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Short-term climate and vegetation dynamics in Lena River Delta (northern Yakutia, Eastern Siberia) during early Eocene

Olesya V. Bondarenko[a,*], Nadezhda I. Blokhina[a], Tatiyana A. Evstigneeva[a], Torsten Utescher[b,c]

[a] *Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch, Russian Academy of Sciences, Prospect Stoletiya 159, Vladivostok, 690022, Russia*
[b] *Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, 60325, Frankfurt Main, Germany*
[c] *Institute for Geosciences, University of Bonn, Nussallee 8, 53115, Bonn, Germany*

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Abstract

Early Eocene climate and vegetation evolution in northern Yakutia (Eastern Siberia) are quantitatively studied for the first time based on paleobotanical records, using the coexistence approach (CA) for paleoclimate, the plant functional type approach (PFT) and the integrated plant record method (IPR). Paleobotanical data of this time-interval were obtained from 18 palynofloras of the coal beds outcropping on the bank of the Bykovskaya Channel in the area of Bulunkan Bay (Lena River Delta). The results indicate the persistence of warm temperate and at times possibly nearly tropical, overall humid climate conditions throughout the early Eocene, and a relatively strong seasonality in precipitation. The vegetation reconstructed is in agreement with the climate conditions determined by the CA. Analyses of the PFT diversity spectra indicate the prevalence of mixed warm temperate evergreen-deciduous forests. Based on the IPR method, plant biomes varied from mixed mesophytic forests during warmer intervals to broadleaved deciduous forest/mixed mesophytic forest ecotone during cooler episodes. The presence of mangroves in our early Eocene records is possibly related to hyperthermal events such as the Paleocene–Eocene Thermal Maximum.

Keywords: temperature evolution; precipitation pattern; climate seasonality; structure of plant assemblages; vegetation type; mangrove taxa

1. Introduction

The early Cenozoic, especially Eocene, is increasingly recognized as a key period for understanding the climate and biogeography of warm intervals of Earth's history (Huber and Sloan, 2000; Westerhold et al., 2020). The early Eocene (Ypresian, ca. 56–47.8 Ma) was an exceptional warm interval with reduced pole-to-equator temperature gradients (Suan et al., 2017) and high atmospheric CO_2 concentrations ranging from ~1000 ppm to 3000 ppm (Beerling and Royer, 2011; Pearson and Palmer, 2000). The beginning of Eocene was marked by one of the fastest and most extreme global warming events known as the Paleocene–Eocene Thermal Maximum (PETM) (55.8 ± 0.2 Ma) which lasted ~170 ky and is commonly attributed to North Atlantic Igneous Province (NAIP) volcanism and methane degassing of seafloor sediments (e.g., Dickens et al., 1995; Dickens, 2000; Westerhold et al., 2009; Charles et al., 2011; Wieczorek et al., 2013; Gutjahr et al., 2017; Jones et al., 2019; Morgan et al., 2019). The PETM brought about noticeable biotic changes, including

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* Corresponding author. Tel.: +7(423)2310410; Fax.: +7(423)2310193.
E-mail addresses: laricioxylon@gmail.com (O.V. Bondarenko), blokhina@biosoil.ru (N.I. Blokhina), evstigneeva@biosoil.ru (T.A. Evstigneeva), t.utescher@uni-bonn.de (T. Utescher).

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extinction and/or diversification of various marine and terrestrial organisms (Kennett and Stott, 1995; Turner et al., 2017; Zhang et al., 2019), and was one of the most significant periods of global change during the Cenozoic (Schmidt and Shindell, 2003; Winguth et al., 2012; Turner et al., 2017).

Globally, early Eocene climate was relatively stable, warm and moist; forested areas expanded to the ice-free poles (Willis and McElwain, 2002). The Eocene polar broadleaved deciduous forests were exposed to long periods of continuous winter darkness and mesothermal humid climate; the forests were very low in diversity with little habitat variation, very few climbers and an open structure (Collinson, 1992; Collinson and Hooker, 2003). The first broadleaved subtropical evergreen (rain) forests appeared in the Paleocene and evolved during the Eocene (Willis and McElwain, 2002; Carvalho et al., 2021), and were variable in time and space (Collinson, 1992; Collinson and Hooker, 2003). Thus, they are potentially important in interpreting plant biomes and their response to global change and provide the unique opportunity for modeling climate changes and understanding the response of the Earth system to various driving forces (Flato et al., 2013; Lunt et al., 2021).

Today, more than 40% of the territory of Yakutia is located within the Arctic Circle and mostly occupied by mountains and plateaus and only 1/3 by lowlands. Most of the territory of Yakutia is located in the middle taiga zone, which is replaced to the north by forest-tundra and tundra zones. Forests occupy about 4/5 of the river valleys and lowlands, while shrubby and herbaceous vegetation and lichens dominate the coast and mountain tops. The Lena River Delta and the Laptev Sea coast are occupied by Arctic tundra. The present-day climate of Yakutia is distinctly continental, characterized by long winters and short summers, with temperature difference of 70–75°C between the coldest and the warmest month and the temperature minima as low as −70°C, unparalleled in the Northern Hemisphere in terms of the annual duration of freezing (from 6.5 to 9 months per year; cf. Tsherbakov, 1975).

The Arctic is warming dramatically, faster than almost all other parts of our planet (IPCC, 2014), attributed to "polar amplification" (Lee, 2014). Extensive studies on climate proxies and models have been conducted for the Cretaceous that revealed paleoenvironmental conditions and vegetation responses in the High Arctic in a "greenhouse" climate (e.g., Spicer and Parrish, 1986; Spicer and Corfield, 1992; Herman and Spicer, 1996, 1997; Amiot et al., 2004; Spicer and Herman, 2010; Spicer et al., 2014, 2019; Herman et al., 2016). By contrast, our knowledge on climate and vegetation dynamics of Eocene is still fragmentary. Analyses of Paleogene deposits in Northeast Russia in general and Yakutia in particular, as well as the reconstruction of the paleoclimate and paleovegetation, were previously tackled by Akhmetiev (1976, 1993, 2015), Akhmetiev et al. (1981, 2010, 2012), Aleksandrova (2016), Bakulina and Zharikova (1989), Baranova and Biske (1979), Belaya and Litvinenko (1989), Fradkina (1995), Fradkina et al. (1979), Grinenko and Kiseleva (1971), Grinenko et al. (1989, 1997), Kulkova (1973, 1987), Kulkova and Laukhin (1975), Laukhin and Fradkina (1984), Laukhin et al. (1988, 1992), L'vova (1989), Narkhinova (1989), Nikitin (2006), Volkova et al. (1990), Volobueva et al. (1988), and others, which were mainly devoted to regional stratigraphy, description of plant fossil remains, new fossil taxa, taxonomic diversity of plants, or paleofloristic aspects and generally included qualitative interpretations of macro- and microfloral successions (Budantsev, 1997, 1999; Akhmetiev, 2015); quantitative studies are largely missing so far.

Recently, quantitative paleoclimate and vegetation studies have been conducted for regions of the southern Russian Far East (Primorye and Amur region) revealing major plant biome changes throughout the Paleogene and providing indications of the average annual temperature and the annual precipitation (Bondarenko et al., 2019, 2020a, 2020b, 2021). Such studies are essential for comparison with results from other proxies or climate models.

Here we present the first high-resolution time series for the climate and vegetation evolution of northern Yakutia (Eastern Siberia) during early Eocene. Our study is based on an investigation of 18 palynofloras sampled from coal beds exposed in the area of Bulunkan Bay (Lena River Delta). We analyze changes in the taxonomic composition and abundance of the floras and establish quantitative records to trace regional climate and vegetation dynamics when early Cenozoic ecosystems became established. In addition, we discuss subtropical climate conditions and mangrove growth in Arctic Siberia during early Eocene and relevant global signals found in northern Yakutia.

2. Geological setting

2.1. Sedimentary succession in the study area

The Tiksinskii coal-bearing area is located within the Primorskii Ridge of the Kharaulakh Mountains, within the northern part of the Kharaulakh segment of the Verkhoyansk fold zone (Parfenov and Kuz'min, 2001). The study section is located on the right bank of the Bykovskaya Channel in the area of Bulunkan Bay (Lena River Delta) (127°90′E, 72°20′N) in the north of the Sakha Republic (Yakutia), in the lower reaches of the Lena, Olenek and Omoloi rivers (Fig. 1A).

Paleogene sediments are ubiquitous, unconformably overlying Paleozoic and Triassic deposits, and are represented mainly by siltstones, poorly cemented sandstones and plastic clays with beds of brown coal with a thickness of 1 m to 3–5 m (Imaeva et al., 2019). Carboniferous deposits are usually gently folded with the limds of the folds dipping at an angle of up to 45°. Faults are widespread, but their amplitude of offset is usually small (less than 5 m).

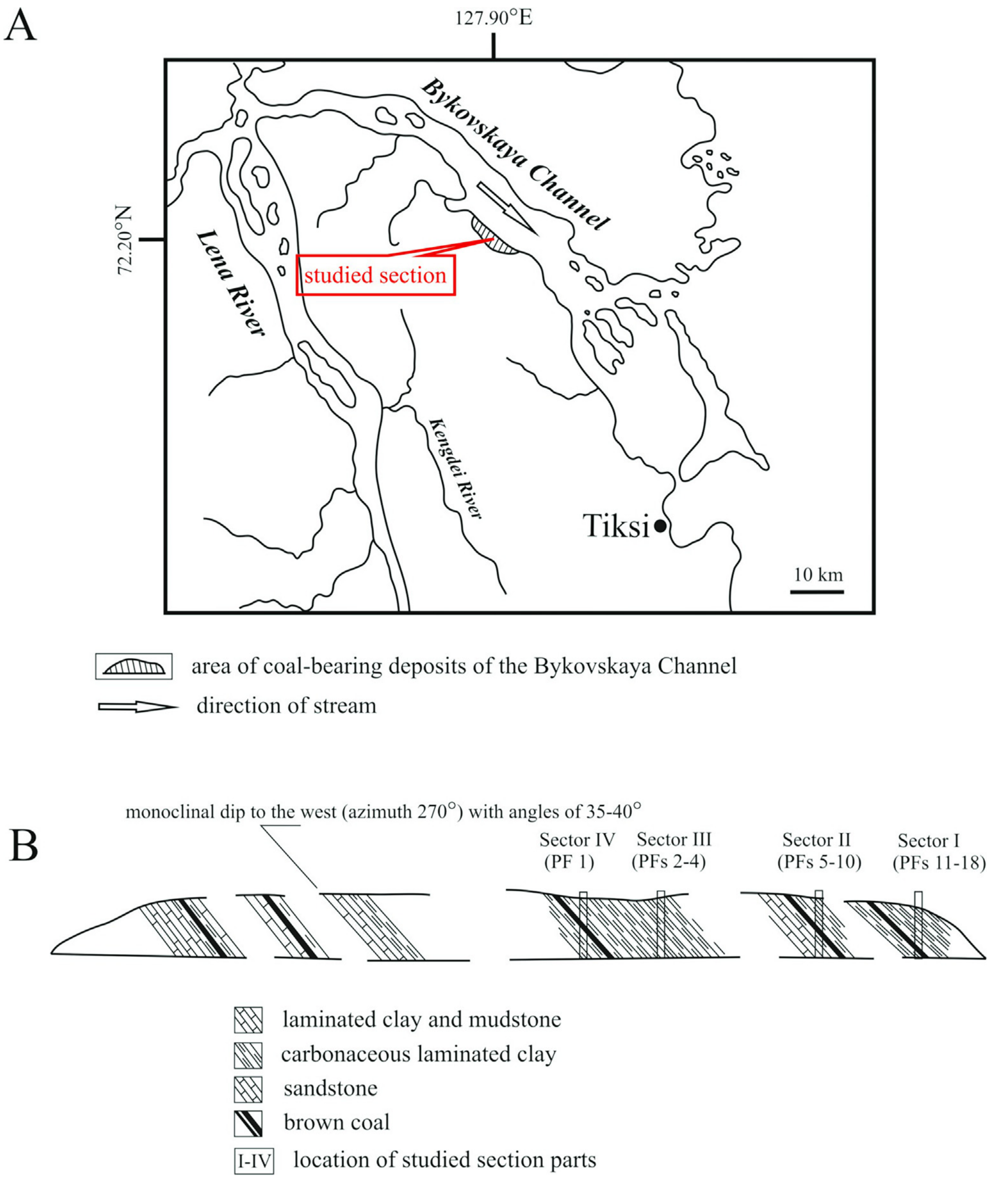

Fig. 1. Map showing the location of study section, distribution area of coal-bearing deposits of the Bykovskaya Channel (A), and stratigraphic profile of the examined sections (B).

