

Subfossil Spore–Pollen Spectra from Larch Forests of Central Evenkia: Special Aspects of Interpretation for Paleoecological Research Purposes

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Abstract—Characteristics of 27 subfossil spore–pollen spectra of recent plant communities in larch forests of Central Evenkia. Although larch forests dominate in the study region, the main components of the spectra are *Betula* sect. *Betula* and *Alnus alnobetula* subsp. *fruticosa*, whereas the proportion of *Larix* pollen is reduced relative to that of larch trees in the vegetation and ranges from 0.6 to 13.5%. The proportion of *Picea* pollen increases at sampling points where spruce is a component of tree stand. *Pinus* pollen is a foreign component of the spore–pollen spectra, and its proportion increases in phytocenoses where the tree layer is sparse or absent. Species characteristic of taiga forests and wetland and meadow habitats and indicators of disturbed grounds and burned-out areas have been identified, which will allow a more detailed and objective reconstruction of paleovegetation.

Keywords: subfossil spore–pollen spectra, surface samples, plant communities, Central Evenkia, larch

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The study of vegetation and environmental conditions of previous epochs based on palynological data is a widespread approach in paleoecological research. In reconstructing changes in the vegetation of any region, an important question arises as to how adequately the composition and ratio of components in the spore–pollen spectra reflect characteristics of the communities that produced them. Numerous studies on sub-recent and subfossil spore–pollen spectra have been published over the period from the 1940s [1–4] to the present [5–10]. Detailed data are available on specific features in the formation of spore–pollen spectra, in different regions of Siberia and the Russian Far East [11–14] and on the composition of pollen rain and surface samples from the tundra and forest–tundra zones in the eastern sector of the Russian Arctic [15–18]. Comparisons of surface spore–pollen spectra with the composition of plant communities in the north of Siberia, the Arctic, and Subarctic have shown that using these data for paleoecological reconstructions is associated with certain difficulties [16, 19, 20]. The subfossil spore–pollen spectra of forest ecosystems in the permafrost zone of Central and Eastern Siberia

remain almost unstudied because of poor accessibility of these regions and generally small number of palynological studies.

The history of development and current dynamics of larch forests are of major interest. During the Last Glacial Period, these forests markedly expanded their range in the periglacial zone [21], and currently they occupy vast areas in Northern Eurasia. Larch pollen has a thin exine and is poorly preserved in deposits, which leads to underestimation of its proportion in fossil spore–pollen spectra [22]. Therefore, new data on the composition of recent spore–pollen spectra of larch forests and the degree of their adequacy to the surrounding vegetation are very important for interpreting the results of palynological analysis.

The purpose of this study was to reveal regional features in subfossil spore–pollen spectra of larch forests in the middle reaches of the Nizhnyaya Tunguska River, Central Evenkia, by analyzing surface pollen samples collected in different types of larch forests, waterlogged sparse stands, floodplain plant communities, and bogs.

MATERIAL AND METHODS

Studies were performed in the middle reaches of the Nizhnyaya Tunguska (a right tributary of the Yenisei) near the village of Tura, in the central part of the Central Siberian Plateau with elevations of 120 to 600 m a.s.l. and low-mountain erosion-denudation topography. The climate is temperate, sharply continental. According to long-term data from the Tura weather station (1936–2018), the average temperatures of January and July and annual average temperatures are -35.7 , 16.6 , and -8.8°C , respectively [23]; annual precipitation averages about 370 mm. The study area lies in the zone of continuous permafrost.

This area is included in the Nizhne-Tungusky district of Angara–Tunguska forest province of the Central Siberian plateau forest region [24]. The vegetation is composed mainly of northern taiga light conifer forests dominated by *Larix gmelinii* (Rupr.) Rupr. that are at different stages of postpyrogenic progressive succession [25]. The interfire interval varies from 61 to 139 years depending on terrain topography and slope aspect [26, 27].

To study subfossil spore–pollen spectra, samples were taken of the surface soil layer (1–2 cm) or 3- to 5-cm moss layer from the central parts of moss cushions. Detailed descriptions of vegetation were made at sampling points [28]. On the whole, 27 plant communities were included in the study.

