Biology Bulletin, Vol. 32, No. 2, 2005, pp. 196–206. Translated from Izvestiya Akademii Nauk, Seriya Biologicheskaya, No. 2, 2005, pp. 240–252.

ECOLOGY

Taphonomic Features of Arctic Pollen

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Received September 10, 2004

Abstract—The composition of the primary pollen changes during pollen transfer and redistribution over the Earth's surface and fossilization. These processes are particularly pronounced in the tundra zone. Patterns of pollen spectra formation in the subaerial and subaqueous deposits of the tundra zone were considered and the differences in the content of palynomorphs with exine rupture were revealed. The changes in the effect of regional and local taphonomic factors on Arctic tundra slopes were traced. Pollen conservation in the deposits of the tundra zone, snowfields, and wedge ice was considered.

Environmental factors affecting the composition of pollen after their production and emission from the maternal plant can be considered as taphonomic. Taphonomic factors are an external mechanism changing the proportions of pollen in the *primary pollen spectrum*, i.e., pollen formed by the floristic community according to its pollen production capacity.

Groups of factors affecting the quantitative and qualitative composition of the primary pollen can be recognized. The first group of factors affects the process of pollen transfer and redistribution over the Earth's surface. These factors underlie different composition of the primary pollen resulting from their transfer. The second group of factors include conditions and processes accompanying pollen fossilization. These factors underlie the degree of pollen conservation.

Taphonomic processes of pollen spectra formation in the sediments can change or remain nearly constant in time. In the second case, they provide for the constant and easily accountable pollen spectra in a given site. Local time-variable taphonomic effects, particularly, in forest-free regions, are hard to reveal in highly variational pollen spectra, which can lead to unjustifiably contrast reconstructions of vegetation conditions and variability of paleofloristic communities.

Specific effect of taphonomic factors in pollen accumulation in wedge ice is due to specific features of wedge ice formation. It results from repeated leaking of water from melted snow into frost-clefts and its nearly instant freezing, which provides for ideal conditions for conservation of pollen not affected by transformations. Hence, pollen spectra from wedge ice reflect the primary pollen rain. The chemical and microbial effects are negligible here. Comparison of these pollen spectra with those from synchronous enclosing deposits allows us to evaluate the effect of taphonomic factors on deposition.

RESEARCH LOCATIONS AND METHODS

Studies were carried out in the Yamal, Mamont, and Gydan Peninsulas as well as Belyi Island in the northern West Siberia, in the Kolyma River valley (Cherskii–Kolymskoe Settlement, Seimchana Town, and Sinegor'e Town), Daurkin Peninsula, and Main River valley in Chukotka.

We studied pollen spectra in peatlands including polygonal ones and those forming the upper part of frost mounds, current warp of rivers and seas, current soils, material from rodent burrows, surface snow, river water, and pollen concentrate from wedge ice. A palynological study of the profiles along the terrace slope (the foot and the upper part) was carried out. For bulk analysis of damaged palynomorphs, one or two samples with average indices were selected from each point.

The following ranks of pollen conservation were recognized for the subfossil samples: intact, ruptured (with signs of physical damage), battered and corroded (with signs of chemical damage), immature/lacking sculptural elements, and charred.

Since some pollen damage results from sample preparation, redeposited palynomorphs were isolated using the standard technique of pollen extraction from sediments excluding the water bath stage during acetolysis.

RESULTS AND DISCUSSION

Ruptures prevailed among disturbance types (over 75–86%) in all deposit types in the surface samples of the tundra zone. Riverbed and beach deposits featured ruptured pollen grains and spores. Battered and corroded grains were observed in the samples redeposited from prepleistocene deposits. Charred pollen grains and spores were common in the waterbed samples from the Kolyma River, which reflects high incidence of fires in the valley. Immature pollen grains were recorded on snowfield surfaces and in the snow fell during the vegetation period in tundra and forest-tundra, while they were absent in the surface sediment samples. This indicates that immature pollen grains decay faster than mature ones and can be conserved only under favorable conditions.

Long-term transfer often flattens and damages pollen covers before they appear in conditions favorable for fossilization. Hence, the degree of pollen conservation and types of the damage carry additional information on pollen spectra. Ruptured pollen grains and spores were common in wedge ice, on the surface of snowfields, and in snow. Apparently, firm pollen covers are ruptured during thawing and freezing when ice crystals are formed as well as during pollen swelling in water and subsequent drying. Berezina and Tyuremnov (1973) experimentally demonstrated that this damage type occurs when fresh or dry pollen is soaked in water and its content and intine considerably swells.

Cracked or cleft pollen usually occurs in acid peats, sapropels, and moss cushions (Cushing, 1967). Rupture and batter damages usually result from pollen transfer in a water flow with a high concentration of sludge particles (Campbell, 1991).

Thus, the ruptures can be induced by drying and moistening, freezing and thawing, and long-term transfer in turbid flows. Battering, stratification, cavitation, and loosening are traces of chemical impact of microbes (Elsik, 1971). Havinga (1984) experimentally demonstrated that pollen became colorless, stratified, and battered, their exine was dissolved, and sporopollenin was oxidized in alkaline environment. Hall (1981) traced the decrease in pollen concentration with depth in sediments formed in dry climate. Pollen concentration was 41–17 000 grains/g on the surface, while it decreased to 0–5000 grains/g at a depth of 0.2–0.4 m. The sediments studied in this work had pH range of 7.5–9.0, which was reflected in the type of pollen damage: pollen grains were largely battered and colorless. The proportion of undefinable pollen grains increased with depth (7–37% of total accounted grains) and the proportion of damaged palynomorphs increased with the decrease in pollen concentration. The concentration of pollen and spores as well as the content of damaged palynomorphs were proposed as a marker of reliable interpretation of pollen spectra. Low pollen concentration coupled with a high content of damaged palynomorphs indicate considerable changes in pollen composition during fossilization prompting inadequate interpretation; this pattern can be observed even in the absence of ligneous vegetation in the Arctic tundra zone. The data on the south-facing slopes were particularly indicative. For instance, subfossil pollen samples from the surface of high pingos (hydrolaccoliths) in Alaska (Prudhoe Bay region) contained 5–8 more pollen and spores of species rare for this region as compared to other slopes (Walker *et al.*, 1991).

