УДК 551.89(571.651):561

VEGETATION RESPONSE TO CLIMATE CHANGE IN POLAR CHUKOTKA FROM 2.510–2.554 MA BP

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The response of vegetation to climate change in Polar Chukotka between 2.510 and 2.554 Ma was determined by a palynological study of sediment cores from Lake Elgygytgyn recovered during the international expedition "El'gygytgyn Drilling Project". Six pollen zones were defined for this interval, which spans marine isotope stages (MIS) 101 and 100. Pollen zones 1 and 2 (MIS 101) as well as zones 3 and 4 (MIS 100) indicate the presence of *Larix* and *Larix-Betula* forests during interglaciations. The plant communities reflected in the spectra of zone 3 represent the warmest climates during the early Gelasian Age. During MIS 100, the period of maximum climate cooling is marked by the regional presence of shrub and herb dominated tundra (pollen zone 5). During the interstade (MIS 100, zone 6), the vegetation was dominated by *Larix* forest tundra. Pollen zones 3 and 4, which have spectra more indicative of interglacial rather than glacial plant communities, are more consistent with climate of MIS 101 and not MIS 100, as suggested by the core's age model. The incorrect age assignment of the boundary between these stages indicates that the Lake Elgygytgyn age model needs revision.

***Keywords*: Gelasian Age, isotope stage, pollen zone, interglaciation, interstade, glaciation.**

DOI: 10.34078/1814-0998-2023-2-42-51

Palynological analysis of a sediment record from Lake Elgygytgyn (67º 30' N, 172º 05' E; Fig. 1) has revealed the responses of vegetation in Polar Chukotka to climate changes between 2.510 and 2.554 million years ago (Ma). The lake is in a crater formed by a meteor impact, which occurred c. 3.58 Ma (Layer, 2000). As part of the International Expedition "El'gygytgyn Drilling Project" (Melles et al., 2012; Nowaczyk et al., 2013; Lozhkin, Anderson, 2020a), a continuous sediment core was raised in the center of the lake (drilling site 5011-1, water depth 176 m; Fig. 1). The interval discussed in this paper includes marine isotope stages (MIS) 100 and 101 (Lisiecki, Raymo, 2005) and corresponds to the earliest part of the Gelasian age.

RESEARCH METHODS

Sediment samples from Lake Elgygytgyn in the interval 2.510–2.554 Ma were prepared for palynological analysis following standard methods used in the study of arctic lakes and estuaries (PALE, 1994). A minimum of 300 pollen grains from terrestrial plants was counted in each sample. The spore-pollen diagrams were constructed using Tilia and Tilia-graph (http://www.tiliat.com) and show the percentages of 3 subsum groups (woody plants; nonwoody shrubs and herbaceous plants; moss and ferns) as well as for individual pollen and spore taxa (Figs. 2, 3). Each pollen taxon is represented as a percentage of the sum of all arboreal and nonarboreal pollen grains. The percentages of spores are based on the same pollen sum. Difficulties in achieving sufficiently high counts due to low pollen concentration occurred in some samples, particularly in intervals 2.5176–2.520 Ma, 2.525–2.5275 Ma, 2.537–2.541 Ma, and 2.544–2.547 Ma. Modern palynological samples taken from the sediment-water interface in lakes from Western Beringia aided the paleovegetation interpretations (Anderson et al., 2002a; 2002b; Lozhkin et al., 2002; Tarasov et al., 2013). The modern spectra from Lake Elgygytgyn itself are dominated by *Alnus* (*Duschekia fruticosa* (Rupr.) Ledeb.), *Betula*, and *Pinus pumila* (Pall.) Regel representing up to 45 % of the modern pollen