To prepare the samples for palynological analysis, they were heated to boiling in 10% KOH solution, washed with distilled water through a 120- μm sieve to remove large plant remains, and then acetolysis was performed [29]. Mineral deposits were additionally treated with hydrofluoric acid to remove silicates. Analysis was performed by examining no less than 500 pollen grains and spores per sample.

The data were processed and spore–pollen diagrams were plotted using TILIA and TGView programs [30]. The sum total of pollen from trees and shrubs (arboreal pollen, AP) and dwarf shrubs and herbaceous plants (nonarboreal pollen, NAP) was taken as 100%. The percent ratios of spores were calculated relative to this sum.

RESULTS

Local Vegetation at Sampling Points

Four sampling points (sp.) were in closed forest communities: bog bilberry–green moss larch forest with undergrowth of *Alnus alnobetula* subsp. *fruticosa* (Rupr.) Raus. (sp. 1); *Ledum*–green moss larch forest (sp. 2); dwarf shrub–*Linnaea* larch forest with *Picea obovata* Ledeb and undergrowth of *Sorbus* sp. (sp. 3) (all three on the watershed slope and the first terrace above the Nizhnyaya Tunguska floodplain); and horsetail birch forest growing in the high floodplain (sp. 4). The tree layer at all points has a crown closure of 0.5–0.6. The shrub layer is formed mainly by *Alnus*

alnobetula subsp. *fruticosa*, *Rosa acicularis* Lindl., and several *Salix* species: *S. lapponum* L., *S. reticulata* L., *S. rosmarinifolia* L., etc.

The projective cover (PC) of the herb–dwarf shrub layer varies from 19 to 45%. Dwarf shrubs are represented by *Ledum palustre* L. and *Vaccinium vitis-idaea* L. The most prevalent herbaceous plants include several *Carex* species, *Equisetum arvense* L., *E. palustre* L., *Calamagrostis langsdorffii* (Link) Trin., and *C. lapponica* (Wahlb.) Hartm. The moss–lichen layer is formed by different species of green mosses and lichens with dominance of *Polytrichum commune* Hedw. and *Pleurozium schreberi* (Brid.) Mitt.

Samples from open larch forests with a crown closure of 0.3–0.4 were taken in six habitats (sp. 5–10) located on the first terrace above the Nizhnyaya Tunguska floodplain (sp. 5, 6, 9, 10) and on the interfluvial (watershed) slope (sp. 7, 8). The tree layer in these communities is 512 m high and consists of *Larix gmelinii*. Forests on the watershed slope (sp. 7, 8) have undergrowth of *Alnus alnobetula* subsp. *fruticosa*. The herb–dwarf shrub layer is dominated by *Ledum palustre* and also includes other dwarf shrubs such as *Vaccinium uliginosum* L., *V. vitis-idaea*, *Betula nana* L., and *Empetrum nigrum* L. Herbaceous plants are almost absent ($\leq 3\%$ PC). The moss–lichen layer is well developed (up to 95% PC) and consists mainly of lichens at sp. 5 (80% PC); green mosses (*Polytrichum commune*, *Pleurozium schreberi*, etc. at sp. 7, 8, 10; and *Sphagnum* species at sp. 6, 9).

Four samples were taken in sparse lichen forests with a crown closure of 0.1–0.2 (sp. 11–14), and one sample was from a burned-out area overgrown by larch forest with sedges (sp. 15). The tree layer is weakly developed, the height of *Larix gmelinii* trees does not exceed 10 m (sp. 11, 12, 14, 15). The forest at sp. 13 has a well-defined undergrowth of *Alnus alnobetula* subsp. *fruticosa*. The shrub layer is formed by various *Salix* species. Among dwarf shrubs, *Vaccinium uliginosum* is the most common species. The herbaceous layer includes *Carex* sp., *Equisetum* sp., *Eriophorum* sp., *Poa* sp., *Hedysarum* sp.. Its projective cover at sp. 11–13 is no higher than 8% but reaches 35% at sp. 14.