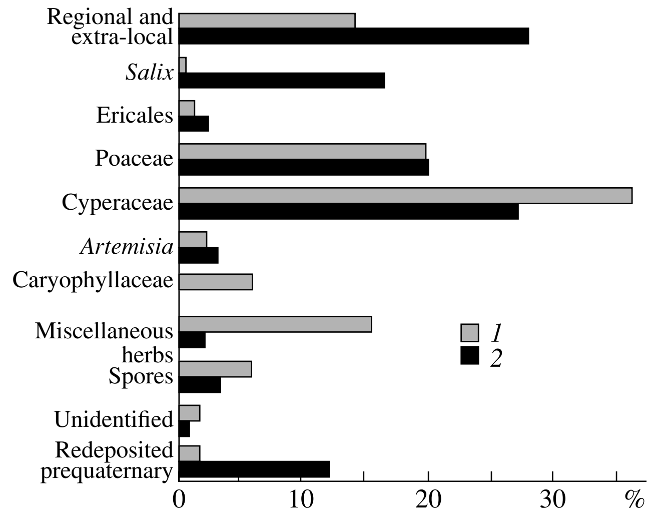

Fig. 1. Proportion of pollen and spores in south-facing slopes of the Kharasavei River terrace in the Arctic tundra zone; *1*, terrace foot; *2*, near-edge region.

We studied the pattern of changes in pollen composition during their transportation and redistribution over the Earth's surface using the profiles of the near-edge and foot regions of a matted slope (15 m) of the south-facing terrace of the Kharasavei River (Fig. 1). The profile length was 200 m and the distance between sites of sample collection was 1–3 m.

In order to avoid the effect of random factors, we traced the patterns using arithmetic means calculated from 50 samples for each profile.

One of the goals of this work was to study the distribution of dominant pollen species in order to determine their role in the subfossil pollen spectra.

Pollen of birch *Betula nana*, which appeared the closest pollen-producing plant to the location of sample collection, was considered as regional. Pollen grains of *Pinus silvestris, P. sibirica, Betula* sect. *Albae*, and *Alnaster* found in the surface samples from the lower and upper parts of the slope were assigned to the extra-local and regional components of pollen spectra.

In the near-edge part of the slope, the extra-local and regional pollen amounted to 27% on average; in the foot, 14.5%. We assigned willow pollen to local, since these plants could be found around. The contrast between the high and low values in the upper and lower parts of the slope (17 and the low 5%, respectively) indicate that most of willow pollen in the upper part of the slope was air-born. Hence, despite the presence of flowering plants around the location of sample collection, willow pollen is as a regional component. Pollen of heathers demonstrated no such contrast, apparently, due to their low concentration in the upper and lower parts of the slope (below 5%), although pollen of this family has features of regional pollen.

The content of cereal pollen was similar in the lower and upper parts of the slope (18–19%). Most likely, local pollen of cereals and heathers reflects their involvement in vegetation cover and has an even surface distribution. Sedge pollen dominated over the whole slope and reflected the zonal pattern of pollen spectra. In the lower part of the slope, its content reached 50%, while the mean content for the whole slope was 38%. In the upper part of the slope, sedge pollen content was lower (28% on average), although samples with sedge pollen content over 50% occurred.

Wormwood pollen had a contrast distribution: 2–5 and 10–14% in the lower and upper parts of the slope, respectively.

Pollen of the pink family was not observed in the upper part of the slope, while its mean content in the lower part was 6%. This suggests that it is easily washed down by rain and accumulates in the lower part of the slope. Representatives of the pink family were found both on the terrace surface and on the slope. The data on the content of pollen of other herbs also demonstrated its accumulation in the lower part of the slope.

Spores of horsetails and green mosses predominated in most samples from the lower part of the slope, while spores of sphagnum and club mosses as well as of true ferns occurred in the upper part of the slope. Prequaternary palynomorphs amounted to 10–11 and below 3% in the lower and upper parts of the slope, respectively.

The obtained data indicate that southern winds transfer pollen not only of Scotch pine, Siberian cedar, and birch, but also of dwarf birch, alder, willow, heathers, wormwood as well as spores of sphagnum and club mosses and true ferns. These palynomorphs are extralocal and regional in the zone of Arctic tundra, which can be used to compare results of pollen analysis in the tundra zone of West Siberia. Surface runoff predominantly redistributed pollen of sedges, pinks, and miscellaneous herbs as well as redeposited prequaternary palynomorphs.

Selective pollen redeposition was reported by Campbell (1999) in the Cattle Camp region in the Yukon. A small drained lacustrine depression 25×20 m and 3 m in depth was studied using core samples from the slope (25 cm) and bottom of the alassy (38 cm). Tephra horizon with an age of 1230 years was used as a marker horizon. Tephra lied at a depth of 12 and 24 cm in the slope and in the depression bottom, respectively. Samples were taken with a 1 cm step on the slope and a 2 cm step on the bottom. This allowed Campbell to trace formation of pollen spectra for each 100 years; i.e., pollen spectra average for 100 years were considered in this case (Fig. 2). The obtained data demonstrated that pine pollen was transferred to the studied region by air and was not washed down to the alassy bottom, since there was more pine pollen on the slope. Regional pollen fell on the bottom in lower quantities before ash bed sedimentation. After the sedimentation, ash became frozen in the slope but remained thawed in the bottom, and the situation changed. Apparently, due to the changes in the underlying surface, pollen started to be washed down to the bottom with surface water runoff. If this process largely involved regional pollen of ligneous forms, one can assume that pollen transfer to the bottom largely occurred during snow melting. Note that, similar to our case, willow pollen accumulated in the upper part of the slope, while cereal and heather pollen was evenly distributed over the surface. Different distribution of pink pollen was observed as well: in our case, they were much more abundant in the near-edge part of the slope; while in the Cattle Camp, on the slope.

Analyzing pollen transfer (Fig. 2), Campbell (1999) compared pollen diagrams from the depression bottom and from the slope using birch-to-spruce and alder-to-spruce pollen ratios. These ratios increased on the bottom but decreased on the slope. Since samples were collected at a distance of 1 km from the nearest tree, this difference can be due to only taphonomic features, particularly, to the transfer capacity. Spruce pollen transfer depends on pollen grain structure (the presence of sacs). It is readily transferred by water, which makes it more susceptible of transfer during snow melting as compared to pollen grains of birch and alder. Quantitative differences in the surface runoff also affect this ratio in the synchronous horizons.

The palynological data obtained on the southern slope in the lower reaches of Kharasavei River and in the Cattle Camp illustrate that even surface runoff affects pollen spectra. Nevertheless, both samples demonstrated signs of zonal pollen spectra. Clearly, pollen spectra are determined by selective washing and redistribution of pollen. Identification of redeposited pollen without signs of degradation by the standard analysis is hard. Only radiocarbon dating of pollen allows us to reveal such redeposition when pollen of different ages are present in the concentrate (Vasil'chuk, 2005).