Paleogene volcaniclastics have not been noted (Bol'shiyanov et al., 2013).

Paleogene deposits are exposed along the Bykovskaya Channel. Seismic profiling indicates that the late Paleocene–Eocene coal-bearing deposits filled large depressions of a subsiding river delta system (Shkarubo et al., 2014). Oligocene layers have not been identified within this delta (Imaeva et al., 2019).

Deposits of the Bykovskaya Formation in the area were studied in detail by Grinenko and Kiseleva (1971). In natural cliffs of a 6–15-meter terrace, mudstones, carbonaceous-argillaceous shales, poorly cemented sandstones, and brown coal seams are exposed (Fig. 1B). They form an angular unconformity with the Middle–Upper Devonian rocks of the Tuoidah Mountain (Grinenko and Kiseleva, 1971). The sediments are mainly continental, but there are interlayers of most likely coastal-marine origin, in which dinoflagellates were found (Grinenko et al., 1989, 1997; Fradkina, 1995, 1996). In the sandstones, leaf imprints have been discovered. According to Grinenko and Kiseleva (1971), the leaf flora collected by M.F. Lobanov and identified by T.N. Baikovskaya and I.V. Palibin contains: *Equisetum arcticum* Heer, *Sequoia langsdorfii* (Sternberg) Heer, *Taxodium dubium* (Sternberg) Heer, *Taxites olrikii* Heer, *Glyptostrobus europaeus* (Brongniart) Unger, *Arundo pseudogoeppertii* Berry, *Betula macrophylla* Heer, *Alnus* sp., *Quercus platania* Hollick, *Trochodendroides arctica* (Heer) Berry, *Tr. smilacifollus* (Newberry) Kryshtofovich, *Tr. richardsonii* (Heer) Kryshtofovich, *Menispermites septentrionalis* Hollick, *Protophyllum* sp. (cf. *P. multinerve* Lesquereux), and *Vitis islandica* Heer. Grinenko et al. (1989) described a small but representative complex of plants collected in ferruginous sandstone layers and white clays, among them *Ginkgo* ex gr. *adiantoides* (Unger) Heer, *Metasequoia occidentalis* (Newberry) Chaney, *Platanus* sp., and *Trochodendroides arctica* (Heer) Berry, with *Juglans lenaense* Budantsev are dominant.

2.2. Stratigraphy and dating

Cenozoic deposits in Northern Yakutia have been known since the end of the 19th century. They were first discovered in the Bykovskaya Channel of the Lena River by A.N. Neelov in 1912 (see Grinenko and Kiseleva, 1971). Gusev and Fleishman (1938), Lobanov (1951, 1959), Mezhvilk (1958), Grinenko and Kiseleva (1971) then studied and dated these deposits to the Paleocene.

In the Kharaulakh region (northern Yakutia), Grinenko et al. (1989) distinguished the Kengdeiskaya (s.s.) and Bykovskaya formations and Kunginskaya strata of the same lithological composition and of the same age. According to Grinenko et al. (1989), the palynological assemblage indicates an Eocene age, also confirmed by the finds of dinoflagellates, widespread in the Eocene deposits of other regions, including Western Siberia (cf. Kulkova, 1987). Grinenko et al. (1997) combined the Kengdeiskaya (s.s.) and Bykovskaya formations and Kunginskaya strata into a single Kengdeiskaya Formation (s.l.), which is a stratotype of the regional horizon (the first half of the early Eocene). Here we follow the stratigraphic scheme of Grinenko et al. (1997).

3. Material and methods

3.1. Floral record

In the present study, microfloras (PFs) from 18 levels are considered, sampled in the study section from the coal beds of the Kengdeiskaya (s.l.) (= Bykovskaya) Formation (Fig. 1A). All palynological data are taken from Grinenko and Kiseleva (1971). The microfloras yield evidence for a total of 103 different taxa (69 angiosperms, 20 gymnosperms, and 14 pteridophytes) identified by A. V. Kiseleva (Grinenko and Kiseleva, 1971). As reported

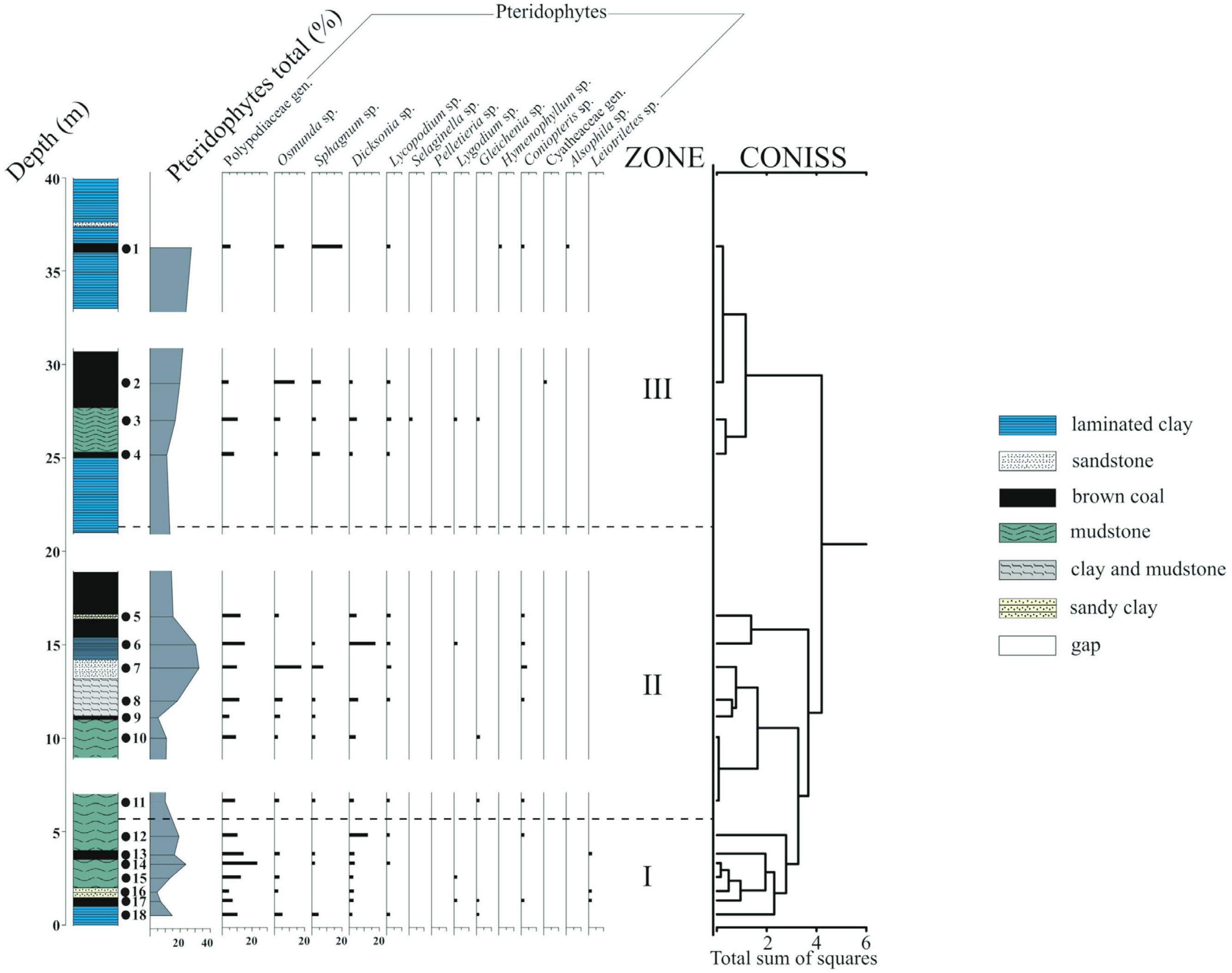

Fig. 2. Palynological diagrams for pteridophytes.

in the original study, 300 or more pollen grains were counted per sample. The material is stored in Diamond and Precious Metal Geology Institute, Siberian Branch, Russian Academy of Sciences (DPMGI SB RAS, Yakutsk).

3.2. Palynological method

The palynological data are represented in diagrams (Figs. 2–4) constructed with the TILIA program (Grimm, 2011). The diagrams were divided into zones using CONISS software (Constrained Incremental Sums of Squares cluster analysis) to estimate variations in the record (Grimm, 2011). The percentages of each taxon were calculated based on the total sum of pollen and spores.

3.3. Quantitative paleoclimate reconstruction — Coexistence Approach (CA)

To reconstruct climate from the palynomorph record, we used the Coexistence Approach (CA) (Mosbrugger and Utescher, 1997; Utescher et al., 2014). This approach is organ-independent, so that both macro- and microfossil plants are eligible as long as their modern botanical affinities are determinable (Mosbrugger and Utescher, 1997; Utescher et al., 2007; Bruch et al., 2011). For climatic requirements of extant plants, we used data sets from the Palaeoflora Database (Utescher and Mosbrugger, 2018). Floral lists with corresponding nearest living relatives (NLRs) employed in this study and their climatic requirements are made available in Appendix A.