Samples characterizing floodplain vegetation were taken from two points in horsetail–reed grass willow forests (sp. 16, 17) and one point in herbaceous alder forest (sp. 18).

The plant cover of bogs (sp. 19–27) has a complex mosaic pattern due to microtopographic heterogeneity of bog massifs [31]. Fossil pollen and spores for paleoecological research are usually extracted from peat cores, and therefore the formation of spore–pollen spectra in bogs requires thorough analysis. Samples from bogs were collected in the following phytocenoses: sparse larch forest with a sedge–dwarf shrub–sphagnum ground layer (sp. 19), sparse larch forest with a *Ledum*–sphagnum ground layer (sp. 20–22), sparse larch forest with a dwarf shrub–sedge–green moss

ground layer and willow undergrowth (sp. 23), sparse larch forest with a *Ledum*–green moss ground layer (sp. 24), and sparse larch forests with sedge–green moss and bog bilberry–green moss ground layers and undergrowth of various willow species (sp. 25, 26). The last sampling point (27) was in closed wintergreen larch forest growing in the mesotrophic part of the bog massif.

The vegetation of bogs is characterized by diversity in the composition of herb–dwarf shrub layer, whose projective cover reaches 30%. Species such as *Vaccinium uliginosum* L., *Ledum palustre* L., *Oxycoccus microcarpus* Turcz. ex Rupr., and *Empetrum nigrum* prevail in abundance; *Carex*, *Eriophorum*, *Rubus chamaemorus* L., *Epilobium palustre* L. are fairly common in this layer. The projective cover of the moss–lichen layer reaches 60–100%. Green moss larch forests (sp. 23–26) grow in flat bog areas where microtopography is formed by flat moss hummocks and cushions with dominance of *Polytrichum commune*, *P. strictum* L. and *Pleurozium schreberi*. In sphagnum larch forests (sp. 19–22), hummocks and cushions near tree trunks are higher and have greater diameter; dominant species are *Sphagnum fuscum* (Schimp.) H. Klinggr. and *Sph. angustifolium* (C.E.O. Jensen ex Russow) C.E.O. Jensen.

The Results of Analysis of Spore–Pollen Spectra in Surface Samples

Arboreal pollen was prevalent in all samples (70–95%), with *Betula* pollen from plants of both tree and shrub forms being most abundant. A considerable proportion of pollen was contributed by *Alnus alnobetula* subsp. *fruticosa*; pollen from *Larix*, *Picea*, *Pinus*, *Salix*, and other tree species was also included in the spectra (Fig. 1).

Although the majority of samples were collected in different types of larch forests, the proportion of *Larix* pollen varied between 0.6 and 13.5%, averaging 5.2% (Fig. 2). Relatively high values (7–10% or higher) were recorded in both closed (sp. 1, 3, 27) and sparse larch forests and even in a burned-out area where tree stand was absent. On the other hand, the spectrum of bog bilberry–green moss larch forest with a crown closure of 0.5 contained only 1.1% of *Larix* pollen. It should be noted that its proportion in the majority of samples—the values between the first and third quartile (Fig. 2)—were in the range of 2 to 7%.

Picea pollen was found at all sampling points. Its proportion in almost all samples varied between 0.6 and 5%, averaging 3.5%, except for one bog habitat where its variation range was higher: from 0.3 to 15.9% (Fig. 2). The content of *Picea* pollen at points where spruce was included in phytocenosis reached 6–9%, being no higher than 2% in other samples. However, the highest contents of spruce pollen in the spectra were recorded in samples from bogs: 13.1 and 15.9% at sp. 20 and 21. Spruce is absent immediately at sampling

points, but the results of our root surveys confirm that it occurs in the vicinity of the bog.

Pine pollen was also found at all sampling points: the proportion of pollen from *Pinus* subgen. *Haploxylon* varied between 0.2 and 10.3%; from *P.* subgen. *Diploxylon*, between 1.2 and 19.6%. In both cases, the highest contents of pollen were recorded at sampling points in bogs (sp. 19–24), in sparse larch stands or open areas.