Palynomorph damage on the slope. Taphonomic features of pollen spectra formation on the slope can be exposed by examination of damaged palynomorphs from parallel profiles along the foot and near-edge regions of the slope in the Kharasavei River valley. Differences in the content of damaged palynomorphs reflect even subtle differences in pollen spectra formation (Fig. 3). In the foot region, 64% samples demonstrated minimum damage (0–10%), while the proportion of palynomorphs with a 10–20% damage was 32%. At the same time, 9 and 1% of samples demonstrated 20–30 and 30–40% damage, respectively. In the near-edge region, 70% palynomorph samples demonstrated a 0–10% damage; while 30% of samples had 10–20% damaged palynomorphs, which was similar to that for the foot region. Water was clearly involved in pollen spectra formation in the foot region of the slope, since pollen grains and spores were damaged and/or sorted.

Palynological data for Arctic tundra in West Siberia allows us to trace relative resistance of the covers of pollen grains and spores. The increasing series of cover resistance of pollen and spores was as follows: *Salix*—

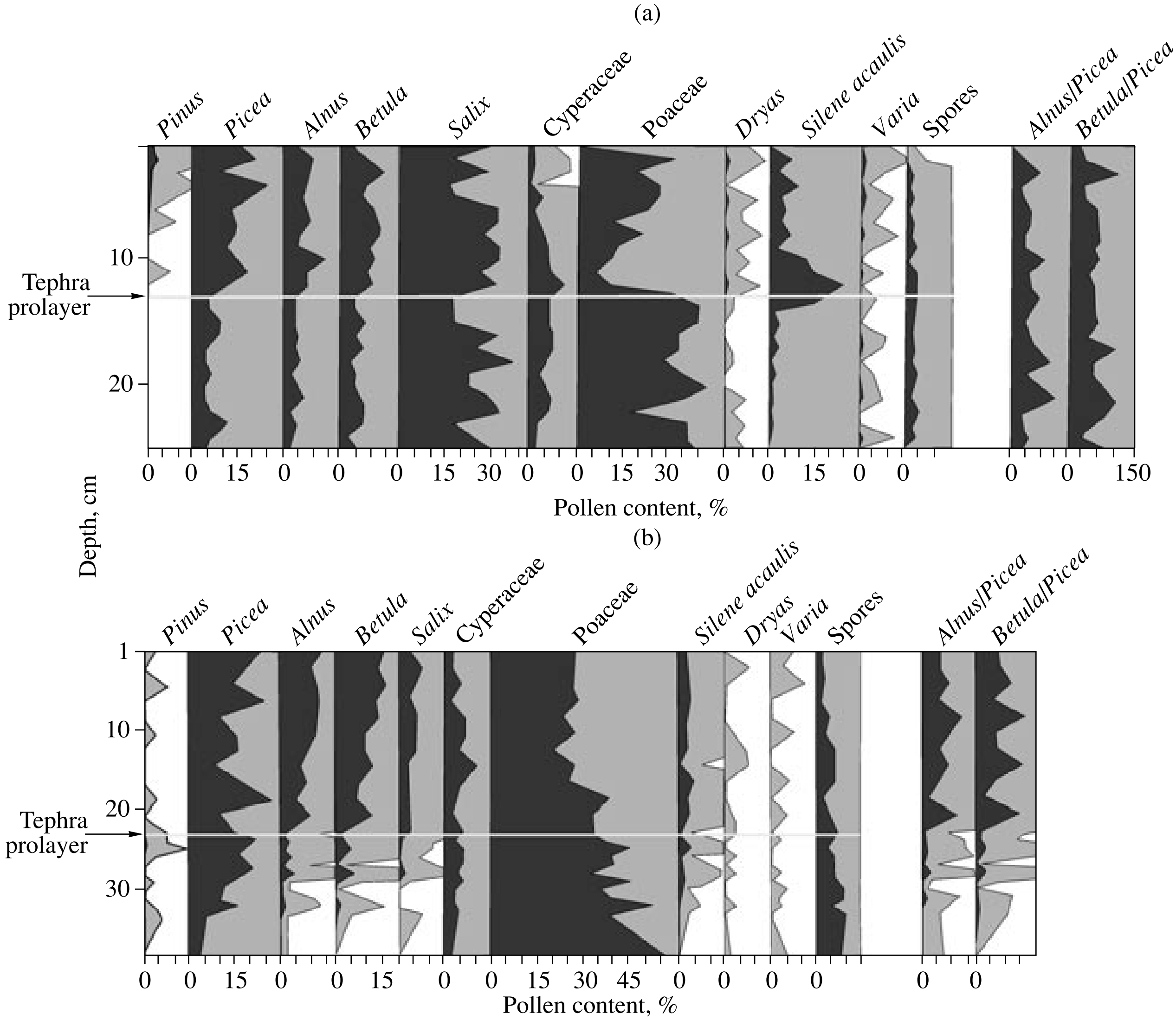

Fig. 2. Pollen diagram for deposits from the slope (a) and bottom (b) of dry lacustrine depression (alassy) in the Cattle Camp region, Yukon (Campbell, 1991).

Cyperaceae—*Sphagnum* and Polypodiaceae—Poaceae—*Betula* sect. *Nanae*—*Alnaster*—Ericaceae, Caryophyllaceae, and *Artemisia.* Three letter taxa demonstrated nearly no damage.

Specific formation of pollen spectra in the zone of permafrost development. Pollen spectra also depend on the pattern of matter mobilization during weathering. Fine rock shattering is hardly possible without “hydration weathering,” which is a physicochemical process coupled with frost weathering. Hence, cryogenic weathering includes at least two processes: frost integration based on the wedging action of ice crystals and aggregates and cryohydration disintegration mediated by oscillating wedging action of fine water films. Fresh pollen appearing in the permafrost soil or ice is exposed to freezing degradation due to the wedging action of forming intracellular ice while the effect of fine water

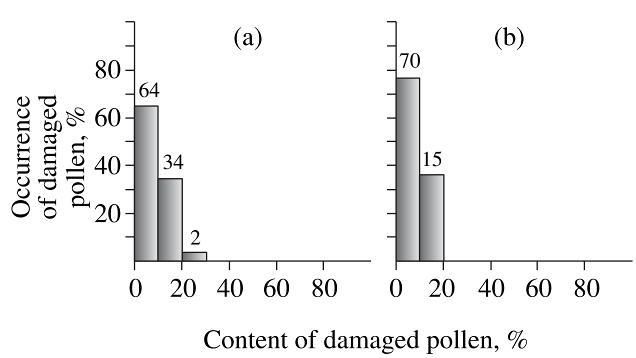

Fig. 3. Histogram of ruptured pollen occurrence in the south-facing slope of the Kharasavei River to raise in the Arctic tundra zone; (a) terrace foot, 50 samples; (b) near-edge region, 50 samples.