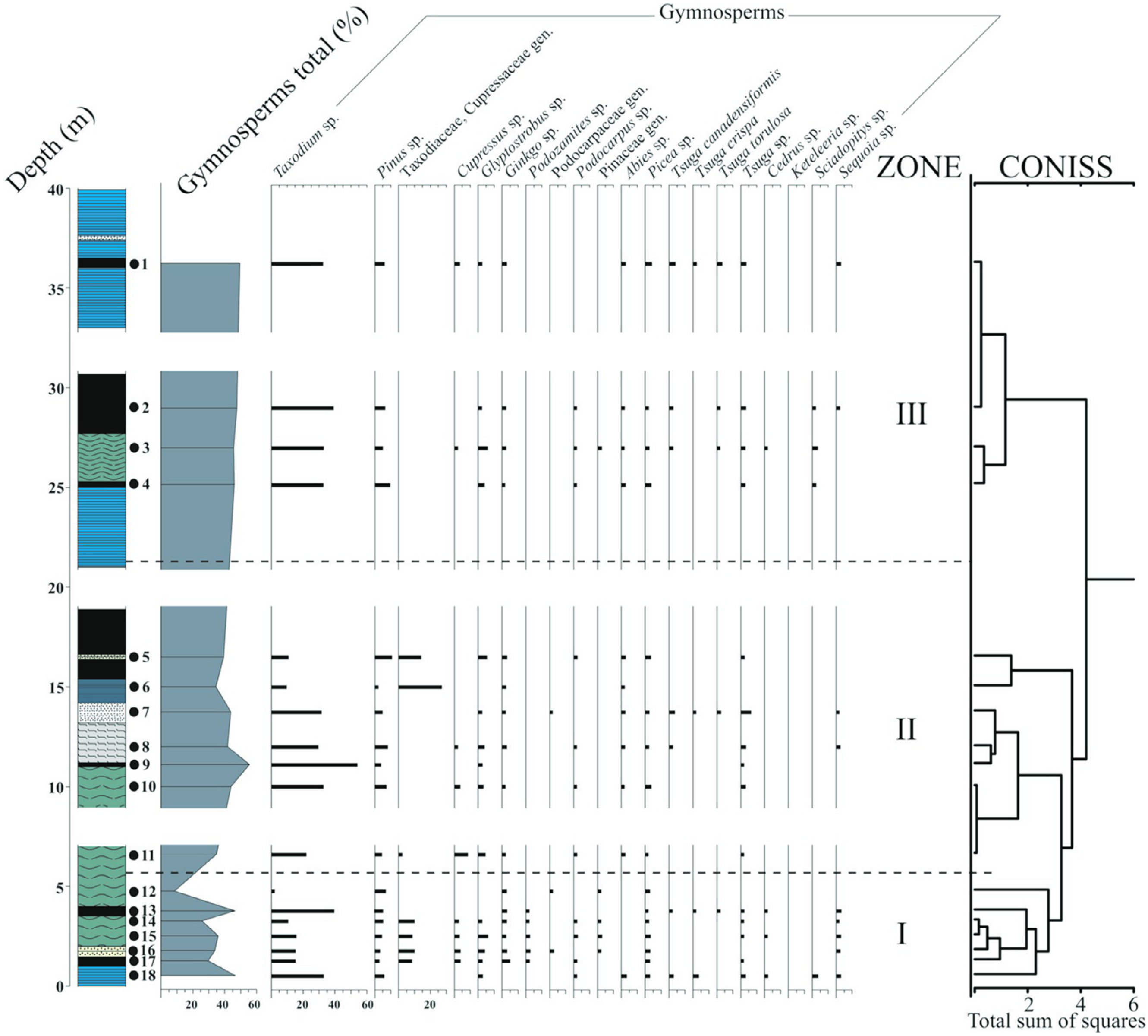

Fig. 3. Palynological diagrams for gymnosperms.

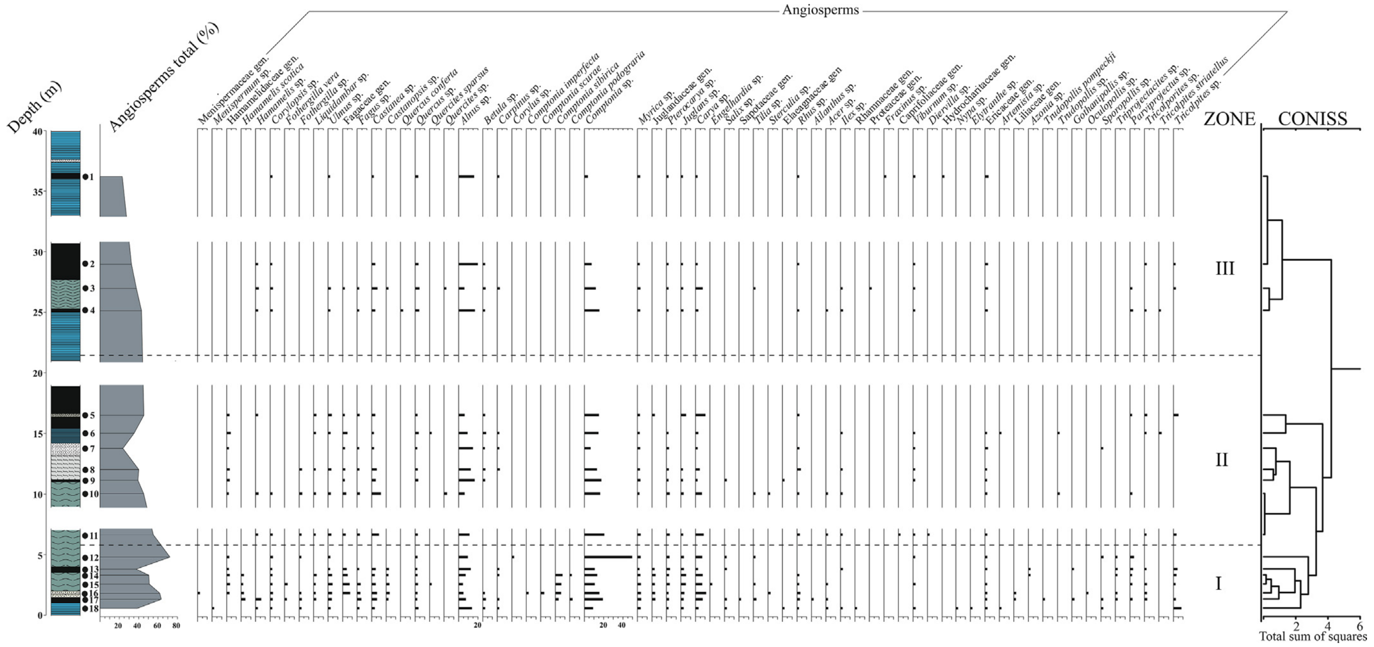

Fig. 4. Palynological diagrams for angiosperms.

In this study, three temperature and four precipitation variables are reconstructed: mean annual temperature (MAT), cold and warm month mean temperature (CMMT, WMMT), mean annual precipitation (MAP), and mean monthly precipitation of the wettest, driest and warmest month (MPwet, MPdry, and MPwarm). Min, max, and mean values of climatic parameters for each flora are given in Tables S1 and S2.

In CA analyses, at least 10 NLR taxa with climate data are required to obtain reliable results (Mosbrugger and Utescher, 1997). The climatic resolution of the CA results also depends on the taxonomical level of NLR identification (Mosbrugger and Utescher, 1997). *Eucommia ulmoides* Oliver, *Ginkgo biloba* Linnaeus and *Sciadopitys verticillata* (Thunberg) Siebold and Zuccarini were excluded from the analysis for being monotypic. For the monotypic genera (but not monotypic families) we used climate data for families (for example, climate data of Myricaceae Blume were used for *Comptonia peregrina* (Linnaeus) Coulter, Taxodioideae Endlicher ex Koch — for *Glyptostrobus pensilis* (Staunton ex Don) Koch and *Taxodium* Richard).

3.4. Climate seasonality

In order to determine temperature seasonality of the early Eocene climate of Yakutia, the mean annual range of temperature (MART) was calculated as the difference of WMMT and CMMT for each level (Table S2). To study precipitation seasonality, the mean annual range of precipitation (MARP — calculated as difference of MPwet and MPdry) was calculated (Table S2). To obtain an estimate of climate seasonality during the early Eocene we use the ratio of MPwet and MPdry on MAP (RMPwet and RMPdry) (Table S2). According to Jacques et al. (2011), the ratios of MPwet and MPdry of MAP provide a good indication of past monsoon intensity, i.e., precipitation seasonality. In general, increasing of RMPwet indicates higher proportion of precipitation in the wet season, while the decreasing of RMPdry suggests lower proportion of precipitation in the dry season.

3.5. Vegetation reconstruction methods

In order to reconstruct paleovegetation based on fossil flora, several methods have been developed aiming at standardized, reproducible and thus comparable results, facilitating the analysis of spatio-temporal trends in the evolution of the vegetation cover. These methods differ mainly by scale of reconstruction from local plant communities (PFT) to biome level (IPR).

3.5.1. Quantitative paleovegetation reconstruction — Plant Functional Type approach (PFT)

The Plant Functional Type (PFT) concept goes back to works of Prentice et al. (1992) and Prentice and Webb (1998), and has been widely used to describe vegetation cover in vegetation modelling. A PFT is defined using traits and climatic thresholds of key taxa, and combines species related by morphological and phenological traits (François et al., 2011). The application of the PFT technique on the Neogene paleobotanical record was first introduced by Utescher et al. (2007). The present study employs an extended PFT classification scheme described in detail in Popova et al. (2013), comprising 26 herbaceous to arboreal PFTs based on physiognomic characters and bioclimatic tolerances of plants, complemented by an aquatic PFT (Table S3). The allocation of fossil taxa to the single PFTs is based on interpretation of their NLRs (Appendix

B), and follows the procedure described in Utescher and Mosbrugger (2007) and Utescher et al. (2007). Proportions of the different groups of PFTs are given in Table S4.

To exclude unlikely PFTs, we used the likelihood procedure according to François et al. (2011) and Henrot et al. (2017). This methodology is similar to that of the CA used in paleoclimate reconstructions from the paleobotanical records. In cases when several classes of arboreal PFTs are possible for a taxon, only those that can coexist with the other classes identified at the site are retained. It narrows the range of PFT types present at the site by suppressing extreme end members, such as cold boreal/temperate and tropical PFTs. A coexistence table is then used to evaluate the likelihood for the presence of each PFT at each site, according to the four following affinity levels of coexistence: H – high, M – moderate, L – low, and I – improbable. Finally, all PFTs of low and improbable levels of coexistence were excluded from the analysis (Appendix B).

The PFT approach requires only information on presence and absence of taxa and thus is comparatively robust towards taphonomic bias. The approach can be applied on all types of fossil floras providing an adequate size of the sample.

3.5.2. Plant biome reconstruction — Integrated Plant Record vegetation analysis (IPR)

The Integrated Plant Record vegetation analysis (IPR) is a semi-quantitative method first introduced by Kovar-Eder and Kvaček (2003) to assess zonal vegetation based on the fossil plant record (leaf, fruit, and pollen assemblages). In order to employ the IPR, thirteen basic taxonomic-physiognomic groups, termed components, defined to reflect key ecological characteristics of an assemblage (Kovar-Eder and Kvaček, 2003, 2007; Kovar-Eder et al., 2008; Teodoridis et al., 2011) are used: conifer component (CONIF), broad-leaved deciduous component (BLD), broad-leaved evergreen component (BLE), sclerophyllous component (SCL), legume-like component (LEG), zonal palm component (ZONPALM), arborescent fern component (ARBFERN), dry herbaceous component (D-HERB), mesophytic herbaceous component (M-HERB). Azonal components, i.e., azonal woody component (AZW), azonal non-woody component (AZNW) and aquatic component (AQUA). The PROBLEMATIC TAXA component includes elements with uncertain taxonomic-physiognomic affinity. For further analysis, all taxa (but not their abundances) of every single assemblage have to be assigned to those components and their relative proportions have to be calculated. The complete flora lists, assigned NLRs, and their allocation to the components are given in Appendix C. The number of taxa assigned to the components for each flora is given in Table S5.