Two birch species of the tree form—*Betula pubescens* Ehrh. and *B. pendula* Roth.—grow in the study region. Since it is difficult to distinguish between pollen of these species by morphological traits, the accepted practice in palynology is to identify this pollen at the level of *Betula* sect. *Betula*. The highest proportion of pollen from the tree form of birch in the spectrum (59.4%) was found in horsetail birch forest. This proportion in other samples varied from 16 to 40%, being higher in habitats where birch is a component of local phytocenosis.

The proportion of *Betula nana* L. pollen in the spectra varied widely, from 0.8 to 47.3%, but in most samples it did not exceed 10% (Fig. 2). The highest values were recorded in palynospectra from sparse dwarf shrub–lichen and *Empetrum*–*Ledum*–*Sphagnum* larch forests (sp. 5, 6). The contribution of *B. nana* pollen to the spectra of samples from bog ecotopes (sp. 19–24) was also considerable, especially in phytocenoses where this species was abundant (cop.₁, cop.₂), while its proportion in other samples dropped abruptly.

Alnus alnobetula subsp. *fruticosa* dominated in the shrub layer of most phytocenoses included in the study, and its pollen was one of the main components of spore–pollen spectra at all sampling points. Its proportion varied from 8.2 to 50.1% (in floodplain alder forest, sp. 18) and was generally higher in samples from habitats where this species was highly abundant in phytocenoses. The range of its values between the first and third quartiles of the samples is 18–36% (Fig. 2).

The content of willow pollen showed strong dependence on local conditions and proportions of willows in a plant community. The proportion of *Salix* pollen in the spectra of floodplain willow forests and horsetail birch forest was 7–10% but increased to 33.5% in sparse sedge–green moss larch forest with undergrowth of different *Salix* species within the bog massif. The pollen of other shrubs (*Lonicera*, *Ribes*, *Sorbus*, *Juniperus*) was represented by single grains in several samples.

Some surface samples included foreign tree pollen transferred from long distance. *Tilia* pollen was found in the spectra from four sampling points; *Ulmus* pollen, in the spectrum from one point. Samples from several habitats contained *Alnus* pollen from species of tree life form, which morphologically differed from the pollen of *Alnus alnobetula* subsp. *fruticosa*.