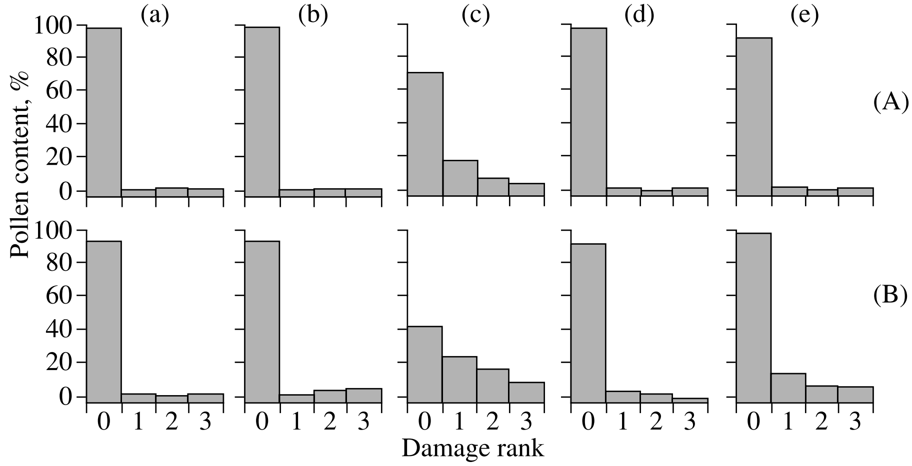

Fig. 4. Experimental packing of pollen; A, before packing; B, after packing; pollen damage ranks: from 0 (intact) to 3 (severe damage) points (Campbell, 1991); pollen: (a) *Coryus*, (b) *Alnus*, (c) *Pinus* sp. (d) *Sal in the x-ray*, and (e) Poaceae.

films is not so significant. Rupture of palynomorphs is partially due to exine rupture by ice crystals inside a pollen grain or spore.

Acidic pH is typical for soils and rocks in most permafrost regions, which favors iron release from the lattice and accumulation of iron hydroxides in the soil. Usually, low temperatures promote their coagulation on soil particles and microfossils as films which are later subjected to irreversible dehydration and recrystallization (Gravis and Lisun, 1971). Precipitation of iron hydroxides is particularly active during acidic-to-alkaline pH shift, which commonly accompanies dehydration. During isolation, pollen grains in iron envelopes are removed with mineral particles; hence, sediments exposed to dehydration can be palynologically silent and isolation of pollen and spores from such deposits requires ultrasonication. Deposits of this kind can be exemplified by prolayers of allochthonous peat in Yedomian strata where pollen concentration is often lower than in the surrounding mineral deposits.

In order to study pollen packing during sediment freezing, Campbell (1991) filled a cylinder with oozy sand, water, and pollen of *Pinus*, Poaceae, *Corylus, Alnus*, and *Salix*. The cylinder was loaded in a hydraulic press with a pressure of 2000 kg/cm^2. The damage (commonly rupture) was evaluated using a scale from 0 to 4 points. *Corylus, Alnus, Salix*, and the largest *Pinus* pollen grains proved the most resistance to pressure; Poaceae were slightly damaged (Fig. 4). Clearly, pollen is relatively resistant to pressure and only a considerable sediment packing can result in selective pollen damage.

Effect of taphonomic factors during pollen transfer in rivers, bays, and seas. Exposure to wind or water can cause secondary redistribution of pollen; lightweight pollen grains are aerodynamically or hydrodynamically displaced while heavy pollen remains. For instance, pollen sorting by morphology in lakes and seas was proposed (Levkovskaya, 1967; Davis, 1968; Davis and Brubaker, 1973). Up to 80% of pollen found on the bottom initially fell somewhere else.

Studies on differential pollen transfer by water (Brush and Brush, 1972) demonstrated considerable sorting of pollen into several types in a stream. Hopkins (1950) experimentally demonstrated that *Quercus* pollen submerged faster than pine pollen and that submergence rate depended on pollen grain size. Different degree of pollen grain conservation is very important during transportation, particularly, in the case of water transfer.

In the littoral and beach zones, pollen spectra are largely affected by water transfer. Fine sand facies accumulating on the beach was palynologically studied in detail on the coasts of the Kara Sea, Gulf of Ob, Tazov Bay, Gydan Bay, Anadyr estuary, and Bering Sea. Histograms of damaged pollen occurrence were plotted, particularly, for this facies, on the basis of the obtained palynological data.

According to our data, fine sand of the Yamal Peninsula contains notable quantities of damaged pollen (Fig. 5a). Over a half of studied samples contained 30–40% damaged pollen, while 18% of samples included 40–50% damaged pollen. In 28% of studied samples, 20–30% palynomorphs were damaged, and 0–20% damage was observed in as low as 3% of samples.

The Gydan and Tazov Peninsulas had a similar distribution of samples containing damaged pollen and spores (Fig. 5b). The highest proportion of damaged pollen (20–40%) was observed in 97% of studied samples. At the same time, 52% of samples included 30–40% of damaged palynomorphs.

In Chukotka (Fig. 5c), most samples (92%) included 20–40% of damaged palynomorphs as well, while as low as 5% of samples had no more than 20% of damaged pollen.

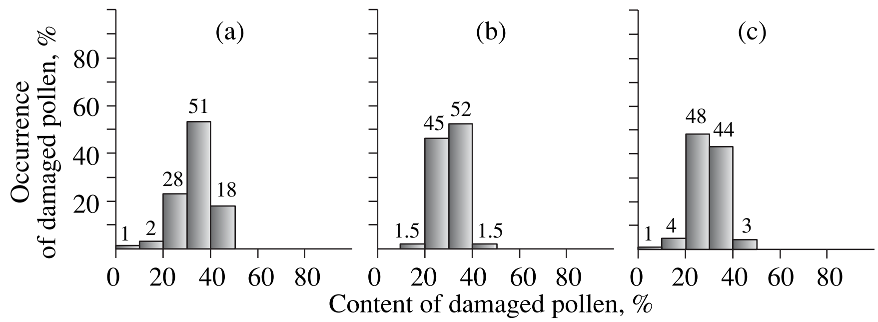

Fig. 5. Histogram of ruptured pollen occurrence in current beach deposits (fine sand); (a) Yamal Peninsula (environs of Kharasavei, Tambei, Seyakha, and Mys Kamennyi Settlements) and Belyi Island, 127 samples; (b) Gydan and Tazov Peninsulas (environs of Tazov, Gyda, Tadibeiyakha, Matyuisale, and Mongatalyang Settlements), 132 samples; and (c) Chukotka (environs of Anadyr Town and Lavrentiya, Provideniya, and Wellen Settlements), 65 samples.