To characterize zonal vegetation, the following proportions of components are regarded as relevant: (a) the proportion of the BLD, BLE, and SCL+LEG components of zonal woody angiosperms, where "zonal woody angiosperms" means sum of BLD+BLE+SCL+LEG+ZONPALM+ARBFERN components; (b) the proportion of the ZONAL HERB (D-HERB+M-HERB) component of all zonal taxa, where "zonal taxa" means sum of the CONIF+BLD+BLE+SCL+LEG+ZONPALM+ARBFERN+D-HERB+M-HERB components. The reliability of the results increases with increasing numbers of zonal taxa preserved. Ten zonal taxa are regarded as a minimum to perform this method (Kovar-Eder et al., 2008). Recently, Kovar-Eder and Teodoridis (2018) raised the former threshold to 15 zonal taxa for the application of the IPR vegetation analysis. The proportions of the components were calculated for each flora and are given in Table S5.

Based on relative proportions of the components, the following six zonal vegetation types are distinguished (Kovar-Eder and Kvaček, 2007; Kovar-Eder et al., 2008): zonal temperate to warm temperate broadleaved deciduous forests (broadleaved deciduous forests, BLDF), zonal warm temperate to subtropical mixed mesophytic forests (mixed mesophytic forests, MMF), zonal subtropical broadleaved evergreen forests (broadleaved evergreen forests, BLEF), zonal subtropical, subhumid sclerophyllous or microphyllous forests (subhumid sclerophyllous forests, ShSF), zonal xeric open woodlands (open woodland), and zonal xeric grasslands or steppe (xeric grassland). Teodoridis et al. (2011) additionally defined ecotones between the BLDF and MMF and the BLEF and MMF and recently, Kovar-Eder and Teodoridis (2018) defined an ecotone between the MMF/ShSF.

4. Results

4.1. Palynological data

Based on Grinenko and Kiseleva (1971), 103 taxa in total (69 angiosperms, 20 gymnosperms and 14 pteridophytes) were identified. Most taxa belong to trees and shrubs. Sporomorphs from herbs were generally rare. Cluster analysis performed with the TILIA software yields 3 palynozones (Figs. 2–4) which are described from base to top as follows.

Zone I (PFs 12–18; Figs. 2–4) has the highest taxonomic diversity of angiosperm and gymnosperm pollen. Angiosperm pollen dominates and reaches 72.3%, with mostly *Comptonia* sp., *Comptonia sibirica* Gladkova, *Alnus* sp., *Carya* sp., *Juglans* sp., *Ulmus* sp., *Myrica* sp. Fagaceae pollen are very frequent in this zone and are represented by *Fagus* sp., *Quercus* sp., *Castanea* sp. and *Castanopsis* sp. A comparatively high percentage of gymnosperm pollen (up to 46.7%) with *Taxodium* sp., Taxodiaceae gen., Cupressaceae gen. and *Pinus* sp. are recorded in this zone. *Picea* sp., *Ginkgo* sp., *Podozamites* sp., *Tsuga* sp., *Glyptostrobus* sp. are continuously present. Pteridophyte spores are represented (up to 23.9%) mainly by Polypodiaceae gen. and *Dicksonia* sp.

Zone II (PFs 5–11; Figs. 2–4): gymnosperm (34.5–55.6%) and angiosperm (23.6–55.0%) pollen dominate. Gymnosperms are represented mainly by *Taxodium* sp.

(up to 52.4%). Taxodiaceae and Cupressaceae pollen is abundant (25.3%) at the top of this zone. Among the angiosperms, *Comptonia* sp. and *Alnus* sp. dominate, accompanied by *Castanea* sp. and *Carya* sp. Pteridophyte spores (up to 33.3%) are represented by Polypodiaceae gen., *Dicksonia* sp. and *Osmunda* sp.

Zone III (PFs 1–4; Figs. 2–4): gymnosperm pollen dominates and reaches 49.5% mostly due to *Taxodium* sp. A comparatively high percentage of angiosperm pollen (23.0–43.0%) with *Alnus* sp. and *Comptonia* sp. is recorded. Pteridophyte taxa occur at a lower frequency (11.0–27.5%) and are represented mainly by Polypodiaceae gen., *Osmunda* sp., and *Sphagnum* sp.

4.2. Paleoclimate reconstruction

The analysis of 18 microfloras is based on 21 to 42 (mean 32.4) climate datasets of extant reference taxa (Table S1), showing over 99% NLR coexistence. When reconstructing CA intervals of the MAT obtained from the microfloras, CA ranges are comparatively wide owing to the commonly high taxonomic level of NLR assignment. For MAT the width of CA intervals is ca. 8.2°C at the mean (varies from 0.2°C to 13.7°C, standard deviation 2.7°C).

The mean values of MAT show a general smooth cooling trend in the lower part and warming trend in upper part (Fig. 5, Tables S1, S2). The highest MAT values are found in PF 18 (Zone I) – 21.8°C (21.7–21.9°C). The lowest MAT values are in PF 9 (Zone II) – 14.5°C (7.6–21.3°C). For the other floras the MAT mean values vary in the range of 16.1–17.6°C.

We show that the CMMT means indicate cyclic variability but in general a cooling trend (Fig. 5, Tables S1, S2). The highest values of CMMTs are found in the PF 18 (Zone I) – 15.2°C. The lowest CMMT values in the PF 9 (Zone II) – 3.5°C (−8.2–15.2°C). For the other floras, the mean values of CMMTs vary from 7.5°C to 11.7°C.

WMMT means vary slightly (Fig. 5, Tables S1, S2). The highest WMMT values are found in PF 18 (Zone I) – 27.7°C (27.2–28.2°C). The lowest values of WMMTs are in PF 9 and PF 7 (Zone II) – 23.8°C (19.3–28.3°C). For the other floras, the mean values of WMMT vary from 25.2°C to 25.9°C.

MAP shows no general trend and varies slightly from 1200 mm up to 1300 mm (Fig. 6, Tables S1, S2). The highest value of MAP is found in the PF 18 – 1299 mm (1215–1383 mm), the lowest in PFs 7 and 9 – 1071 mm (529–1613 mm) and 1127 mm (529–1724 mm), respectively.

MPdry means in the early Eocene of northern Yakutia were at ca. 25–66 mm (Fig. 6, Tables S1, S2).

The mean values of MPwet attain very high values (160–277 mm) throughout the early Eocene (Fig. 6, Tables S1, S2).

4.3. Climate seasonality

Temperature (MART) and precipitation (MARP) seasonality parameters and the mean values of related climatic parameters for each flora are given in Table S2 in comparison to the present-day values. The MART ranges in 12.5–20.3°C (mean value of MART is 15.8°C). The MARP

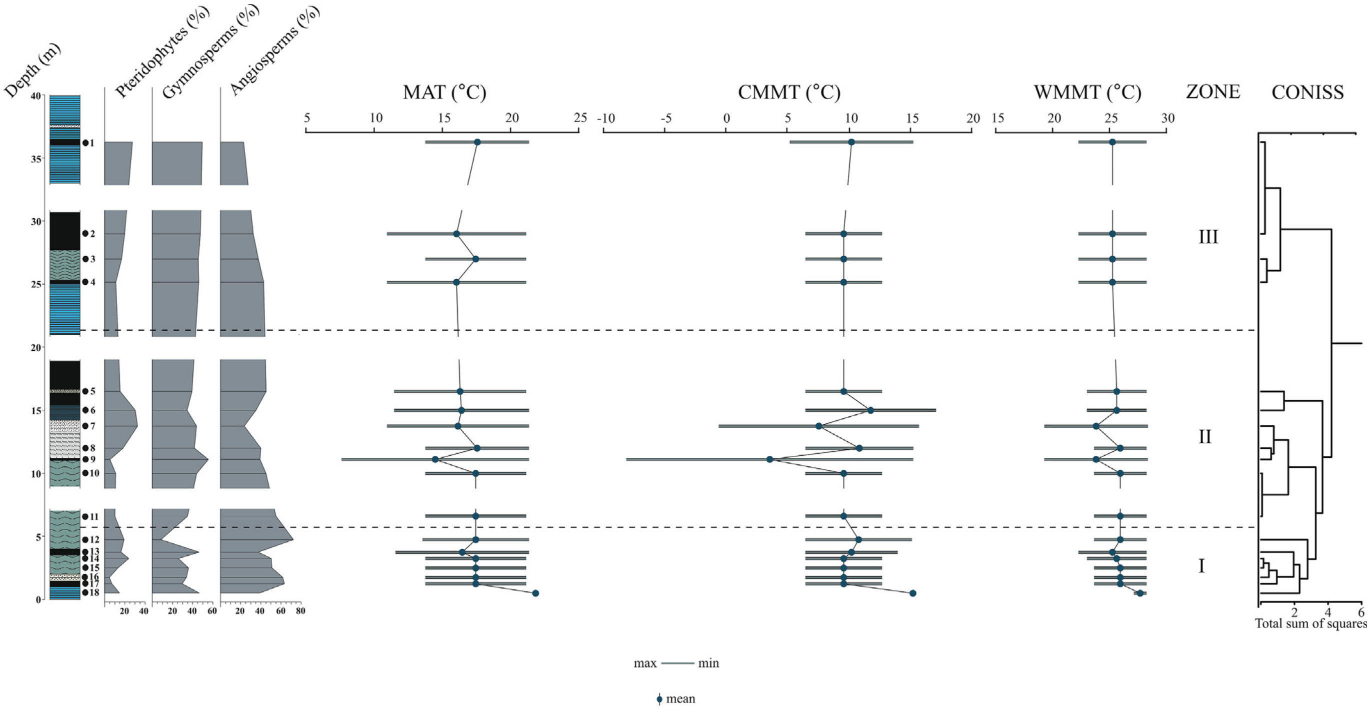

Fig. 5. Estimates for temperature variables. MAT – mean annual temperature, CMMT – cold month mean temperature, WMMT – warm month mean temperature. Cluster analysis with CONISS (Grimm, 2011) at right.