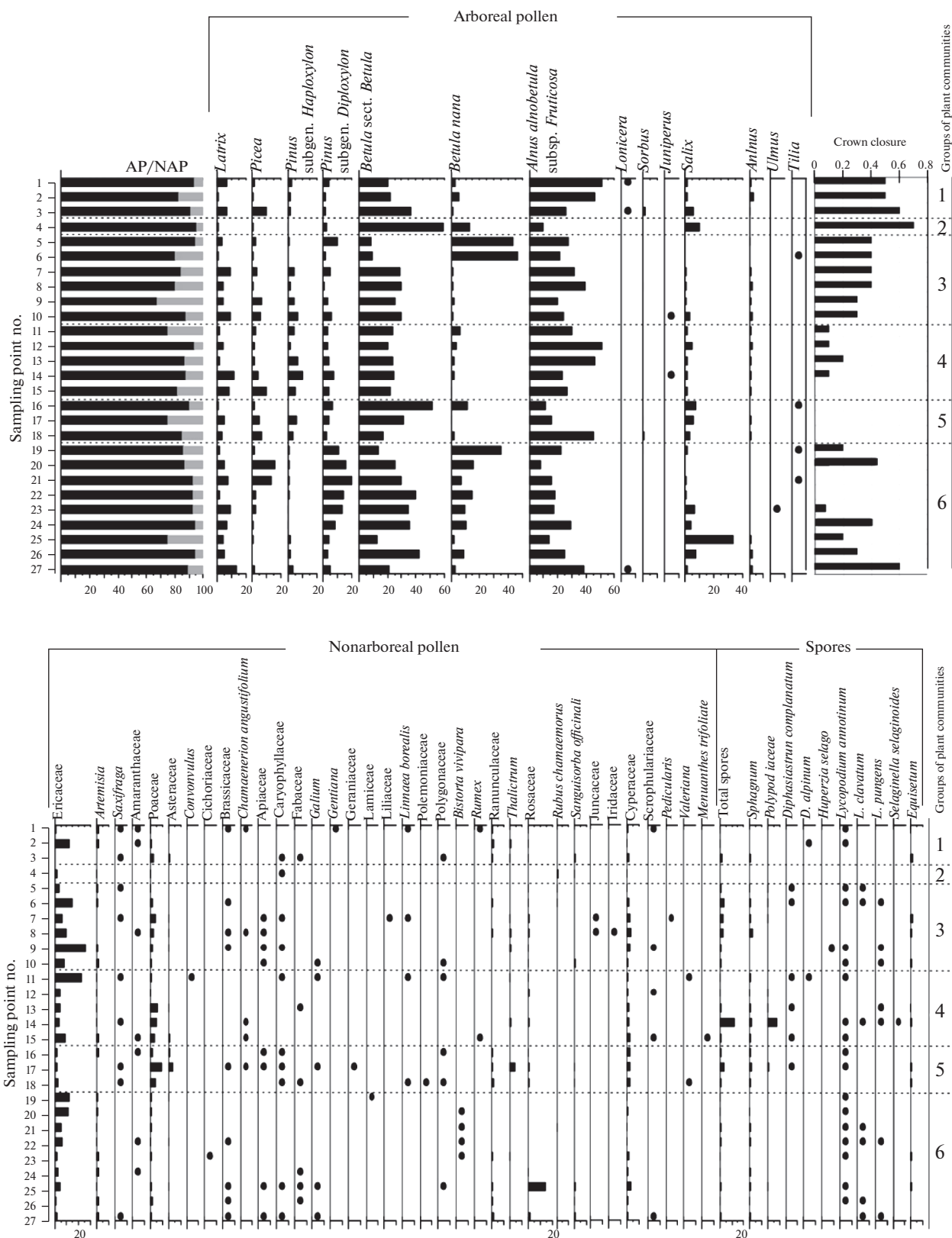


Fig. 1. Spore–pollen diagram of surface samples from plant communities in the region of Tura, Central Evenkia: (1) closed larch forests, (2) birch forest, (3) open larch forests, (4) sparse larch forests, (5) floodplain vegetation, (6) bogs.

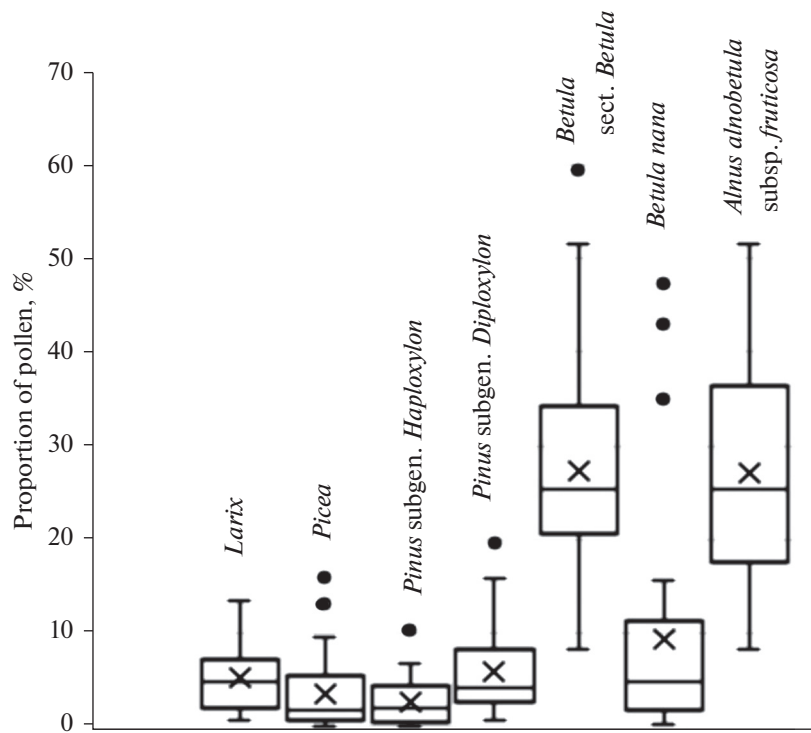


Fig. 2. Proportions of pollen from the main tree and shrub species in spore–pollen spectra of surface samples.