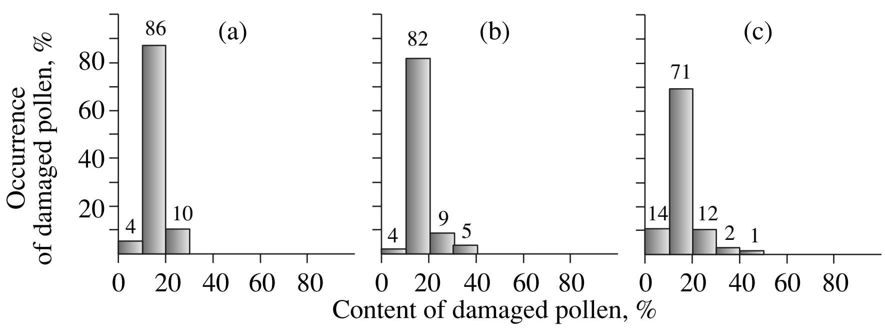

Fig. 6. Histogram of ruptured pollen occurrence in current riverbed deposits (fine sand); (a) Yamal Peninsula (environs of Kharasavei, Tambei, Seyakha, Lyakkatose, and Er''yakha Rivers), 117 samples; (b) Gydan and Tazov Peninsulas (Gyda, Tanama, Tadibeiyakha, Antipaetayakh, and Salemlekabtamda Rivers), 103 samples; and (c) lower (Cherskii-Kolymskoe Settlement) and middle reaches of Kolyma River (the region of Seimchana and Sinegor'e Towns), 100 samples.

Comparison of the proportion of damaged palynomorphs in beach sediment samples from different regions of northern Russia demonstrated that palynomorph damage depended on the facial conditions of pollen spectra formation. Fine sand of the littoral zone included 20–40% of damaged palynomorphs in most studied samples from northern West Siberia and Chukotka.

For comparability of data on pollen damage in alluvial deposits, we selected fine sand samples from riverbed and floodplain facies in the Yamal Peninsula (Kharasavei, Tambei, Seyakha-Zelenaya, Syambileiyakh, Lyakkatose, and Er''yakha Rivers), Gydan and Tazov Peninsulas (Gyda, Tanama, Tadibeiyakha, Antipaetayakh, and Salemlekabtamda Rivers), and lower (Cherskii-Kolymskoe Settlement) and middle reaches of Kolyma River (the region of Seimchana and Sinegor'e Towns). Histograms of damaged pollen occurrence in the fine sand facies were plotted.

Analysis of alluvial deposits demonstrated lower proportions of damaged pollen in them as compared to the beach. Deposits of small rivers in the Yamal Peninsula (Fig. 6a) had the highest proportion of samples (86%) with 10–20% of damaged pollen; 1/10 samples included 20–30% of damaged palynomorphs; and only 4% samples included less than 10% of damaged pollen.

In the Gydan and Tazov Peninsulas (Fig. 6b), the distribution of alluvial sediment samples with damaged pollen was quite similar to that in the Yamal Peninsula. Samples were also collected from alluvial deposits of small rivers. Most samples (82%) included 10–20% of damaged palynomorphs; samples containing 20–30% of damaged palynomorphs amounted to 9%; 30–40%, 5% samples; and 0–10%, 4% samples.

The distribution of damaged palynomorphs in Kolyma River deposits was slightly different (Fig. 6c). Although the majority of samples (71%) included 10–20% of damaged palynomorphs, a considerable fraction of samples (14%) included a low proportion of damaged pollen (0–10%). This can be due to a more pronounced involvement of pollen and spores brought to the alluvial deposits by surface runoff. A small fraction of samples (11%) included 20–40% damaged pollen. In contrast to the rivers of the Yamal and Gydan, the alluvial deposits of the Kolyma included 1% of samples with 40–50% of damaged pollen among which damaged horsetail spores predominated.

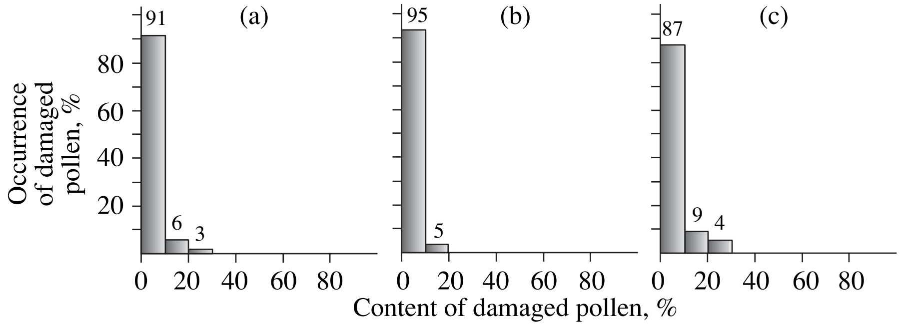

Fig. 7. Histogram of ruptured pollen occurrence in grass–moss cover of terraces and watersheds: (a) Yamal Peninsula (valleys of Kharasavei, Tambei, Seyakha, and Syambileiyakha Rivers and evirons of Mys Kamennyi and Novyi Port Settlements), 94 samples; (b) Gydan and Tazov Peninsulas (valleys of Gyda, Tadibeiyakha, Salemlekabtamda, Indik"yakha, Aderpaetayakha Rivers and Napakovo Trading Station), 96 samples; and (c) Chukotka (valley of Chul'kheveem River, environs of Koolen' Lake, and Provideniya, Lavrentiya, and Wellen Settlements), 101 samples.

For the analysis of damaged pollen in subaerial deposits, we collected samples from the grass–moss cover on various relief elements, largely, terrace and watershed surfaces: the Yamal Peninsula (valleys of Kharasavei, Tambei, and Seyakha Rivers and evirons of Mys Kamennyi and Novyi Port Settlements), Gydan and Tazov Peninsulas (valleys of Gyda, Tadibeiyakha, Salemlekabtamda, Indik"yakha, Aderpaetayakha Rivers and Napakovo Trading Station), and Chukotka (valley of Chul'kheveem River and environs of Koolen' Lake and Provideniya, Lavrentiya, and Wellen Settlements).