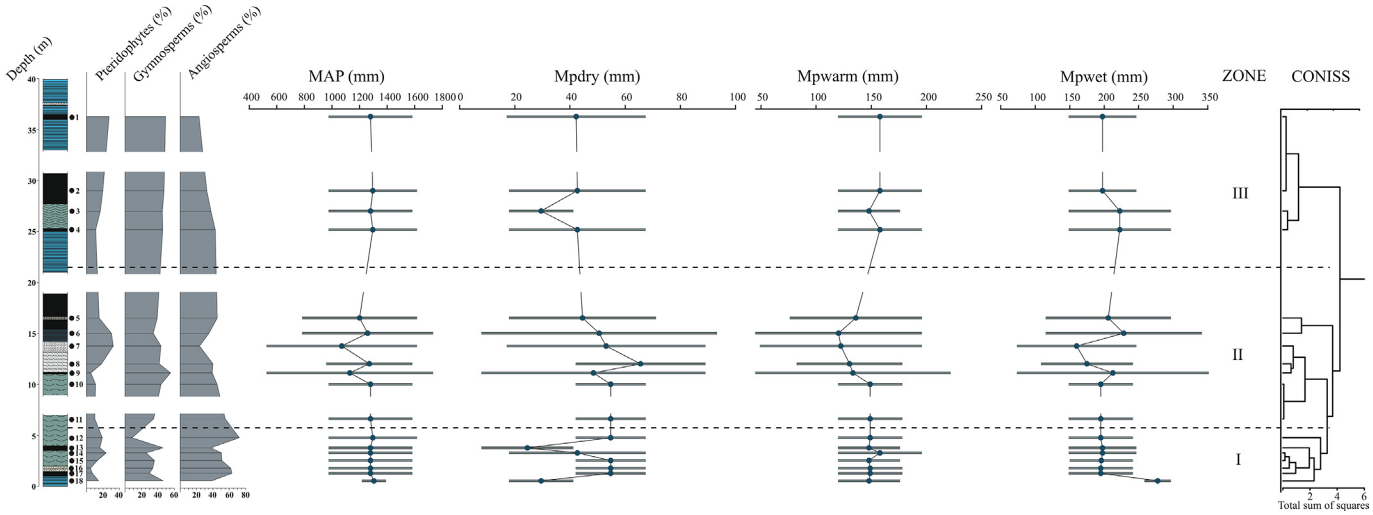

Fig. 6. Estimates for precipitation variables. MAP – mean annual precipitation, MPwet – mean monthly precipitation of the wettest month, MPdry – mean monthly precipitation of the driest month, MPwarm – mean monthly precipitation of the warmest month.

varies from 107 mm to 247 mm. The RMPwet fluctuates within 13.8–21.3%, while the RMPdry varied from 1.9% to 5.2% (Table S2).

4.4. Vegetation

4.4.1. PFT approach

Using the PFT approach, paleovegetation data of Yakutia were obtained from 18 palynofloras. The number of PFTs encountered in each sample is lower than that of fossil taxa contributing with PFT data (Table S4), which we consider meaningful. Aquatic plants (PFT 27) are present in two palynofloras only in upper part (Zone III), and the proportion of aquatic plants does not exceed 1.4% (Fig. 7, Table S4). Herbaceous plants (PFTs 1–3) are present in all floras. The diversity of herbaceous PFTs varies from 2.7% to 8.0% of total diversity of the flora (Figs. 7, 8, Table S4). Shrubs (PFTs 4–11) are presented in all floras studied — from 17.3% to 34.2% (Fig. 7, Table S4). Arboreal plants (PFTs 12–26) are present in all floras studied

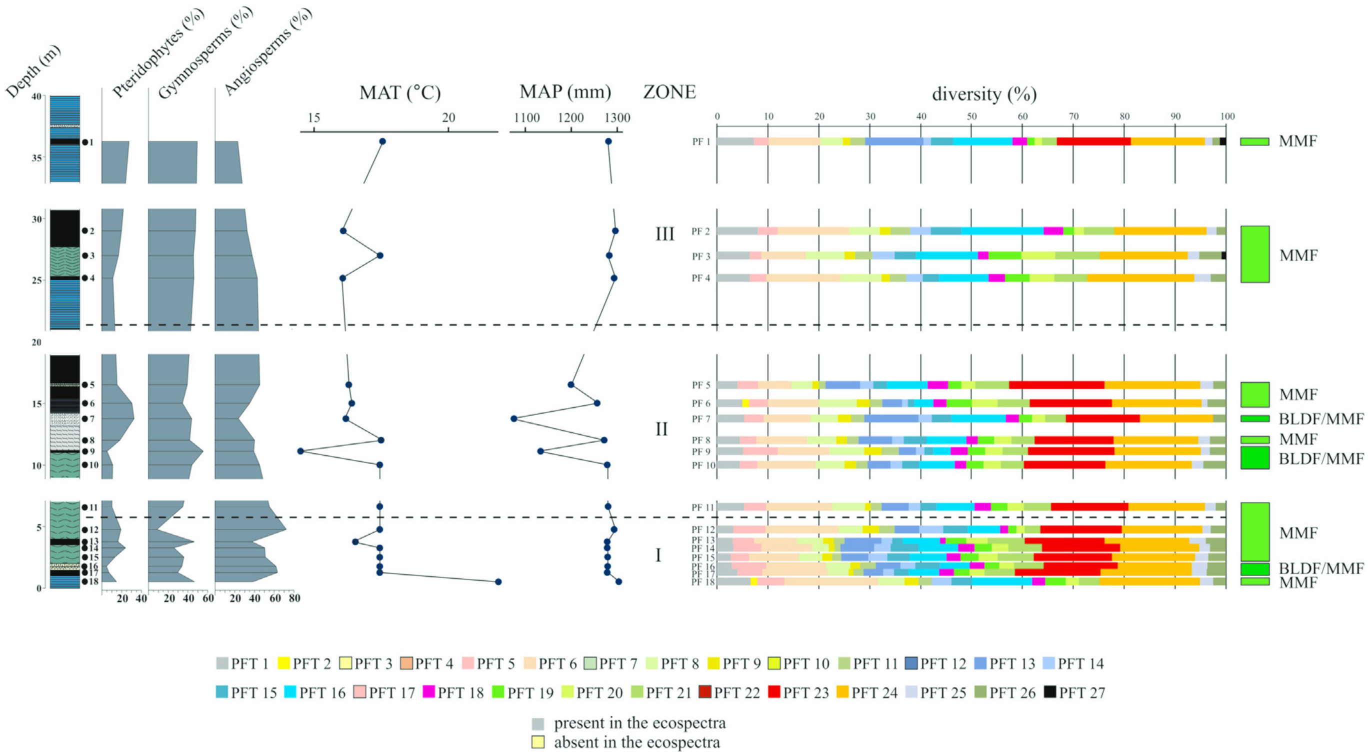

Fig. 7. Ecospectra of PFT diversity and vegetation types of the study setion along with curves of MAT and MAP. MAT – mean annual temperature, MAP – mean annual precipitation, MMF – mixed mesophytic forest, BLDF/MMF – ecotone between broadleaved deciduous forest and mixed mesophytic forest.

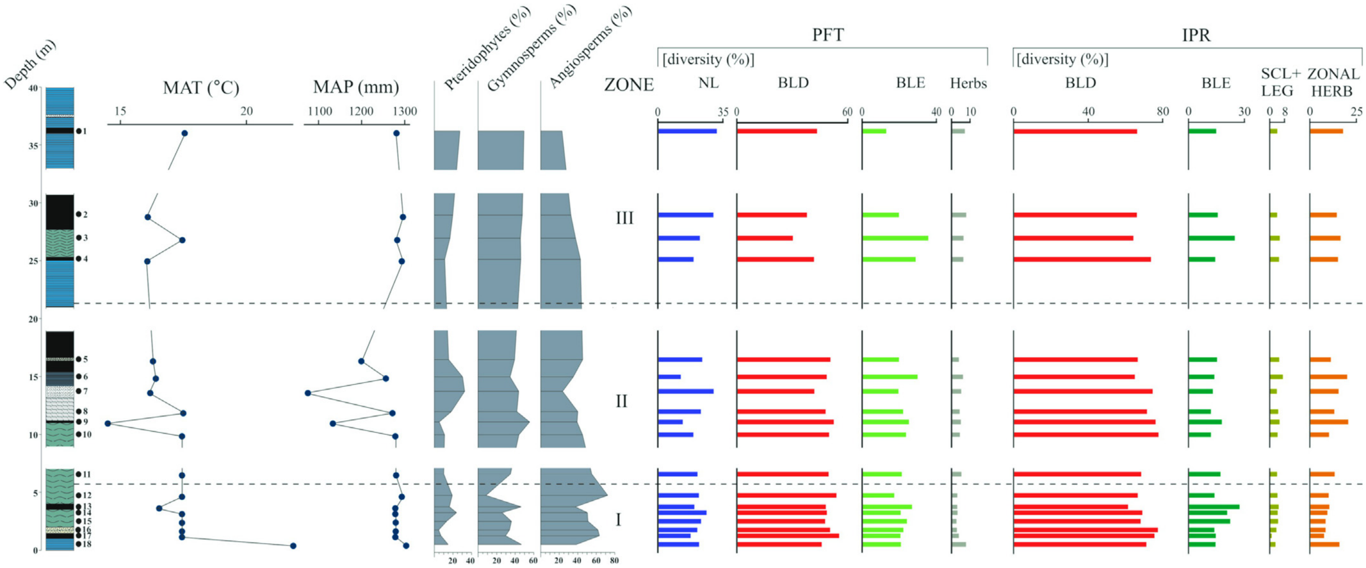

Fig. 8. Quantitative characteristics of the main groups of plants according to palynology, PFT, and IPR methods of the study section along with curves of MAT and MAP. MAT – mean annual temperature, MAP – mean annual precipitation, NL – needleleaved plants, BLD – broadleaved deciduous plants, BLE – broadleaved evergreen plants, SCL+LEG – sclerophyllous and legume-like plants.

57.9–78.7% of total diversity (Fig. 7, Table S4). Needleleaved (PFTs 12–18) are present in all floras. The proportion of conifers varies within the range of 12.5–31.9% of total diversity of the flora (Figs. 7, 8, Table S4). Broadleaved deciduous plants (PFTs 4–6, 22–25) are present in all floras. The diversity of deciduous PFTs varies from 30.4% to 55.4% of total diversity of the flora (Table S4). Broadleaved evergreens (PFTs 7–9, 19–21, 26) are present in all floras. The proportion of broadleaved evergreens varies from 13.0% to 35.9% of total diversity of the flora (Figs. 7, 8, Table S4).

The diversity spectra of the early Eocene floras analyzed (Fig. 7) show that broadleaved summergreen shrubs and trees (PFTs 5, 6, and 23/24) are the most important functional types, followed by broadleaved evergreen shrubs and trees (PFTs 8/9 and 19–21) and needleleaved evergreens (PFTs 13–16 and 18). Broadleaved summergreen arctic shrubs (PFT 4), broadleaved evergreen boreal or temperate cold shrubs (PFT 7), needleleaved evergreen boreal or temperate cold trees (PFT 12), needleleaved summergreen boreal trees (PFT 17) and broadleaved summergreen boreal or temperate cold trees (PFT 22) are absent in the spectra after having applied the likelihood procedure. Needleleaved summergreen subtropical swamp trees (PFT 18) are present in all floras (Fig. 7). Broadleaved raingreen tropical trees (PFT 25) and broadleaved evergreen tropical trees (PFT 26) also are presented in all floras (Fig. 7) but in very low proportion. Herbaceous plants in the early Eocene floras of Yakutia are mainly represented by humid herbs (PFT 1).

