and good, allowing identification of plants to the level of species. Normally, the seeds of the sampled gramineous plants look somewhat darkened but they also may have a natural color, preserve their shape, venation and rods, as well as the pattern and the structure of the surface. The preservation degree is varied in different samples, which is explained by the conditions of burial, the composition of the enclosing strata and the degree of ripeness of the seeds themselves as they reach the soil. According to our observations, carpoids are best preserved in the peaty horizons of the modern soils of the region, in boggy habitats, silts on the bottoms of frost cracks, lakes and other water reservoirs. In the samples from larch forests, up to a half of all the carpoids were composed of larch seeds, but about 60 % of them were damaged by insects or mice. Seeds of plants producing eatable

tasty berries (blueberry, red bilberry, cranberry) are often missing or occur only singly in the samples.

A number of the grass *geni* are not always found in the spore-and-pollen spectra (and if they are, the representation not always quantitatively adequate). The pollen of gramineous plants occurring in significant amounts on the sites of rare larch forests studied is found continuously in significant amounts. It may be likely that, due to the high productivity and the high transport capacity, part of the pollen of gramineous plants, as well as of sagebrush (*artemisia*) in the spectra is transported. Gramineous plants are characterized by high palynological productivity: the pollen of this family has smooth exine without sculptural outgrowths, contributing to its fast propagation in the air and transport to long distances. It is to be noted that the seeds of the *ericaceous* and gramineous plants are stably present in the larch forest seed banks. The pollen of entomophilous families *Caryophyllaceae*, *Onagraceae*, *Lamiaceae*, *Ranunculaceae* and *Liliaceae* is represented insignificantly, even if representatives of these families are present on the territories under study (with the exception of the spectrum of sample 266 with the pollen of the *Onagraceae*, sampled directly from a willowweed meadow) prevailing, which seems to be due to the method of its transport.

The pollen of a number of herbal families (*Scrophulariaceae*, *Lamiaceae*, *Rubiaceae*), present among the vegetation was not found in the spectra, possibly due to the low pollen productivity of these plants under severe climatic conditions and their transition to vegetative reproduction. Thus, the pollen of grasses and dwarf shrubs not always reflects the qualitative variety of the local vegetation, which is caused both by the biological features of the plants (the structure of pollen, pollen productivity, and the method of pollination), and the specific method of distribution and preservation of the pollen of different plant species. The seeds of grasses, on the contrary, are often present in the seed banks and rather adequately reflect the composition of the vegetation of the sites under study. The variety of the morphological phytolith types allows the qualitative diversity of the grassy vegetation to be determined, although it is not always easy to identify the systematic appurtenance of certain forms. This method allows the presence of sedges and gramineous plants to be identified with sufficient confidence. The variety of phytoliths has been recorded in open steppe areas, whereas in the surface samples from the larch forests they occur singly and do not display any qualitative diversity.

Mosses play a significant role as local vegetation, primarily leafy, although no carpological remains were found in the seed banks. The content of spores, identified to the order of *Bryales*, is insignificant in the spectra, possibly due to the transition of these

plants to vegetative reproduction. The spores of the rock spikemoss, clubmoss, horsetails, polypody ferns, and *dicranum* occur singly in all the spectra and are transported. On the contrary, phytolith analysis allows reliable verification of the presence of mosses on the studied sites. Mosses produce well-diagnosed specific forms of phytoliths (the group of rounded phytoliths). In addition, due to the specific character of the processes of modern soil formation in this region, a sufficient amount of tissues is present in the sample macerate, which allow individual moss *geni* to be identified.

CONCLUSIONS

For the first time, comparative analysis of spores and pollen, phytoliths and carpological remnants from a number of surface samples of the area of the lower course of the Kolyma River has been made. Subrecent plant remains from the area with near-surface permafrost are well preserved due to low microbial activity and short stay in the active layer. The carpological analysis of the surface samples rather adequately reflects the composition of the surrounding vegetation. Transported taxa are present in all the studied seed banks, with their number most prevalent on open sites – steppified areas and the bottom of a dry lake covered with vegetation. The proportion of transported pollen of trees and shrubs in the studied spectra often shadows the content of the pollen of plants growing in the areas of sampling. The presence of this pollen in the spectra does not carry information about the composition of the vegetation; it testifies to atmospheric circulation in the region and to the landscape in the area. Transported taxa in the phytolith spectra are absent, which allows the vegetation growing directly on the sampling site to be characterized.

Analysis of the spore-and-pollen spectra from the larch forest has shown that the amount of poorly preserved larch pollen is scanty, whereas an opposite picture is observed in the seed banks – larch seeds dominate there. This genus does not produce phytoliths; however, it is quite well identifiable by the characteristic micro formations on the bark. Willows and the shrub species of the birch growing in the undergrowth of these woods are consistently recorded in the spore-and-pollen spectra and in the seed banks. Phytoliths of these *geni* have not been found. The carpet plants of the larch forests are reflected in the prevailing pollen of the *Ericaceae* and *Poaceae* families which have been identified in the seed banks. The participation of the gramineous plants and sedges in the vegetative cover is also confirmed by the results of the phytolith analysis. Moss remains from the larch forests cannot be identified by the palynological and carpological methods, but specific phytoliths and remains of their tissues have been found in the macerates in large amounts.

The spectra from the southern slopes of the step-plicated areas within rare larch forests do not show motley grass communities growing in them; transported pine pollen prevails in them, which is likely to belong to the dwarf Siberian pine. In the seed banks from the areas under study, both the grass species growing in them and transported taxa have been identified, which distort the picture of the local vegetation reflected by the carpological method. Phytolith analysis allows identification of the diversity of the grasses growing in the sampling areas. Unlike in the spore-and-pollen analysis, remains of coniferous trees have not been identified by this type of analysis.

The three types of analysis provide a rather realistic picture of the composition of vegetation covering the bottom of the drained lake (the prevalence of the Onagraceae family and of gramineous plants). However, a significant proportion of transported forms has been noted in the seed bank.

The data of the palynological and carpological analyses do not comply with the actual vegetative cover of a sphagnum bog. Single occurrences of palynological remains in the surface samples may be due to washing out of spores and pollen from the moss turf by water flows or by their eating by phytophagous organisms. The seed bank contains only single representatives of the ericaceous plants, not reflecting the actual role of the other taxa in the vegetative cover. However, due to the specific character of the processes of modern soil formation in this region, a sufficient amount of the remains of the tissues of mosses, ericaceous plants, and shrubs are present in the sample macerate, and phytoliths of mosses and sedges have been identified. In this case, phytolith analysis, unlike the palynological and carpological analyses, proves to be more resultative and reflects the composition of the bog vegetation.

When carrying out reconstructions of the vegetative cover, the probable transition of a part of plants to vegetative reproduction under severe climatic conditions and the resulting low productivity of the local phytocenoses should be taken into account.

Subrecent spore-and-pollen spectra, studied in the lower course of the Kolyma River, do not always adequately reflect the composition of the surrounding vegetation but provide a clear idea of its edificators, except for the larch. A significant proportion, and often prevalence, of transported pollen, in the spectra results from the openness of the studied landscapes. The autochthonous genesis of the carpological remains and phytoliths allows reconstruction of the local type of vegetation within a broader floristic environment determined according to the palynological analysis data. A complex botanical analysis, where the local component is regarded through the prism of the regional vegetation and taking it into account, seems to be the most appropriate approach to reconstruction of the Quaternary vegetation.

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