In the Yamal Peninsula (Fig. 7a), the highest proportion of samples (91%) contained intact pollen and spores (0–10%) and as low as 9% of samples included 10–30% of damaged palynomorphs.

In the Gydan and Tazov Peninsulas (Fig. 7b), 95% of samples included 0–10% of damaged palynomorphs while only 5% of samples included more damaged palynomorphs (10–20%).

In Chukotka (Fig. 7c), the majority of samples (87%) included intact (0–10%) palynomorphs as well; 10–20 and 20–30% damaged palynomorphs were observed in 9 and 4% samples, respectively.

These palynomorph damages largely included ruptures. The samples most commonly included damaged pollen of *Larix, Pinus silvestris, Pinus sibirica, Salix, Picea*, and spores of *Equisetum.* Further resistance to rupture increased in the following order: pollen of Cyperaceae and *Potentilla*, *Poaceae* spores of *Sphagnum* and Polypodiaceae, pollen of *Betula* sect. *Nanae, Alnaster*, and *Betula* sect. *Albae.* No damaged pollen of *Artemisia* and only singular damaged pollen grains of Ericaceae, Caryophyllaceae, and *Draba* were observed.

Pronounced differences were revealed for ruptured pollen content in the samples formed under subaquatic (transferred by water) and subaerial (largely transferred by wind) conditions. About 70% pollen samples formed under subaquatic conditions included 20–40% ruptured pollen and spores. Over 90% pollen samples formed under subaerial conditions included 0–10% damaged pollen. Thus, the content of ruptured pollen grains can be used as a facial index of deposition. At the same time, damaged palynomorphs that arrived from other deposits are not considered.

Pollen transfer by water leaves them virtually undamaged as demonstrated experimentally (Catto, 1985; Fall, 1987). Smirnov *et al.* (1999) proposed that pollen grains and spores are damaged by redeposition in the river when they are exposed to drying and then come back to water flow. We believe that ruptures also result from pollen freezing and thawing, which is reflected in pollen samples from snow cover and wedge ice. Ruptures also appear after sediment freezing when freezing of a fraction of water increases the salinity and osmolality. Studies of the degree of pollen conservation for certain taxa demonstrated sensitivity of certain pollen grains to osmolality changes in water with variable salinity (Campbell, 1991). Pollen grains with grooves and/or pores conserved well in water of any salinity (pollen of birch and potentilla) (Fig. 8). Pollen grains with sacs (pine pollen) were inclined to ruptures in distilled water but proved resistant in water with salinity of at least 1%. Particularly sensitive aspen pollen started to degrade in distilled water even before sedimentation due to high osmotic pressure in the pollen cell. Alete pollen of aspen and larch degraded in distilled water but preserved well at a salinity of 1%. At higher salinities, pollen of *Populus* shrank while pollen of *Larix* ruptured. Larch pollen is often found in wedge ice in quantities similar to or exceeding those in the synchronous deposits; at the same time, ruptured pollen grains are very frequent. We observed singular aspen pollen in the Holocene wedge ice from the peat bog near the Seimchan Settlement, while they were absent from the enclosing deposits (sphagnum bog).

Almost distilled water naturally occurs after rainfall and thawing of snow or glassier. Hence, *Populus* pollen appears in conditions favoring its degradation if aspen anthesis starts before going of snow cover. Such event is quite frequent, which can partially explain poor con-

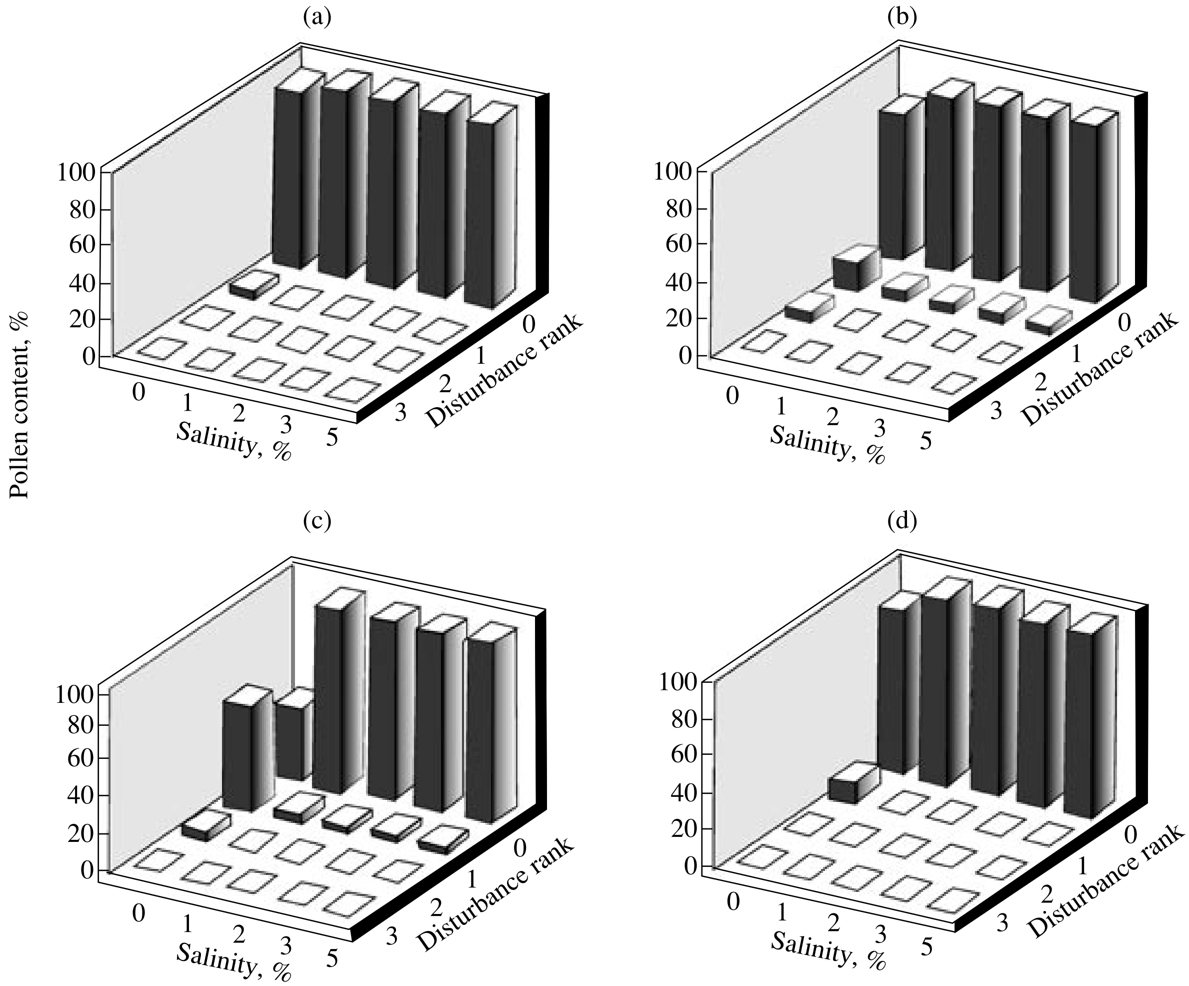

Fig. 8. Degree of experimental pollen disturbance (%) in solutions with different salinity (Campbell, 1991); (a) *Betula*, (b) *Populus*, (c) *Pinus*, and (d) *Potentilla*.