4.4.2. IPR vegetation analysis

To apply IPR vegetation analysis, 18 microfloras were analyzed. Based on the relative proportions of the components, one zonal vegetation type and one ecotone were revealed for the early Eocene of northern Yakutia (Fig. 4, Table S5). Warm temperate to subtropical mixed mesophytic forest (= mixed mesophytic forest, MMF) was obtained for most floras (13 out of 18). The floras assigned to this zonal vegetation type are characterized by proportions of the BLD component from 61.7% to 74.4%, BLE component – 12.1–27.5%, SCL + LEG component – 1.3–7.1%, and 8.6–23.7% of herbs. The ecotone BLDF/MMF was revealed only for five floras, characterized by 75.2–78.4% of BLD, 12.2–18.0% of BLE, 1.0–5.3% of SCL + LEG, and 7.8–20.8% of herbaceous components (Figs. 4, 5, Table S5).

5. Discussion

5.1. Evolution of early Eocene palynomorph complexes in northern Yakutia

According to Grinenko and Kiseleva (1971), the palynological complex of the Bykovskaya Formation is characterized by high content of Taxodioideae pollen (up to 53%), a noticeable presence and species diversity of pollen of broad-leaved thermophilic taxa and pollen of *Alnus* Miller and *Betula* Linnaeus. There are rare occurrences of pollen of Late Cretaceous relics, but sporadically, pollen of *Parviprojectus* sp., *Sporopollis* sp., *Trudopollis* sp., *Tricolpites striatellus* Mtchedlishvili, *Quercites sparsus* (Martynova) Samoilovitch are present. Single grains of *Triprojectacites* sp., *Azonia* sp., *Oculopollis* sp., *Trudopollis pompeckii* (Potonie) Pflug are noted only in the lower part (Zone I). According to Samoilovich (1965), Taxodioideae pollen is rarely encountered in the Danian deposits of Yakutia. Their content is also low in the Eocene of the south Siberian Platform, the North-East and the Far East of Russia (Khaikina, 1959; Bolotnikova, 1966; Litvintsev and Tarakanova, 1967). Pollen of broad-leaved thermophilic taxa and the pollen of *Alnus* and *Betula* are scarce in the Late Cretaceous and Danian deposits of Yakutia (Samoilovich, 1965), while in the Eocene complexes, they prevail quantitatively and are richer in species composition (Bolotnikova, 1966; Litvintsev and Tarakanova, 1967). The peak distribution of relict pollen (*Trudopollis* sp., *Oculopollis* sp., *Sporopollis* sp.), as well as pollen belonging to Triprojectacites and Kryshtofoviacites, occurs in the Maastrichtian–Danian (Khaikina, 1959; Mtchedlishvili, 1961; Samoilovich, 1965).

This palynological assemblage is most similar to thatfrom the Kengdei River section (right tributary of the Lena River) (Grinenko and Kiseleva, 1971). However, as stated above, the Kengdeiskaya (s.s.) and Bykovskaya formations and Kunginskaya strata have the same lithological composition and were combined by Grinenko et al. (1997) into the Kengdeiskaya (s.l.) Formation. According to Grinenko et al. (1989, 1997) and Fradkina (1995, 1996), the Kengdeiskaya (s.l.) Formation is characterized by typical palynomorph complexes for the early Eocene of the northeastern part of Russia.

Kulkova (1973) reported that the palynomorph complex of the Kengdeiskaya (s.l.) Formation was similar to the early–middle Eocene complex of the Tastakhskaya Formation in terms of the percentages of the main forms (*Pistillipollenites mcgregorii* Rouse, *Castanea* sp., *Rhus* sp., *Nyssa* sp., *Engelhardia quietus* (Potonie) Elsik). However, these forms, somewhat different in composition in the Kengdeiskaya (s.l.) Formation complex, in which angiosperm pollen and spores alternately dominate, may not be considered time equivalent, as the polynomorph spectra of the Tastakhskaya Formation are represented by tricolporate and tricolpate pollen, namely *Ulmoideipites* Anderson, and *Pistillipollenites* Rouse, while in the Kengdeiskaya (s.l.) Formation, Betulaceae pollen, *Quercites sparsus*, and Polypodiaceae spores are dominant (Kulkova, 1973). According to Boitsova (1966), *Quercites sparsus* had a very wide range in the Paleocene and was replaced in the Eocene by other characteristic species, such as *Quercus graciliformis* Boitzova and *Q. conferta* Boitzova. In turn, *Quercus graciliformis* and *Q. conferta* are very typical taxa of the complexes of the Tastakhskaya Formation (Kulkova, 1973).

In addition, the Paleocene and older forms, not found in the spectra of the Tastakhskaya Formation, but noted in the Kengdeiskaya (s.l.) Formation, include *Psophosphaera lanceolata* Bolkhovitina, *Psophosphaera magnoloides* Bolkhovitina, *Dicksonia densa* Bolkhovitina, *Podozamites bilateralis* Bolkhovitina, *Parviprojectus echinaceus* Mtchedlishvili, and *Beaupreaidites elegnasiformis* Cookson. There are morphotaxa, such as *Loranthus elegans* Kulkova, *L. mirus* Kulkova, *Cardiespermum notablle* Kulkova, *Tetraporites lubomirovae* Kulkova, *Pleurospermaepollenites tastacliensis* Kulkova, only observed in the palynomorph complex of the Tastakhskaya Formation and absent from the Kengdeiskaya (s.l.) Formation (Kulkova, 1973). Moreover, it is shown that palynomorphs considered by Fradkina (1995) as typical Paleocene elements and Late Cretaceous relicts are absent from the palynomorph complex of the Tastakhskaya Formation. This indicates that the Tastakhskaya Formation complex is younger than the Kengdeiskaya (s.l.) Formation complex.

According to Fradkina (1995), pollen of *Fothergilla* Murray, *Hamamelis* Linnaeus, and *Pistillipollenites* made their first appearance in the palynological complexes of the Kengdeiskaya (s.l.) Formation, while they are absent from those of late Paleocene. The Eocene age is confirmed by regional correlation with palynological assemblages in other regions of Siberia, in particular, early Eocene of the Yenisei Ridge (Kulkova and Laukhin, 1975), based on the appearance of characteristic Eocene pollen such as *Quercus graciliformis Castanea* sp., Juglandaceae gen., *Tricolpopollenites liblarensis* (Thomson) Thomson and Pflug, *Fothergilla vera* Lubomirova, as well as *Trudopollis* sp., and *Sporopollis* sp. Notabaly, *Fothergilla* sp. is one of the key taxa for Eocene sediments of Siberia (Kulkova, 1973) and the Far East (Brattseva, 1969). Common taxa were also found in early Eocene palynological assemblages of Western Siberia (Fradkina, 1995). In addition, the Eocene age of the palynological assemblage of the Bykovskaya Formation (= Kengdeiskaya (s.l.) in the location of Bykovskaya Channel) is also confirmed by dinoflagellates (cf. Kulkova, 1987), including *Wetzeliella articulate* Eisenack, *Deflandrea phosphoritica* Eisenack, and *Isabellidinium* sp., which have not yet been found in strata younger than early Eocene (Grinenko et al., 1989).

Therefore, the palynological assemblage of the Kengdeiskaya (s.l.) Formation can be attributed to the first half of the early Eocene (Grinenko et al., 1997). Additional age evidence comes from a freshwater mollusk assemblage of *Lanceolaria* sp., *Margaritifera* sp., and *Hyriopsis* sp. (Grinenko et al., 1989), indicating early Eocene. Laukhin et al. (1988) reported leaf impressions from the Kunginskaya strata (= Kengdeiskaya (s.l.) Formation), at Kunga River, suggesting Eocene age close to the boundary with Paleocene. The identified leaf flora included representatives of *Liquidambar* Linnaeus, *Quercus* Linnaeus, *Fagus* Linnaeus and *Alangium* Lamarck, which are widely present in Eocene and Oligocene floras. A characteristic feature of the Kengdei flora is the large leaf size noted for *Platanus*, *Trochodendroides* Berry, *Alnus*, *Acer* Linnaeus, and *Alangium*. The Arctic large angiosperm leaves (Herman, 1994) are considered an adaptation to low and predominantly diffuse sunlight situations with sufficient water supplies. This feature is also a charactreristic of Cretaceous and Paleogene high latitude floras, e.g., the early–middle Eocene flora of Tastakh Lake (Kryshtofovich, 1958; Budantsev, 1983). Although there are differences between the Tastakh flora and the Kengdei flora, Grinenko et al. (1989) point to the continuity in their development through common taxa, such as *Trochodendroides arctica*, *Liquidambar*, *Acer arcticum*, and *Alangium*.

5.2. Climate evolution

Given the scarcity of quantitative continental paleoclimate data for the early Eocene, we here provide valuable estimates on the early Eocene climate of the high-latitude northern Yakutia. With an MAT of at least ca. 16°C and CMMT ca. 10°C in the warmer floras and ca. 14.5°C/3.5°C in the coolest flora, a warm temperate or possibly near-tropical climate persisted throughout the deposition of the strata (Fig. 5). The climate was overall humid, with high MAP rates of at least ca. 1200 mm in the warmer phases and over ca. 1000 mm during the cooler phases (Fig. 6).

Considering the paleolatitude of the study section at about 76°N (ODSN Plate Tectonic Reconstruction Service using 55.0 Ma and the hotspot reference frame 1), the CMMT in the study area was warmer than present by around 55°C (modern climate data from WorldClim). This result and CMMT anomalies of middle Eocene paleobotanical sites of Eurasia of 60°N, including Spitsbergen and Greenland (Utescher et al., 2011) are in line with a reconstruction based on early to middle Eocene palynofloras of coastal plain sediments on the Belkovsky and Faddeevsky Islands (New Siberian Islands, Russia) (Suan et al., 2017). In the Faddeevsky Island record, quantitative climate data were obtained with the Climatic Amplitude Method (Fauquette et al., 1998), with most likely values varying between ~16°C and 21°C for MAT, ~6°C and 14°C for CMMT, ~25°C and 28°C for WMMT, and 1100 mm and 1370 mm for MAP, similar to those of the present reconstruction. The Faddeevsky Island succession was deposited between the PETM and Eocene Thermal Maximum 2 (ETM2) (early Eocene) at 56–54 Ma, when temperature rose globally before reaching a long-term maximum known as the EECO (Zachos et al., 2008; Westerhold et al., 2020). Comparing the Faddeevsky Island succession with our record, significant differences are observed. The earlier part of our record (up to ca. 25 m) shows an intermittent cooling trend, coinciding with the global marine signal (cf. declining trend in the oxygen isotope record postdating the PETM, Zachos et al., 2008), while the Faddeevsky record displays a strong warming signal succeeding the PETM (Suan et al., 2017).