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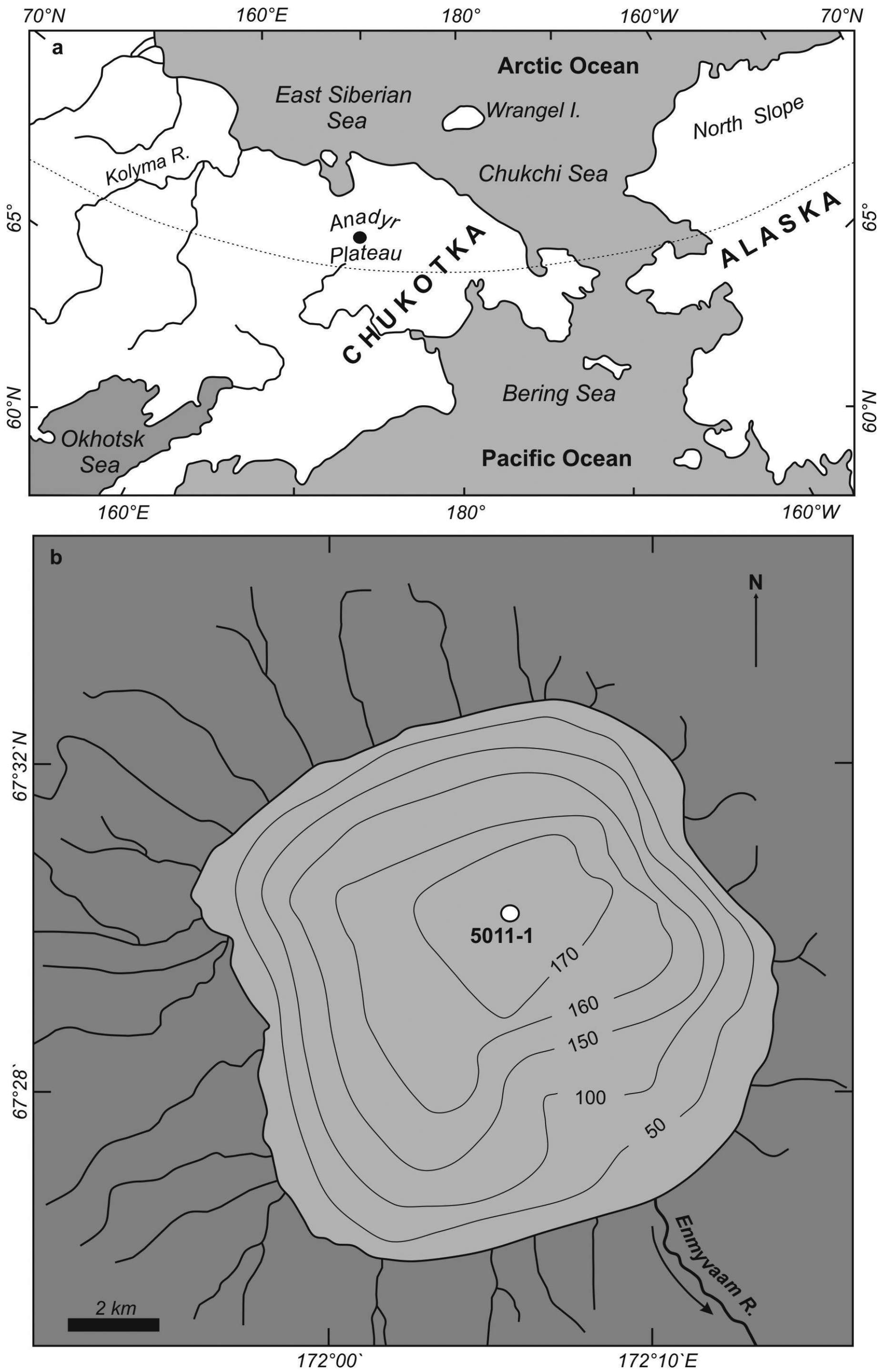

Рис. 1. (a) Географическое положение оз. Эльгыгытгын (темный кружок); пунктирная линия – Полярный круг. (b) Батиметрия оз. Эльгыгытгын (глубины озера даны в метрах), место отбора керна озерных осадков (белый кружок), ручьи, впадающие в озеро, и вытекающая из озера р. Энмываам

Fig. 1. (a) Map showing the location of Lake Elgygytgyn (dark circle); dotted line represents the Arctic Circle. (b) Lake Elgygytgyn bathymetry (lake depths are given in meters); coring site (white circle); inflowing streams and the Enmyvaam River outlet

assemblage, and primarily reflect the long distance transport of these pollen taxa from other areas of the Anadyr Plateau (Lozhkin et al., 2002). The present-day vegetation near the lake is dominated by lichens and graminoid species. Plant cover is discontinuous at higher elevations within the crater. Low shrubs of *Salix krylovii* E. Wolf and *S. alaxensis* Cov. occupy protected sites in upland valleys and are found along the Enmyvaam River. *Betula exilis* Sukacz. is limited to valley areas, where organic matter has accumulated (Kozhevnikov, 1993). Thus, the modern pollen spectra from Lake Elgygytgyn reflect