servation of aspen pollen; in particular, it was observed in the Seimchan. Maximum content of *Populus tremula* pollen in Alaska in the early Holocene can be due both to the northward advancement of this species and specific pattern of phenological phases of this period. Apparently, snow cover managed to thaw before the peak of *Populus tremula* anthesis. This is confirmed by the absence of its pollen in northern Alaska in the early Holocene, although its macroremains were identified in the deposits.

Considering certain factors such as low content of sporopollenin, the absence of apertures, and inability to identify damaged *Populus* pollen, one should admit that conservation of this pollen requires a narrow range of conditions. Note that *Populus* is well conserved in the digestive tract of extinct bodies of mammals. For instance, pollen samples including *Populus* pollen were isolated from the stomach of the Kirgilyakhsky baby mammoth (Belaya and Kisterova, 1978), although it was absent from all transects of sediments possibly synchronous to its death. In addition, pollen of larch and willow conserved much better in the digestive tract of the baby mammoth as compared to the deposits of a similar age. Abundant intact pollen of *Populus* was also found in the gut content of *Daphnia* (Hadden, 1978).

Thus, most pollen samples formed in the tundra zone with the involvement of water included 20–40% ruptured pollen. The samples formed under subaerial conditions largely included 0–10% ruptured pollen.

Manifestations of taphonomic factors in pollen accumulation on the snow cover surface and in wedge ice. We studied pollen damage in the tundra zone on the surface of snowfields and in wedge ice in West Siberia and Yakutia (Fig. 9). Analysis of pollen from snowfields demonstrated that the content of ruptured palynomorphs in snow which was maintained until midsummer is similar to that in the surface samples of the grass–moss cover. In northern West Siberia (Fig. 9a), 58% of snowfield samples contained 0–10% damaged pollen and spores; one-third (32%) of samples, 10–20%; and 9%, 20–30%. Damaged palynomorphs were better conserved on the snowfield surface, as indicated by the

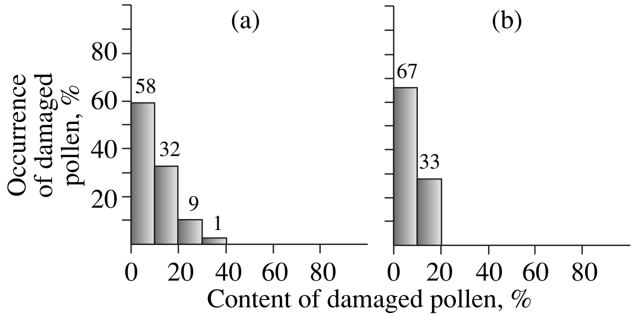

Fig. 9. Histogram of ruptured pollen occurrence in (a) snowfields of the Yamal Peninsula (valleys of Kharasavei, Tambei, and Seyakha Rivers) and the Gydan Peninsula (valleys of Gyda, Tadibeiyakha, and Salemlekabtamda Rivers), 88 samples; (b) wedge ice of the Yamal and Gydan Peninsulas, 92 samples.

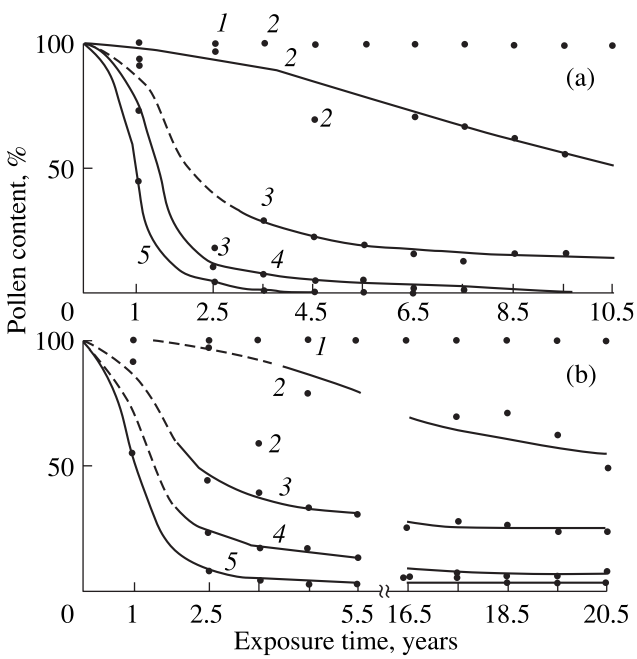

Fig. 10. Degree of experimental pollen conservation (Havinga, 1984) in (a) floodplain soil for 10 years and (b) forest litter for 20 years; *1*, *Lycopodium*; *2*, *Polypodium* and *Taraxacum*; *3*, *Betula*, *Fagus, Juniperus, Pinus, Quercus, Taxus*, and *Tilia*; *4*, *Acer, Carpinus, Fraxinus, Populus, Salix*, and *Ulmus*; and *5*, *Alnus, Corilus*, and *Myrica*.

presence of vacuoles in pollen grains. At the same time, pollen grains were often damaged by ice crystals formed at low temperature as compared to the subfossil samples from subaerial deposits. Immature tricolpate pollen and contorted pollen of cereals were also found on the snowfield surface; apparently, they fell on ice during flowering of these plants growing nearby. Immature tricolpate pollen grains were not considered as damaged, while ruptured immature pollen grains of cereals were recognized as a particular type apart from palynomorphs. According to the data obtained by Berezina and Tyuremnova (1973) in transects of peat-bogs and sapropels, ruptured palynomorphs are degraded first.