The main contributions to the group of nonarboreal pollen were from plants of the families Ericaceae, Poaceae, and Cyperaceae. The proportion of Ericaceae pollen reached 8–24% at points where these dwarf shrubs were abundant in phytocenosis—e.g., in *Ledum*–green moss, dwarf shrub–lichen, and dwarf shrub–sphagnum–green moss larch forests—but did not exceed 2–3% in all other samples. The contribution of Poaceae pollen was 4–5% in samples from floodplain phytocenoses and dry larch forests, reached 9.4% in horsetail–reed grass willow forest (apparently on account of *Calamagrostis* pollen), and varied between 1 and 2% in other samples. Cyperaceae pollen (0.8–3.2%) was a permanent component of the spectra. The pollen of *Artemisia* and *Amaranthaceae* was also found at certain sampling points.

Surface samples proved to contain pollen from a variety of forbs (0.1–0.3%): Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Fabaceae, Geraniaceae, Gentianaceae, Lamiaceae, Polemoniaceae, Scrophulariaceae, *Valeriana* sp., *Thalictrum* sp., *Bistorta vivipara* (L.) Delarbre, *Sanguisorba officinalis* L., etc. The palynospectrum from sp. 15 (sparse sedge–green moss larch forest with undergrowth of various *Salix* species) contained 14.2% of Rosaceae pollen, which could be explained by local conditions. Its content in other samples was only 0.2–1.5%, or this pollen was absent from the spectrum. The pollen of plants characteristic of disturbed habitats, such as *Convolvulus* and *Rumex*, was represented by single grains in

samples from one or two points, and five samples contained the pollen of *Chamaenerion angustifolium* (L.) Scop. Pollen from bog species—*Rubus chamaemorus*, *Menyanthes trifoliata* L., *Pedicularis* sp.—was also found in the samples.

The total sum of spores relative to that of pollen counts (AP + NAP) varied from 0.5 to 11%. Spores that occurred most frequently were those of *Sphagnum* (0.2–2.2%), ferns (0.2–7.9%), *Lycopodium annotinum* L. (0.2–1.5%), and *Equisetum* (0.2–1.5%). Samples from several points contained spores of club mosses *Diphasiastrum complanatum* (L.) Holub, *Lycopodium clavatum* L., and *L. pungens* (Desv.) Bach. Pyl. ex Iljin, and spores of species such as *Huperzia selago* (L.) Bernh. ex Schrank & Mart. and *Selaginella selaginoides* (L.) P. Beauv. ex Schrank & Mart. were found in only one spore–pollen spectrum. The proportions of *Sphagnum* and horsetail spores were slightly higher in the spectra of plant communities that included these species, while at all other sampling points they occurred in single cases or were absent. Ferns and club mosses were not found immediately at sampling points, but they grow in the study region and could appear in the spore–pollen spectra due to transfer of spores from neighboring forest habitats.

DISCUSSION

The results of this study show that a thorough analysis of data on the composition and ratio of compo-