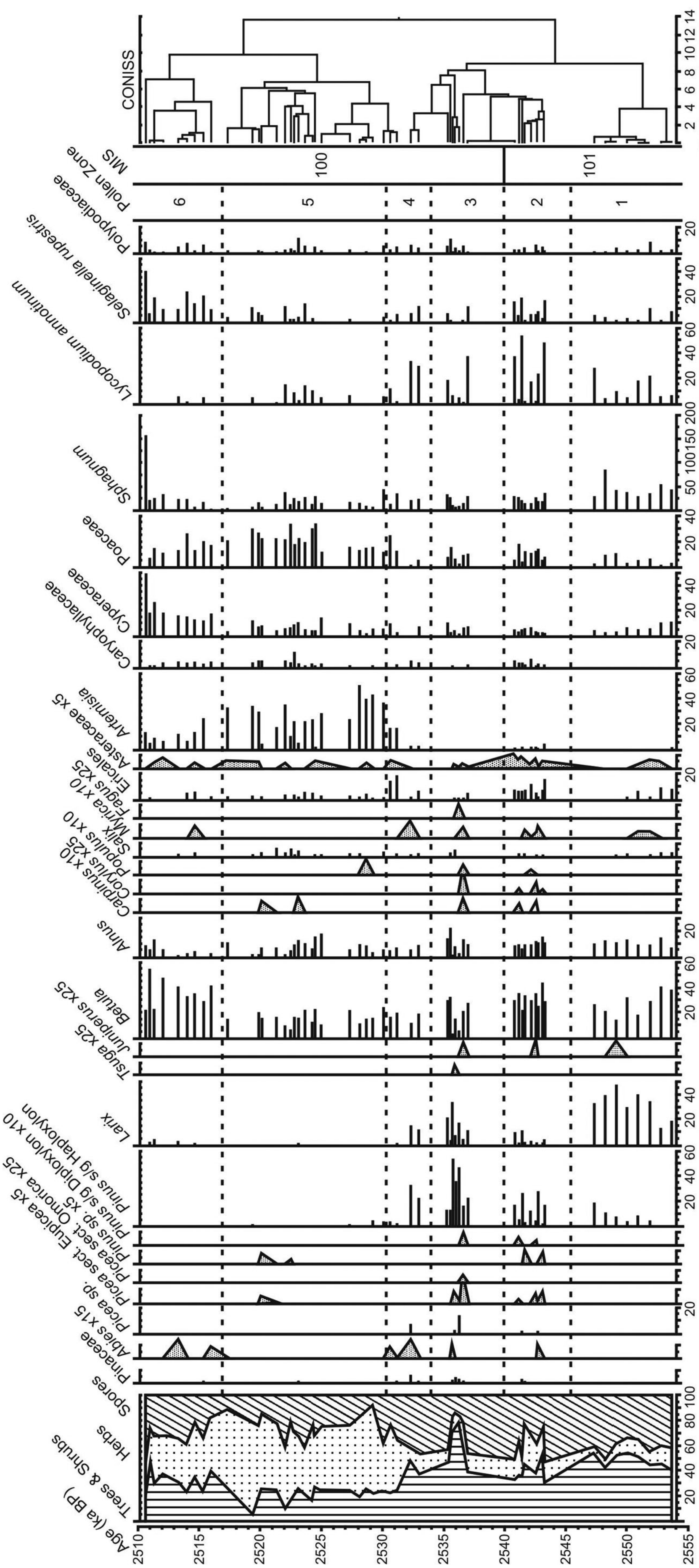

Рис. 2. Процентные соотношения групп растительности, основных пыльцевых и споровых таксонов в спектрах осадков оз. Эльгыгытгын (морские изотопные стадии 101–100)

Fig. 2. Percentage diagram showing vegetation groups and the main pollen and spore taxa from Lake Elgygytgyn sediments (marine isotope stages 101–100)