Analysis of pollen from Holocene and Pleistocene wedge ice in Yamal and Gydan Peninsulas (Fig. 9b) demonstrated a lower degree of palynomorph damage as compared to snowfields. Samples with the minimum damage (0–10%) amounted to 65%, while 3% of samples had 20–30% of damaged palynomorphs, which is much lower as compared to snowfields. No samples with more than 30% of damaged palynomorphs were found in wedge ice. Possibly, a fraction of ruptured pollen grains and spores has time for degradation during wedge ice formation. This is indicated by the absence of ruptured immature pollen grains of cereals and a lower content of immature pollen grains as compared to snowfields. However, pollen spectra from snowfields and wedge ice generally demonstrate more similarities than distinctions.

Selective resistance of the exine of pollen grains and spores. In the region of permafrost development, sediment freezing decelerates destruction of pollen. This is confirmed by high incidence of ruptured pollen grains and spores. In addition, the degree of pollen destruction partially reflects the degree of exine resistance in a particular taxon. Selective destruction of willow, larch, and aspen pollen has a considerable impact on pollen patterns. Thus, the proportion of well and poorly conserved palynomorphs can be used to evaluate the conditions of pollen sample formation.

Havinga (1984) experimentally studied pollen damage under various edaphic conditions for 20 years (1964–1984). Concentrated pollen and spores of 19 species were mixed with river sand and placed into different types of soil and peat (Fig. 10). Acidic deposits (sphagnum peat, sedge peat, and podzol) featured low microbial activity, while neutral ones (floodplain soil and forest litter) had high microbial activity. In soils with low microbial activity, pollen damage largely included thinning and, to a lesser extent, degradation. In soils with high microbial activity, cavitation damage clearly predominated among pollen damage, while thinning and degradation were less pronounced.

The data obtained by Havinga on pollen conservation in floodplain soil with high microbial activity and neutral pH for 10 years and in forest litter with pH 6.2 for 20 years allow us to arrange pollen grains and spores occurring in the surface samples of the Eurasian tundra zone by their resistance (the proportion of conserved grains is given in parentheses): *Lycopodium* (100%)—*Taraxacum* (50–65%)—*Polypodium* (40–46%)—*Fagus* (26–28%)—*Juniperus* (20–23%)—*Tilia* (18–26%)—*Quercus* (17–40%)—*Betula* (8–10%)—*Pinus* (5–18%)—*Populus* (5–8%)—*Salix* (2–8%)—*Alnus* (1–4%). Note high degree of conservation of deciduous pollen as compared to that of *Pinus, Betula*, and *Alnus* frequent in the tundra zone. This means that considerable quantities of deciduous pollen suggest evaluation of pollen conservation conditions and, particularly, microbial activity.

Cover degradation took place in the most sensitive pollen and spores for 18 months (Fig. 10), after which the rate of degradation decreased and pollen spectra stabilized in the environment with high microbial activity after 18 years. In deposits with low microbial activity, degradation of pollen and spores proceeded much slower and the stabilization occurred later. Nearly no changes in pollen composition were observed although the exine of many grains became considerably thinner. The series of pollen resistance in acidic deposits slightly differed from that in the neutral environment. Havinga presented the following series of decreasing exine resistance: for sphagnum peat, *Lycopodium—Pinus—Taraxacum—Tilia—Alnus—Fagus—Betula—Quercus—Juniperus—Salix—Populus—Polypodium*; for sedge peat, *Lycopodium—Pinus—Taraxacum—Tilia—Alnus—Fagus—Betula—Juniperus—Populus—Quercus—Salix—Polypodium*; and for podzol, *Lycopodium—Pinus—Taraxacum—Tilia—Alnus—Fagus—Juniperus—Betula—Populus—Polypodium—Quercus—Salix.*

Pine pollen is conserved well in acid soil and peatland (as opposed to neutral deposits with high microbial activity), which is important for the analysis of tundra pollen spectra. Havinga recognized the following series of decreasing cavitation resistance: *Lycopodium—Tilia—Salix—Alnus—Betula—Populus—Quercus—Fagus.*

Since even syngenetically (i.e., nearly simultaneously) accumulating and freezing deposits and soils become permafrost within decades, the data obtained by Havinga are partially applicable to the tundra zone. However, if fossil pollen included considerable quantities of damaged palynomorphs, it is reasonable to suppose that the sediments became permafrost much faster so that damaged palynomorphs had not been destroyed. This can be exemplified by pollen samples from certain late Pleistocene transects in Yakutia with a high content of immature pollen of dicotyledons which are quickly degraded by microorganisms in conditions of slower freezing.

CONCLUSIONS

Studies of subfossil pollen spectra in the Kharasavei River valley in the region of Arctic tundra (south-facing slopes) demonstrated that southern winds transfer pollen of not only Scotch pine, Siberian cadar, and birch, but also of dwarf birch, alder, willow, heathers, wormwood as well as spores of sphagnum and club mosses and true ferns. These palynomorphs are extra-local and regional in the zone of Arctic tundra. Hence, they can be used to compare results of pollen analysis of quite distant transects. Surface runoff mostly redistributes pollen of sedges, pinks, miscellaneous herbs as well as redeposited prequaternary palynomorphs. Hence these local components are indicative of secondary changes in pollen spectra induced by surface runoff.

Studies of rupture of pollen grains and spores allowed us to compare exine resistance in individual taxa on the basis of the proportion between damaged and intact palynomorphs and to generate the series of exine resistance to rupture in individual taxa: *Salix*—Cyperaceae—*Sphagnum*—Polypodiaceae—Poaceae—*Betula* sect. *Nanae—Alnaster*—Ericaceae, Caryophyllaceae, and *Artemisia.* Three letter taxa demonstrated nearly no damage.

The tundra pollen samples formed with the involvement of water largely included 20–40% ruptured pollen, while those formed under subaerial conditions included 0–10% ruptured pollen.

Pollen of *Larix* and *Populus* are poorly conserved even in permafrost deposits due to low sporopollenin content; however, they occur in wedge ice and ice of polar glaciers. Such pollen is also conserved in deposits with salinity around 1%, which provides for optimal osmolality conditions. Pressure arising during deposit freezing cannot selectively destroy pollen and spores.

High content of ruptured and immature pollen (over 20%), i.e., the palynomorphs primarily susceptible to degradation, indicates rapid freezing of deposits (within 1–2 years). Action of the taphonomic factors provide for different composition of pollen rain and pollen samples formed on the surface of snow, water, soil, etc.

ACKNOWLEDGMENTS

We are grateful to Prof. Yu.K. Vasil'chuk for the help in field studies and geocryological advice. This work was supported in part by the Russian Foundation for Basic Research (project no. 02-05-64177).

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