In general, paleoclimate proxies indicate exceptional warmth in both the southern and northern high latitudes during the early Eocene, with SSTs and MATs exceeding 8°C to 18°C (Weijers et al., 2007; Eldrett et al., 2009; Huber and Caballero, 2011; Pross et al., 2012; West et al., 2015). The above-mentioned Paleocene–Eocene continental warming trend coincides with the global marine isotope stack (Zachos et al., 2008) and is likewise mirrored in other marine proxies such as faunal patterns in Tethyan carbonate platforms (Scheibner and Speijer, 2008). Hence, this warming trend represents a global pattern that appears to be at odds with the generally declining atmospheric CO_2 reported for that time-span (Zachos et al., 2008; Huber and Caballero, 2011). At the same time, there is a so-called "equable climate problem" which has not yet been solved in paleoclimate modelling (Huber and Caballero, 2011). Most recent studies, considering cloud feedback mechanisms, provided some overlapping of model data and continental proxies at high northern latitudes, in model runs with strongly raised atmospheric CO_2 (Zhu et al., 2019).

Warmest conditions with peaks for MAT, CMMT, and WMMT are found in the lowermost part of the section (PF 18; Fig. 9). The subsequent cooling (up to depth levels 12–14 m) and the warming trend setting on in the upper part of the section roughly coincide with coeval trends in the global $\delta^{18}O$ values of the earlier early Eocene (Zachos et al., 2008). According to the palynostratigraphical constraints outlined above, this warmest peak would comprise the global hypothermal event (PETM).

Very warm conditions in the early Eocene at high latitudes, as evident from our data for PF 18, are supported by results from other continental and marine proxies. High MAT (~18–25°C, Weijers et al., 2007; and ~16–21°C, Suan et al., 2017) and SST (~18–25°C, Sluijs et al., 2009)

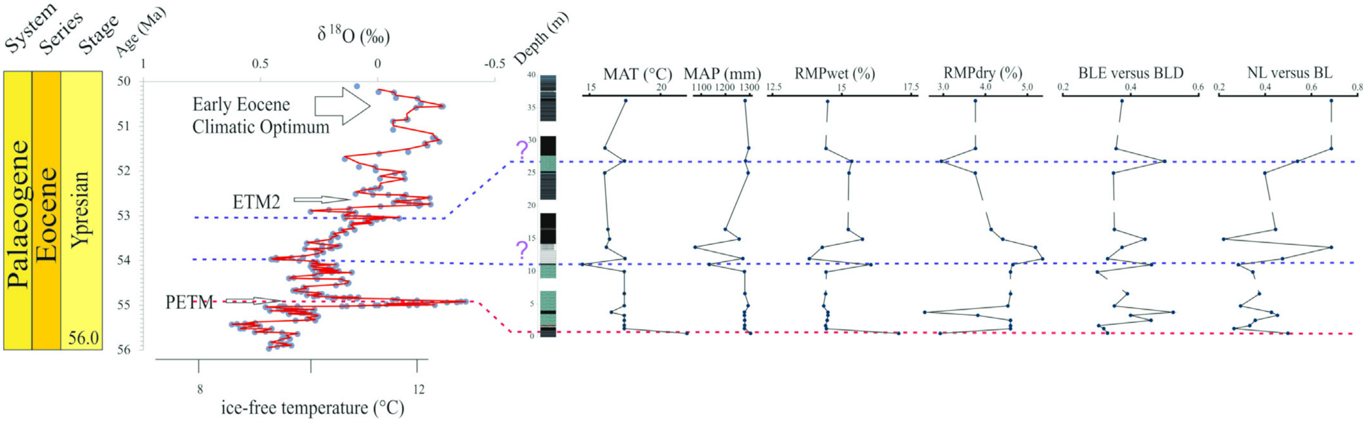

Fig. 9. Curves of various climate and vegetation characteristics for the study succession versus the composite deep-sea benthic foraminiferal oxygen isotope record after Zachos et al. (2008). Red dashed line – correlation based on the stratigraphical concept of regional stages by Grinenko et al. (1997); blue dashed lines – alternative correlation suggested by climate stratigraphy.

values based on tetraether membrane lipids are reported from Arctic lower Eocene strata of IODP Site 302, Lomonosov Ridge (Willard et al., 2019). The lower to middle Eocene strata of Arctic Canada and Greenland yielded floral and faunal data, indicating high temperatures with MAT (8°C and 17°C) and CMMT (3–9°C) (Eldrett et al., 2009; Huber and Caballero, 2011; Wolfe et al., 2012; West et al., 2015). Suan et al. (2017) reported multiproxy data from early Eocene coastal plain sediments of the New Siberian Islands (Russia), showing that taxodioid Cupressaceae, palms, and the mangrove *Avicennia* grew in Arctic Siberia above 72°N under air temperatures averaging 16–21°C annually and 5.5–14°C in winter, as well as exceptionally high kaolinite contents (up to 60% of clay assemblages) that is comparable to those found in present-day subtropical soils formed under high MAP (> 1000 mm) and MAT (> 15°C). The *Avicennia* pollen records the northernmost mangrove growth ever documented and indicates early Eocene SSTs exceeding 13°C in winter and 18°C in summer (Suan et al., 2017).

Other paleontological evidence of warm climates includes crocodiles living in the higher latitudes (Sloan and Rea, 1995; Huber, 2009), the presence of frost-intolerant flora such as palm trees (Huber, 2009; Huber and Caballero, 2011), and fossil snakes that presently live in the tropics (Huber, 2009). Oxygen isotope ratios of mammal teeth and fish scales ($\delta^{18}O$) and fossil plants suggest an Early Eocene MAT ranging from 8°C to 15°C (Greenwood and Wing, 1995; Weijers et al., 2007; Eberle et al., 2010). WMMT probably reached 19–20°C or higher, and CMMT were above freezing (Weijers et al., 2007; Sluijs et al., 2008; Eberle et al., 2010).

Long-standing evidence for a warm Arctic climate was first indicated by the Eocene fauna on Ellesmere Island (Nunavut, Arctic Canada) that included alligators, a varanid lizard, boid snakes, giant tortoises, tapirs and primates (Dawson et al., 1976, 1993; Estes and Hutchison, 1980; Markwick, 1994; Eberle, 2005). The physiological stresses on plants growing in warm polar latitudes are unique — these plants, even in greenhouse conditions of the past, tolerated the same extreme photoperiod that currently exists above the Arctic Circle (McKenna, 1980; Irving and Wynne, 1991; Royer et al., 2003). Many of these polar plants were deciduous (Basinger et al., 1994; McIver and Basinger, 1999) and dormant during the dark winter months, but physiologically active during the low intensity 24 h summer light regime (Royer et al., 2003; Jahren and Sternberg, 2008).

As is shown in Figs. 7 and 8, our early Eocene data suggest a strong impact of climate change and variability on vegetational composition in northern Yakutia, based on the ratio of broadleaved evergreen versus deciduous PFTs.

5.3. Vegetation change

Pollen evidence presented here indicates that mixed conifer-broadleaved forests occupied land masses in the region during early Eocene. The relatively high percentages of bisaccate pollen (*Pinus* Linnaeus, *Picea* Dietrich, *Abies* Miller) suggests that conifer forests were present in upland sites; the common occurrence of juglandaceous and taxodioid pollen and fern spores indicates that broadleaved forests and forested wetlands occurred near rivers and/or the coastline. The occurrence of these assemblages at high latitudes suggests that the land surface from the mid-latitudes of North America and Europe to the Arctic were covered by mixed conifer-broadleaved forests (Boulter and Manum, 1989; Greenwood and Basinger, 1994; Jolley and Whitham, 2004; Jolley and Morton, 2007; Smith et al., 2007; Jolley et al., 2009; Greenwood et al., 2010; Daly et al., 2011; Kender et al., 2012; Eldrett et al., 2014; West et al., 2015; Suan et al., 2017; Willard et al., 2019). Macrofloral data from Ellesmere Island show that the late Paleocene to early Eocene lowland terrestrial vegetation included coal-forming swamp forests dominated by conifers such as *Glyptostrobus* Endlicher and *Metasequoia*, whereas upland forests were dominated by broadleaf taxa including Betulaceae Gray, Cercidiphyllaceae Endlicher, Trochodendraceae Eichler, Juglandaceae, Platanaceae Lestiboudois ex Dumortier, *Ulmus* Linnaeus, and *Tilia* Linnaeus (Eberle and Greenwood, 2012).

The PFT diversity spectra (Fig. 7, Table S4) indicate that the vegetation of northern Yakutia in the early Eocene was of mixed evergreen-deciduous type, generally in accordance with our data from IPR approach. Based on IPR, the MMF zonal vegetation type dominated in northern Yakutia during the early Eocene. The cooler vegetation type, represented by the ecotone BLDF/MMF, was found in five levels (Fig. 7, Table S5). However, in both cases zonal forest biomes have a warm temperate character.

It is known that vegetation changes are often induced by climate change. Our study shows that the change in the proportion of some groups of PFTs (needleleaved versus broadleaved, broadleaved deciduous versus broadleaved evergreen) throughout the early Eocene in the study succession reflects changes in climatic parameters (Fig. 9). The constant presence of PFT 18 in all studied floras herein suggests high humidity in general, and agrees with the precipitation reconstruction considerably wetter conditions than at present. PFT 18 is also indicative for the existence of swamps at places and intrazonal swamp forest communities, suggesting the presence of inundated areas during early Eocene. The constant presence of humid herbs (PFT 1) also indicates high humidity. High humidity in the Arctic under greenhouse climates is already known for Late Cretaceous, based on leaf floras from Alaska and Northeast Russia using CLAMP (Spicer et al., 2019). The humid polar conditions are probably referrable to the enhanced hydrological cycle and formation of clouds in the Arctic, that may also explain the warm polar conditions, due to the radiative forcing effect (Niezgodzki et al., 2017).

The tropical PFTs (PFTs 25 and 26) are present in almost all floras but in low proportions (1.3–3.2% and

1.4–4.5%, respectively) (Fig. 7). Many taxa scoring for tropical PFTs may represent temperate types (for example, *Castanopsis* (Don) Spach, Hamamelidaceae Brown, *Ilex* Linnaeus, Juglandaceae, Menispermaceae Jussieu, *Myrica* Linnaeus, Proteaceae Jussieu). Nevertheless, the warmer IPR vegetation type and higher broadleaved evergreen PFT diversity observed agree with the inferred climate evolution. The presence of megathermic elements near the base of the Faddeevsky record described by Suan et al. (2017), as well as the high proportions of mega-mesothermic elements near the PETM, supports the presently observed occurrence of tropical and warm temperate PFTs.

Our analyses suggest that early Eocene high-latitude vegetation of northern Yakutia was basically a warm temperate mixed forest. In contrast to northern Yakutia, the early Eocene of Primorye was found to be of mainly zonal subtropical broadleaved evergreen forests (BLEF), zonal warm temperate to subtropical mixed mesophytic forests (MMF) and the ecotone MMF/BLEF, using IPR (Bondarenko et al., 2019), and of mixed mesophytic forests based on PFT (Bondarenko et al., 2021). The vegetation of northern Yakutia in the early Eocene includes a lower proportion of evergreen broadleaved PFTs and has a more temperate character compared to the more southern vegetation of Primorye (Bondarenko et al., 2021). From early Neogene carpofloras of the eastern RFE, Popova et al. (2013) reconstructed a high diversity (40–50%) of warm temperate woody plants, including evergreen broadleaved trees.