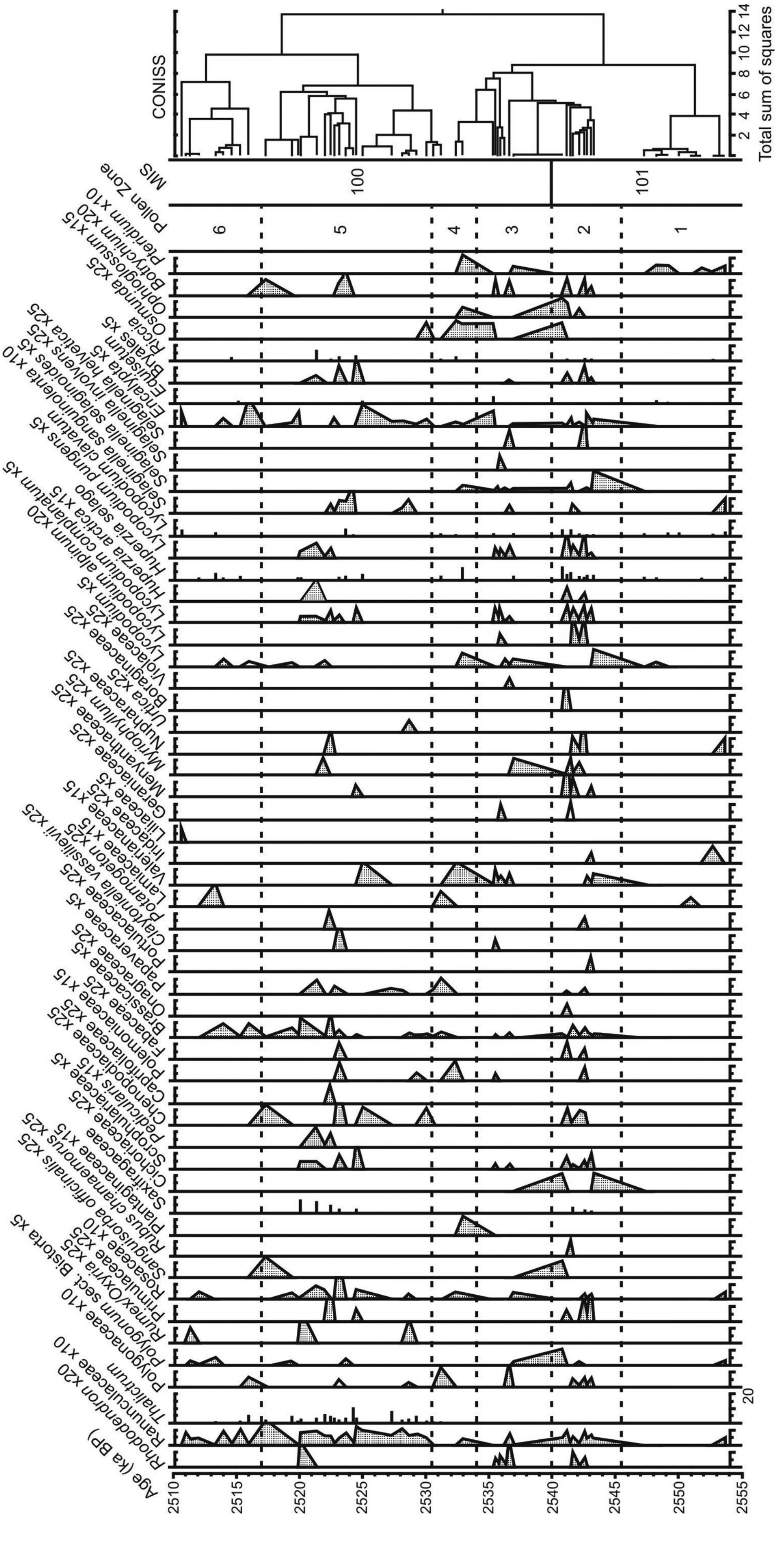

Рис. 3. Второстепенные пыльцевые и споровые таксоны в спектрах осадков оз. Эльгыгытгын (морские изотопные стадии 101–100)

Fig. 3. Percentage diagram showing the minor pollen and spore taxa from Lake Elgygytgyn sediments (marine isotope stages 101–100)

the regional vegetation of northern Chukotka and not the local plant communities, which are characterized by a discontinuous vegetation cover and low pollen productivity.