nents in the arboreal pollen group is necessary for their correct interpretation. The proportion of *Larix* pollen is significantly underestimated relative to the role of this species in phytocenoses. According to our data, there is no relationship between the content of *Larix* pollen in the spectra and the degree of crown closure in larch stands. The discrepancy between the role of larch in plant communities and the proportion of its pollen in the spectra has been repeatedly noted in palynological studies on the history of larch forests and changes in the vegetation of the regions where these forests grow. Thus, the content of *Larix* pollen in surface samples from larch forests of the Middle Timan Range (Komi Republic) was found to vary from 0.6 to 5.0% [22]. Here and below, the percent ratios of pollen taxa are given relative to the sum of AP + NAP (the ratios computed in a different way were recalculated). The proportion of *Larix* pollen in larch forests of Northern Sakhalin averages 1.5% but may reach 12.3% [12]. As shown in studies by Raschke and Savelieva [16] in near-tundra sparse larch forests in the Lena River delta, *Larix* pollen as single grains occurs ubiquitously, but its proportion increases to 4–10% in plots established near mature larch trees. The average proportion of *Larix* pollen in the spectra from larch forests in the Indigirka River basin is about 3% [17].

The question is still debatable as to what is the threshold proportion of *Larix* pollen in the spectra that allows the conclusion about the growth of larch in the area under consideration. The proportion estimated by Lisitsyna et al. [32] for northern Europe is 0.5%, while Klemm et al. [17], based on a large series of surface samples from the north of Eastern Siberia, consider that this value is underestimated and suggest that the threshold is at 2%. Our results show that the proportion of *Larix* pollen even in closed larch forests may be in the range of 0.6–1.5%. It should be noted that pollen in our samples was very well preserved and a great number of pollen grains were examined, which reduced the probability of errors in analysis.

Picea obovata occurs in the study area as an admixture in larch forests, and the proportion of its pollen in the spectra is low, adequately reflecting the role of this species in the vegetation. There is a distinct tendency toward increase in the proportion of *Picea* pollen in the spectra from sampling points where spruce is a component of phytocenosis or grows nearby.

Pine pollen (*Pinus* subgen. *Haploxylon* and *P.* subgen. *Diploxylon*) occurs in the spectra of all surface samples. The range of *Pinus sibirica* Du Tour extends over the study region [33], but it is located close to the range boundary, and this species appears to be very rare in this region. The northern boundary of Scots pine (*Pinus sylvestris* L.) in the middle reaches of the Nizhnyaya Tunguska passes approximately 200 km south of the study region [33]. According to personal communication from A.S. Prokushkin, there is an isolated habitat of *P. sylvestris* located approximately

100 km east of the study region (64°05'59.3" N, 102°56'33.1" E). It should be noted that the proportion of pollen from both pine species reached a peak at sampling points in bogs, where the forest canopy was thin or absent. It is known that the amount of pollen brought by wind from distant regions is much lower in areas beyond the forest canopy than in open habitats due to the filtering effect of tree crowns [34]. Logically, the proportion of pine pollen increases in communities where crown closure is very low or tree stand is absent, in which the content of foreign pollen as a whole is higher. All pine species are characterized by high pollen production, and air sacs on pollen grains facilitate their transfer by air to considerable distances. Klemm et al. [18] have used the content of *Pinus* pollen or variation in the *Pinus/Larix* ratio as an indicator of landscape openness in arctic regions.

The pollen of *Tilia*, *Ulmus*, and *Alnus* is also foreign for the study region. The boundaries of their ranges lie thousands of kilometers away from this region. The transfer of pollen of various broadleaf and conifer species far beyond their ranges, to the Arctic and other regions with severe climate, has been often reported by palynologists working in such regions [35–37]. For example, single grains of linden and alder pollen have been found in surface samples from the Polar Urals [7] and northern Taimyr [37], and input of pollen from different pine species is a typical phenomenon for arctic regions both in Europe [10, 36] and Siberia [16, 37, 38].

The data on the ratio of components in the spectra of surface samples from larch forests show that their main components are contributed by birch and Siberian alder (*Alnus alnobetula* subsp. *fruticosa*), which is expectable from wind-pollinated plants with high pollen production. The contributions of birch and Siberian alder pollen in the majority of samples vary from 20 to 35% and from 18 to 36%, respectively (Fig. 2). The relative content of birch pollen markedly exceeds the proportion of this species in tree stands. This phenomenon has been observed not only in larch but also in spruce forests [8, 9] in which pollen production of the main forest-forming species is lower than that of birch.