According to Collinson (1990, 2000, 2001), a thick tropical, subtropical and deciduous forest existed in the early Eocene around the globe, and from the late middle Eocene, subtropical evergreen forest vegetation gradually changed into vegetation characterized by the loss of paratropical elements and increasing proportion of temperate deciduous elements resulting in the establishment of broadleaved mixed deciduous and evergreen forests in the Oligocene (Collinson, 1992). For most of the early Cenozoic, a remarkable expanse of humid, warm-temperate to temperate forests spread across Northern Polar regions (Wolfe, 1977; Hickey et al., 1983; Basinger et al., 1994; McIver and Basinger, 1999; Sluijs et al., 2008; Eldrett et al., 2009).

The succession in this study is characterized by a high variety of conifers, among which Taxodioideae (17.8–39.0%) predominate, except for PF 12 (Fig. 3). PF 9 with the highest Taxodioideae content (53.3%) correlates with the lowest temperatures (MAT, CMMT and WMMT). Generally, forests with high proportion of *Taxodium* may represent azonal vegetation connected to phases with increased extension of peat bog facies. According to Willard et al. (2019), during the PETM recovery, taxodioid Cupressaceae-dominated swamp forests were important elements of the landscape, representing intermediate climate conditions between the early Eocene hyperthermals and background conditions of the late Paleocene.

Today, Yakutia has a very heterogeneous vegetation cover (Tsherbakov, 1975), rich in fluvial and lacustrine environments. It includes taiga, forest-tundra and tundra, representing the subarctic, arctic and temperate climatic zones; forests in general cover about 4/5 of the territory. Our study shows that the early Eocene vegetation cover in the study area fundamentally differed from the present vegetation. Based on the low proportion of herbaceous PFTs (2.7–8.0%), northern Yakutia was entirely covered by forest vegetation during early Eocene, similar to the early Eocene of Primorye (Bondarenko et al., 2020a). The results obtained from the PFT approach are largely in accordance with those of IPR approach. According to Kovar-Eder et al. (2008) and Teodoridis et al. (2011), with zonal herb proportions ranging from 7.8% to 20.8%, no open woodland is reconstructed for northern Yakutia during early Eocene based on the IPR vegetation analysis. Popova et al. (2013) showed a steep declining trend of the arboreal component in Western Siberia after Eocene.

5.4. Temperature and precipitation seasonality

Yakutia is currently characterized by a pronounced temperature seasonality but no humidity seasonality; MART is at the very high level of 45.0°C at a mean, MARP around 18 mm. The cold period (November–March) accounts for approximately 20–25%, and the warm (April–October) 75–80% of MAP. The minimum precipitation is observed in most of the territory in February–March. The modern RMPwet and RMPdry calculated based on the mean values using station data of Tiksi (Müller and Hennings, 2000; New et al., 2002), are 14.1% and 7.6%, respectively (Table S2).

Before ~3.6 Ma, the high latitudes of the Northern Hemisphere generally were substantially warmer than today and there were no widespread Arctic ice sheets (Herbert et al., 2016; Karas et al., 2020). Paleogene temperature gradients on the Northern Hemisphere were shallow in general as was reconstructed from paleobotanical proxies (Greenwood and Wing, 1995; Utescher et al., 2011). Shallow meridional gradients and considerably warmer-than-present higher northern latitudes were also obtained in various Cretaceous to Paleogene model runs under substantially raised atmospheric CO_2 (e.g., Lunt et al., 2012; Zhu et al., 2019) while it was shown that modified cloud schemes in the model may simulate increasing warming at high latitudes and at the same time do not lead to overheating of the tropics. Our climatic data suggest a relatively weak seasonal control of the early Eocene climate of northern Yakutia. The significantly higher early Eocene WMMTs in combination with significantly higher CMMTs indicate a distinctly lower-than-present seasonality of temperature during the early Eocene. Our MART values for the early Eocene generally range from 15–16°C, occasionally dropping below 13°C and rising above 20°C (Fig. 9, Table S2). Moreover, seasonal temperature reconstructions show that the warming was primarily a winter phenomenon, with little variability in summer temperatures throughout the profile (Fig. 9). Comparable patterns resulted from CLAMP studies on Arctic floras of the Late Cretaceous (Spicer et al., 2019).

According to Akhmetiev (2015), warming in the transitional interval of the Paleocene and Eocene, revealed by fossil plants in the Arctic coast of Eastern Siberia was caused by atmospheric heat transfer from the Tethys, from low to high latitudes in the period preceding the beginning of the formation of the latitudinal Alpine-Himalayan orogenic belt, which appeared from the middle Eocene. In addition, oceanic heat transfer may have added to Eocene Arctic warmth, such as the meridional current connecting the Tethys and the Arctic Ocean through the marine basins of the Northeastern Peritethys, the Turgai Strait, and the West Siberian Inland Sea. This is confirmed by the presence of warm-water microplankton in the northern sections of Western Siberia and in the high SSTs established by isotope studies. SST increase of up to 20°C and even higher, reported from transitional layers at the Paleocene–Eocene boundary on the Lomonosov Ridge (Backman and Moran, 2004; Backman et al., 2006), likely due to oceanic heat transfer from southern regions of Asia. The pronounced seasonality of precipitation (MPwet 175–277 mm; MPdry as 25–66 mm) in northern Yakutia weakly fluctuated during the early Eocene. The early Eocene MARP was significantly higher-than-present. However, the much higher past MPwet coupled with distinctly higher MPdry indicate that, during early Eocene, the climate of northern Yakutia was significantly more humid. The calculated proportions of MPwet and MPdry to yearly precipitation (MPwet: 13.8–21.3%; MPdry: 1.9–5.2%) are almost twice as high for MPwet and 2–4 times lower for MPdry compared to present-day (Fig. 9, Table S2), suggesting pronounced precipitation seasonality in comparison to the present-day. CLAMP analysis of Late Cretaceous Actic floras revealed comparable seasonal precipitation patterns, under the enhanced hydrological cycle at times of global warmth (Spicer et al., 2019).

The precipitation reconstruction points to conditions considerably wetter than those of present, evidenced by the distinct increase in MAP for the early Eocene and moderately declined throughout the Oligocene (Utescher et al., 2014). The regional rainfall pattern of Primorye in the early Eocene also differed from modern conditions (Utescher et al., 2015; Bondarenko et al., 2020a), as was the pronounced seasonality of climate of the Amur Region throughout the Paleocene (Bondarenko et al., 2021). The Paleogene pattern of the southern part of the Eurasian Pacific Coast (low and middle latitudes) was possibly related to an early established monsoon-type circulation over East Asia (Quan et al., 2011, 2012) and enhanced flow of humid air masses from the Pacific to inland areas of northeast Asia.

The ratio of the wet month precipitation of the total amount of annual precipitation (RMPwet) is commonly used as a good proxy for East Asian monsoon intensity (Jacques et al., 2011). However, at high latitudes, precipitation seasonality can not be explained by monsoon signals. Eldrett et al. (2014) associated seasonally wetter summers, briefly prior to and during the PETM interval in the North Sea, with enhanced hydrological cycling, a mechanism also operational in the Artic during the late Cretaceous (Spicer and Herman, 2010).

5.5. Mangrove taxa in the Yakutia record and their climatic implications

Among the most interesting pollen in the studied microfloras is that of *Nypa* sp. (Fig. 4). In general, fossil *Nypa* pollen occur from Late Cretaceous to the Recent (Frederiksen, 1985; Thanikaimoni, 1987; Westgate and Gee, 1990; Lenz et al., 2021). *Nypa fruticans* Wurmb, the only extant species, thrives in mangrove communities found in a belt straddling the equator from India to Southeast Asia to northern Queensland (Tomlinson, 1986). Assuming the habitat of extinct *Nypa* Steck is similar to that of the extant species *N. fruticans*, the presence of *Nypa* fossils may indicate monsoonal or at least seasonal rainfall regimes, likely indicative of tropical climates (Pole and Macphail, 1996). At present, mangroves are salt-tolerant, adapted to harsh coastal conditions (e.g., Tomlinson, 1986; Stewart and Popp, 1987; Ball, 1988; Duke et al., 1998). The worldwide distribution of *Nypa* in the Eocene, especially in deposits from polar latitudes, indicates that Eocene was a time of global warmth, prior to the formation of modern polar ice-caps at the end of the Eocene.

High latitude fossil *Nypa* has been reported from late Paleocene microflora of Chukotka (Belaya and Litvinenko, 1989) and early–middle Eocene microflora of Tastakh Lake in northern Eastern Siberia (Kulkova, 1973). Other mangove pollen — *Avicennia* Linnaeus — appears in the early Eocene in Europe (Sein, 1961; Chandler, 1964) and New Siberian Islands (the paleolatitude of ca. 72°N) (Suan et al., 2017; Suc et al., 2020). Based on ODSN Plate Tectonic Reconstruction Service for 55.0 Ma and the hotspot reference frame 1, the paleolatitude of New Siberian Islands is about 78°N.

In our record (at a paleolatitude of ca. 76°N), *Nypa* pollen occurs as single grains in PF 18 (Zone I; see Fig. 4) from fine-grained, laminated, predominantly clayey and coal deposits. The dark, clayey sediments and high content of taxodian pollen and fern spores suggest extensive wetland habitats in lowland, favorable for the growth of *Nypa* in the early Eocene in the study area, where the deposits are characterized by dark color (anoxic habitat), fine-grained and layered sediments (stable conditions), coastal-marine interlayers containing dinocysts (associated with increased salt content), and pronounced seasonal precipitation. The occurrences of single grains of *Nypa* pollen may be due to poor preservation of materials of these low pollen producing plants, and transportation to distant burial sites. However, no evidence for reworking is found and aeral dispersal of insect-pollinated *Nypa* pollen is quite delimited

(Gastaldo, 1992), indicating a (par)autochthonous origin of the pollen grains. Previous studies show that fossil records of *Nypa* are rare throughout the Cenozoic (e.g., Collinson, 1983; Biosca and Via, 1987).

Mangroves in our records are represented by only one taxon, probably indicating a time of decline of mangroves in the vegetation immediately after the PETM.

6. Conclusions

We provide the first quantitative climate and vegetation analyses for the high latitudes of the Far East of Russia, important for understanding the conditions following the PETM. Our temperature data indicate a strikingly high anomaly with respect to present-day climate, with a CMMT difference of up to 55°C. Seasonality of temperature was comparatively low. Precipitation was at a high level of over 1000 mm in wet climate phases and over 600 mm in dry phases. Seasonality of precipitation was lower in the earlier part of the studied succession pointing to equable conditions near the PETM, thereafter increasing throughout the early Eocene. Climate conditions supported a dense forest cover comprising various warm temperate vegetation types and at times the presence of tropical PFTs.

According to IPR vegetation analysis, MMF vegetation existed over most of the time-span, including diverse broadleaved deciduous components that thrived under long-lasting polar darkness at a paleolatitude near 77°N. Persistent occurrence of swamp vegetation indicates favourable conditions for peat forming in the lowlands. The sporadic occurrence of mangrove elements near the base of the study section suggests a phase with almost tropical climate conditions at such high latitudes, and can possibly be related to the PETM. Our quantitative climatic and vegetational reconstruction supports the hypothesis of early Paleogene warmth in the High Arctic based on a variety of proxy data.

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Supplementary data

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