POLLEN ZONES AND THEIR CORRESPONDING ISOTOPE STAGES

Changes in the percentages seen in both subsums and individual taxa delineate 6 pollen zones for the 2.510–2.554 Ma interval. These zones characterize the vegetation during interglaciations (zones 1–4), glaciations (zone 5) and interstades (zone 6). Pollen zones 1 and 2 belong to MIS 101, whereas the remaining zones fall within MIS 100. According to the lake age model, the boundary of pollen zones 1 and 2 dates to 2.545 Ma. The boundary of pollen zones 2 and 3 coincides with the boundary of MIS 101 and MIS 100, whose age has been determined to be 2.54 Ma (Lisiecki, Raymo, 2005). Following the lake age model, the boundaries of pollen zones 3 and 4 date to 2.534 Ma, zones 4 and 5 to 2.5305 Ma, and zones 5 and 6 to 2.517 Ma.

FEATURES OF SPORE-POLLEN SPECTRA

Betula pollen is present consistently throughout the 2.510–2.554 Ma interval of the Elgygytgyn record. However, *Betula* percentages can reach 40–55 % in zones with interglacial and interstadial climates. The taxon also remains quite high (up to 20–25 %) in samples from glacial stages. *Alnus* pollen occurs in equal amounts during glaciations and interglaciations (up to 15–20 %). *Pinus* subgen. Haploxylon pollen is consistently present in interglacial samples, reaching peaks of up to 55 %. In glacial and interstadial spectra, *Pinus* subgen. Haploxylon pollen occurs more sporadically, being absent in some samples, and never exceeds 4%. *Larix* pollen is characteristic of interglacial assemblages only. The same is true for pollen of *Picea* sp. and *Picea* sect. Eupicea. *Larix* pollen reaches 35 % in pollen zone 3 and 50 % in zone 1. *Picea* sp. is at maximum (15 %) in zone 3. Pollen from the more thermophilus taxa *Corylus*, *Myrica*, and *Fagus* occurs intermittently in this part of the Elgygytgyn record. Cyperaceae plays a significant role in all the pollen zones, but its percentages increase significantly in pollen zone 6 (up to 27–48 %), which is associated with interstadial conditions. Poaceae pollen is a dominant taxon throughout all zones. During glacial stages, the taxon can be up to 34 %, but its percentages decrease during interglaciations. *Artemisia* pollen is another important herb taxon associated with glacial vegetation (up to 50 %), but the taxon is reduced to < 4 % during times of warm climates. Increased percentages of *Artemisia* pollen correspond to samples with a greater number of *Selaginella rupestris* (L.) Spring spores, especially in zone 6 (up to 25–40 % of the pollen sum). *Sphagnum* and *Lycopodium annotinum* L. spores appear consistently throughout all zones but with higher values (35–55 %) during interglaciations.

CHARACTERISTICS OF POLLEN ZONES AND PLANT COMMUNITIES

The palynological spectra of pollen zone 1 reflect the vegetation present during the first half of MIS 101. Of note are the very high percentages of *Larix* pollen, which are unique within Beringian paleovegetation records. The dominance of *Larix* pollen in these spectra suggests the tree's importance both locally and regionally. *Larix* forests established in areas of the surrounding Anadyr Plateau, as well as establishing characterizing the vegetation to the south and west. A dense shrub understory of *Alnus* (*Duschekia*), *Betula*, *Salix,* and *Pinus pumila* was an important feature of this light coniferous forest. The species of *Larix* probably was one that was close to the modern *Larix sibirica* Ledeb., and not to *Larix cajanderi* Mayr, the latter being the only coniferous tree that now forms forests in northeastern Siberia. As shown by A. P. Vaskovsky (1957), this assumption is based on the fact that the pollen of *Larix cajanderi* is extremely poorly preserved even in modern palynological spectra. In the river valleys, gallery forests of *Larix*, *Alnus hirsuta* (Spach.) Rupr., *Populus* (probably *Populus suaveolens* Fish.), and *Chosenia arbutifolia* A. K. Skvortsov developed. Moderately mesic Ericales-*Sphagnum* communities played a significant role in the ground cover. Features of the palynological spectra of pollen zone 1 show that the first half of MIS 101 was characterized by warm climates and corresponds to one of the Gelasian interglaciations.