Alnus alnobetula subsp. *fruticosa* is widespread in the study region, and the contribution of its pollen is expectably high. However, there is a tendency toward further increase in this contribution up to 45–50%, especially in alder thickets. The proportions of *Betula nana* pollen adequately reflect the role of the species in phytocenosis and depend on its abundance in the local vegetation. The relative content of *Salix* pollen also depends of specific local conditions for the formation of spore–pollen spectra.

The composition and ratio of main components in the groups of nonarboreal pollen and spores also reflect the patterns of species richness and abundance of different species in the vegetation to the degree allowed by the method of palynological analysis. Detailed studies on the composition of present-day

flora and vegetation in the region have shown that species of the families Ericaceae, Rosaceae, and Poaceae are the main contributors to the palynospectra among dwarf shrubs and herbaceous plants [25], with their pollen most frequently occurring in the samples. The proportion of Cyperaceae pollen increases in bog habitats, where sedges and cotton grass play a significant role in phytocenoses.

Palynospectra from the majority of sampling points include the pollen of plants typical for ruderal habitats of areas with the disturbed or poorly formed soil–plant cover, such as Amaranthaceae, *Artemisia*, *Convolvulus*, and *Rumex*. The family Amaranthaceae is represented in the study region by only three species: *Chenopodium acerifolium* Andr., *Ch. rubrum* L., and *Ch. suecicum* Murr. [39], which grow along roadsides, riverbeds, and lake shores on pebble soils. The genus *Artemisia* is represented by five species, with two of them occurring more frequently: *Artemisia vulgaris* L., which grown in burned-out areas and larch forest margins, and *A. laciniata* Willd., a meadow–steppe species [40]. The pollen of *Chamaenerion angustifolium* found in the samples is an indicator of burned-out areas, which often occur in the study region.

Although the group of spores was relatively small, it was possible to reveal species characteristic of taiga forests. These are *Lycopodium annotinum* and *L. clavatum*, which are most frequent in the study region, and also *Diphasiastrum complanatum* and *Huperzia selago*. It is noteworthy that one sample proved to contain spores of *Selaginella selaginoides*, a circumpolar hypoarctomontane species that is very rare in the Angara–Tunguska province [40] and has not been previously found in the study region.

CONCLUSIONS

Analysis of composition and the ratio of components of spore–pollen spectra in surface samples from different types of plant communities in larch forests of Central Evenkia provided a basis for the following conclusions:

Although larch forests dominate in the study region, the main components of the spectra are *Betula* sect. *Betula* and *Alnus alnobetula* subsp. *fruticosa*, which is explained by differences in pollen production, distribution pattern, and fossilization between representatives of the genera *Alnus*, *Betula*, and *Larix*. The proportion of *Larix* pollen is reduced relative to that of larch trees in the vegetation, which has been repeatedly noted in palynological studies. Our data show that in palynospectra formed mainly due to pollen transfer by air, in the absence of input with river waters, the proportion of *Larix* pollen may be as low as 0.6–1.5% even in closed larch forests. The proportion of *Picea* pollen in the spectra is relatively low (on average, 3.5%) but increases at sampling points where spruce is a component of tree stand.

(2) *Pinus* pollen is a foreign component of spore–pollen spectra in the study region. The proportion of pollen from both *Pinus* subgen. *Haploxylon* and *P.* subgen. *Diploxylon* increases in phytocenoses where the tree layer is sparse or absent, which allows pine pollen to be used as an indicator of increase in the proportion of open habitats in the study area. More accurate interpretation of fossil spore–pollen spectra and conclusions about the former presence of pine in the study region will be possible if additional evidence is obtained (e.g., findings of seeds, needles, bark, wood, etc.).

(3) The ratio of components in the palynospectra of plants from the herb–dwarf shrub layer largely depends on local conditions. Species characteristic of taiga forests, bog and meadow habitats, and indicators of disturbed lands and burned out areas revealed in this group will allow a more detailed and objective reconstruction of paleovegetation.

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CONFLICT OF INTERESTS

The authors declare that they have no conflict of interest.

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