Plant communities that developed in the second half of MIS 101 reflect the presence of a more diverse composition within the *Larix-Betula* forests. The zone 2 forest included *Picea* sect. Eupicea (*Picea obovata* Ledeb.) as individual trees or within small stands in well-drained areas in river valleys, *Abies* and, possibly, the moderately thermophilus shrubs *Corylus* and *Myrica*. An additional feature of zone 2 is an increase in *Pinus* subgen. Haploxylon pollen, which probably represents the shrub *Pinus pumila* and a tree form close to the modern species *Pinus sibirica* (Rupr.) Mayr. The regional distribution of mossy coniferous forests and dwarf forests (yernik) is also indicated by the high percentages of *Lycopodium annotinum* spores. Heather communities were also more common as compared to zone 1, as were *Artemisia* and *Selaginella rupestris* communities, the latter populating well-drained slopes within the stream valleys. The limited, trace occurrence of *Populus* pollen suggests the presence of *Populus suaveolens* in the gallery forests in association with *Alnus hirsuta*, *Chosenia arbutifolia*, *Larix*, and *Picea obovata.*

Further climate warming is indicated by the zone 3 pollen assemblage, where the pollen of trees and shrubs (up to 80 %) is at a maximum with peaks in *Pinus* subgen. Haploxylon (55 %) and *Larix* pollen (up to 33 %). The regional vegetation was *Larix-Bet-*

ula forests, which included moderately thermophilus trees and shrubs (*Fagus* sp., *Myrica* sp.). Coniferous forests composed of *Pinus* spp., *Picea* spp. (up to 15 % of the pollen from *Picea* sp. and *Picea* sect. Eupicea), and *Abies* occurred at higher elevations (e. g., foothills and mid-elevations in the mountains). *Picea obovata* perhaps formed subalpine woodlands. The wide distribution of forests within the lowlands and mountains is further emphasized by the constant presence of *Lycopodium annotinum* spores in the zone 3 assemblage. The *Tsuga* pollen found in this zone represents long-distance transport from more southerly forest communities.

The palynological characteristics of zone 3 indicate the presence of interglacial conditions and represent the warmest climates in the interval 2.510–2.554 Ma BP. Average temperatures during the growing season were > 16 °C.

Pollen zone 4 also is characterized by interglacial vegetation. The forest possibly included moderately thermophilus deciduous shrubs with *Lycopodium annotinum* common in the ground cover. Compared to zone 3, Ericales-*Sphagnum* communities played a somewhat larger role within the forest communities. *Artemisia* and *Selaginella rupestris* were important on the well-drained slopes of the numerous inflowing streams to the lake.

A sharp restructuring of the vegetation occurred at the zone 4 – zone 5 boundary. This change is reflected in the shift in palynological spectra, which indicate that a significant cooling occurred in the younger zone. As seen in other parts of the Lake Elgygytgyn record, the transition from pollen zones characterized by interglacial vegetation to ones indicative of glacial conditions is usually very pronounced (Lozhkin, Anderson, 2020a; Lozhkin et al., 2020). The main feature of pollen zone 5 is the absence of coniferous pollen taxa, except for the occurrence of single grains of *Pinus* subgen. Haploxylon. *Larix* pollen was not found in any of the samples prepared for palynological analysis. The zone 5 assemblage indicates the dominance of open tundra landscapes. Shrub *Betula* (likely a species close to modern *Betula exilis* Sukacz. and/or *B. middendorffii* Trautv. & C. A. Mey) probably played a significant role in the local and regional vegetation, perhaps forming dense thickets (yerniks) on the slopes of river valleys. During this cold stage, shrub *Alnus* (*Duschekia*) likely occurred as isolated thickets in the most protected places in the Elgygytgyn area. Even considering the underrepresented nature of *Salix* pollen, this taxon was probably the most common shrub in the tundra vegetation based on its present-day ecology.

Zone 5 also is characterized by high percentages of Poaceae pollen (peak of 35 %), indicating a wide distribution of open places, such as wet meadows that included members of the Cyperaceae, Ranunculaceae, Saxifragaceae, and Caryophyllaceae families, near the lake. These taxa along with *Salix* commonly appear during Quaternary with glaciations in of northeastern Siberia. Additionally, the high percentages of *Artemisia* pollen (peaks of up to 50%) indicate the presence of gravel-rich and rocky areas, especially along slopes with southern exposures, and/or coarse-grained, well drained soils. The presence of *Selaginella rupestris* spores (up to 14 %), a species adapted to debris covered slopes, also indicates areas of disturbed ground.

Late Pleistocene palynological assemblages from Beringia, dominated by herb taxa with especially high percentages of *Artemisia* pollen, have been interpreted as steppe or steppe-tundra (Hopkins et al., 1982). This conclusion is based partially on the need for a productive vegetation, which is required to support the populations of large mammals that occupied the region. Biome reconstructions for other portions of the Elgygytgyn record indicate the presence of steppe during glacial times (Tarasov et al., 2013). The high percentages of *Artemisia* pollen and other xeric taxa found in zone 5 are like the Late Pleistocene assemblages, suggesting the presence of a similar paleovegetation during the early Gelasian age. However, a different biome reconstruction, which included both steppe and dry tundra options, showed that at least during the Late Pleistocene, the Beringian vegetation was probably tundra rather than extensive grasslands associated with Asian steppes (Bigelow et al., 2003). Even with the high percentages of *Artemisia* pollen, the dominance of total herb taxa and presence of taxa indicative of mesic settings most likely indicates the presence of tundra, and not steppe, both within the crater and across the region. In fact, the increased pollen percentages from zone 4 to zone 5 of relatively xerophilic herbaceous taxa is consistent with a shift towards colder, drier conditions. Such a change in paleoclimate could reasonably influence the local vegetation with a greater presence of disturbed substrates (e.g., rubbly slopes and slopes with disturbed soils in the valleys of numerous streams) that can be common in the modern tundra.

Larix pollen, reaching up to 5 %, appears again in zone 6. The relatively low percentages, as compared to zones 1–4, suggest the establishment of *Larix* forest-tundra. The dominance of *Betula* pollen (peaks of 47–56 %) among the shrub taxa suggests the presence of *Betula* thickets (yernik) on mountain slopes and in the bordering uplands. However, it is possible that tree *Betula* formed isolated stands on the slopes surrounding the lake. Another feature of the zone 6 assemblage is the low percentages of *Alnus* pollen. Most likely, shrub *Alnus* (*Duschekia fruticosa*) was restricted to isolated thickets in protected microhabitats in the Lake Elgygytgyn region. Other areas supported graminoid forb meadows, mesic Ericales-*Sphagnum* communities, and xeric plant associations (e. g., *Artemisia*, *Selaginella rupestris*) on well-drained, disturbed substrates.

The features of the palynological spectra of zone 6, indicate a noticeable warming of the climate, in comparison with zone 5. However, the palynological data suggest a vegetation indicative of interstadial rather than interglacial conditions.

CONCLUSION

Palynological analysis of the sediments from Lake Elgygytgyn, which accumulated between c. 2.510 and 2.554 Ma, permits the following conclusions:

Pollen zones 1 and 2 (MIS 101) and zones 3 and 4 (early MIS 100) represent interglacial vegetation. This warm climate vegetation is characterized by *Larix* and *Larix-Betula* forests with a dense shrub understory of *Betula*, *Alnus* (*Duschekia*), *Salix*, and *Pinus pumila.* Tree species of *Pinus*, *Betula*, and *Alnus* were also present as were *Abies* sp. and *Picea* sp., the latter two taxa associated with modern day dark coniferous taiga. Gallery forests were formed by *Populus suaveolens*, *Chosenia arbutifolia*, *Alnus hirsuta*, *Picea obovata*, and *Larix* sp.

The zone 3 pollen assemblage characterizes the vegetation associated with the warmest climate in the 2.510–2.554 Ma interval. The presence of pollen from a variety of coniferous taxa underscores the importance of coniferous forest in northern Chukotka during Quaternary interglaciations; this vegetation contrasts sharply to herb and shrub tundra that predominate in this region today (Lozhkin and Anderson, 2020b). Most of these warm intervals occur during the Early Pleistocene (MIS 93, MIS 91, MIS 81, MIS 71) and are characterized by pollen assemblages that indicate the widespread distribution of light coniferous forests with tree spp. of *Larix*, *Betula,* and *Alnus*. The most extreme warming events over the last ≈ 2.6 Ma occurred during MIS 31, MIS 11, and MIS 5. At these times, dark coniferous forest with *Picea*, *Pinus*, and *Larix* formed the regional vegetation, representing an expansion of the northern range limit for some species of ≈ 2000 km. Only the interglaciations include peaks in pollen percentages of *Pinus* subgen. Haploxylon.

Maxima in coniferous pollen percentages set pollen zones 3 and 4 apart from the previous and subsequent zones. The plant communities reflected in the zone 3 – zone 4 spectra clearly characterize one of the Gelasian climatic optima. In this regard, these zones are more consistent with an age assignment to MIS 101 and not the cooler MIS 100, as indicated by the current Elgygytgyn age model. The boundary between MIS 100 and MIS 101 has been dated to c. 2.5305 Ma in the deep-sea records (Lisiecki, Raymo, 2005), whereas according to the palynological data and the Elgygytgyn age model, the shift from warm (MIS 101) to cool (MIS 100) climate occurred c. 2.535 Ma. Thus, the lake age model for this portion of the core needs revision. A deep cooling of the climate is marked by zone 5 and was characterized by forest being replaced by shrub and herb tundra. The vegetation was dominated by Cyperaceae-Poaceae communities with various forb taxa indicating a variety of mesic to xeric microhabitats. The abundance of *Artemisia* pollen and *Selaginella rupestris* spores in the assemblages indicate the importance of well-drained substrates and disturbed sites, certainly within the crater and perhaps regionally. Although high percentages of *Artemisia* and graminoid pollen has led some paleoecologists to infer the regional presence of steppe or steppe-tundra during Pleistocene glaciations, the presence of mesic taxa as well as the broad ecology of Poaceae and Cyperaceae spp. suggest that a mosaic of mesic to xeric environments were present and that a dominance of steppe communities is unwarranted. Additionally, the high percentages of *Betula* pollen are more consistent with tundra rather than steppe.

During the interstade marked by pollen zone 6, the vegetation near Lake Elgygytgyn and that surrounding the Anadyr Plateau was dominated by *Larix* forest-tundra with tree *Betula*. Additionally, *Betula* shrub thickets (yernik) dominated on mountain slopes and in the uplands. Tree *Betula* perhaps also formed isolated stands on the hillslopes surrounding the lake. Shrub *Alnus* (*Duschekia fruticosa*) in the Lake Elgygytgyn region occurred as small, isolated thickets growing in the most protected sites. Graminoid-forb meadows were important parts of the landscape, as were mesic Ericales-*Sphagnum* communities and associations of *Artemisia* and *Selaginella rupestris* found on well-drained, disturbed slopes. *Chosenia arbutifolia* and *Populus suaveolens* probably formed isolated stands, which included *Larix* and small numbers of taxa that today are found in the dark coniferous taiga (*Abies* sp.).

Unusual plant communities, not found in North East Siberia in other intervals of the Quaternary period, reflected by pollen zones in the interval of 2.510–2.554 Ma, show the wide range of past climates and suggest that arctic plant communities as we know them will likely disappear in response to future global warming.

We are grateful to L. N. Kotova for her assistance in the chemical preparation of samples for palynological analysis.

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Received 26.04.2023.
Received after revision 04.05.2023.

РЕАКЦИЯ РАСТИТЕЛЬНОСТИ ПОЛЯРНОЙ ЧУКОТКИ НА ИЗМЕНЕНИЯ КЛИМАТА 2510–2554 ТЫСЯЧИ ЛЕТ НАЗАД

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Реакция растительности Полярной Чукотки на изменения климата в интервале 2510–2554 тысячи лет назад была установлена при исследовании керна осадков оз. Эльгыгытгын, полученного международной экспедицией «El'gygytgyn Drilling Project». Этот интервал включает 101 и 100 морские изотопные стадии (MIS). Палинологический анализ позволил выделить шесть пыльцевых зон. Пыльцевые зоны 1 и 2 (MIS 101), а также 3 и 4 (MIS 100) отражают лиственничные и лиственнично-березовые леса межледниковий. Растительные сообщества, отраженные спектрами зоны 3, характеризуют один из климатических оптимумов гелазия. К периоду максимального похолодания климата в MIS 100 относится региональное распространение кустарниково-травянистой тундры (пыльцевая зона 5). В течение интерстадиала (MIS 100, зона 6) в растительном покрове господствует лиственничная лесотундра. Пыльцевые зоны 3 и 4 со спектрами межледниковых растительных сообществ более соответствуют MIS 101, чем MIS 100, и границу между этими стадиями следует проводить на уровне 2530.5 тыс. л. н. Корреляция возрастной седиментационной модели оз. Эльгыгытгын с палеомагнитными событиями нуждается в ревизии.

***Ключевые слова*: гелазий, изотопная стадия, пыльцевая зона, межледниковье, интерстадиал, ледниковая стадия.**

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