



Temporal climate and vegetation gradient of the Paleocene in the Amur Region (Far East of Russia)

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ABSTRACT

Paleocene climate and vegetation evolution in the Amur Region (Far East of Russia) are quantitatively studied for the first time in detail, based on a palaeobotanical record. Palaeobotanical data for this time interval were obtained from a total of 25 palynofloras from Core 154 drilled in the Erkovetskii Brown Coal Field. In this first integrative study we apply the Coexistence Approach (CA) for quantification of palaeoclimate, the Plant Functional Types (PFT) approach and Integrated Plant Record (IPR) vegetation analysis for quantification of palaeovegetation. Our investigation documents the persistence of warm to cool temperate, overall humid climate conditions throughout the Paleocene. The reconstructed temperature records indicate relatively cool conditions for the early Paleocene part of the succession near the K-T boundary combined with distinctly seasonal conditions. The late Paleocene samples reveal a distinct warming trend and a tendency to more equal climate conditions that can be correlated with declining oxygen isotope values observed in marine archives. Our climate data indicate a relatively strong seasonality in precipitation suggesting the existence of a proto-monsoon in the Amur Region during the Paleocene. Vegetation data as reconstructed are in good agreement with the climate evolution. Based on PFT diversity spectra, our data indicate the prevalence of mixed evergreen-deciduous forests of warm temperate character. Based on the IPR method, plant biomes varied from the mixed mesophytic forest / mixed broadleaved evergreen forest ecotone in the warmer parts to the broadleaved deciduous forest / mixed mesophytic forest ecotone in the cooler parts of the studied sedimentary succession.

Keywords: temperature evolution, precipitation pattern, monsoon intensity, structure of plant assemblages, vegetation type

РЕЗЮМЕ

Бондаренко О.В., Утешер Т., Блохина Н.И., Евстигнеева Т.А., Кезина Т.В. Временной градиент климата и растительности Амурской области (Дальний Восток России) в палеоцене. Эволюция климата и растительности Амурской области (Дальний Восток России) в палеоцене впервые детально количественно изучена на основе палеоботанических данных. Палеоботанические данные для этого временного интервала были получены на основе анализа 25 палинофлор из ядра 154, пробуренного в Ерквецком буровом месторождении. В этом первом комплексном исследовании мы применяем метод Coexistence Approach (CA) для количественной оценки палеоклимата, Plant Functional Types (PFT) подход и Integrated Plant Record (IPR) анализ – для количественной оценки палеорастительности. Наше исследование документирует сохранение тёплых до прохладно умеренных, влажных климатических условий в течение всего палеоцена. Реконструированные температурные параметры указывают на относительно прохладные условия для раннего палеоценового участка сукцессии вблизи мел – палеогеновой границы в сочетании с отчётливо сезонными условиями. В поздних палеоценовых образцах прослеживается отчётливая тенденция потепления и тенденция к более ровным климатическим условиям, которые могут быть связаны с уменьшением значений изотопов кислорода, наблюдаемых в морских отложениях. Наши климатические данные указывают на относительно сильно выраженную сезонность осадков, предполагающую существование прото-муссона в Амурской области в палеоцене. Реконструированные данные о растительности хорошо согласуются с эволюцией климата. Наши данные спектров разнообразия PFT указывают на распространение смешанных вечнозелёных лиственных лесов теплоумеренного характера. На основе данных метода IPR, биомы растений варьировали от экотона между смешанным мезофитным / смешанным широколиственным вечнозелёным лесом в более тёплых частях до экотона между широколиственным листопадным / смешанным мезофитным лесом в более холодных частях изученной осадочной сукцессии.

Ключевые слова: динамика температуры, характер осадков, интенсивность муссона, структура растительных сообществ, тип растительности

INTRODUCTION

The Paleocene, as the first geological epoch of the Paleogene, lasted from about 66 to 56 Ma and was bracketed by two major dramatic events in Earth's history: a mass extinction and a rapid global warming. The mass extinction event started at the end of the Cretaceous (66.02 Ma), known as the Cretaceous – Paleogene boundary (KPB). Rapid climate warming in the last 350 kyr of the Maastrichtian and climate cooling during the first 500 kyr of the early Paleocene are linked to a large impact of the Chicxulub asteroid and Deccan volcanic eruptions (Schulte et al. 2019, Punekar et al. 2014). The end of the Paleocene was marked by one of the fastest and most extreme global warming events recorded in geological history. It was a geologically brief interval known as either the Paleocene – Eocene Thermal Maximum (PETM) or the Initial Eocene Thermal Maximum (IETM). The PETM event (55.8 ± 0.2 Ma) lasted ~ 170 ky, and it 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, Wicczorek et al. 2013, Gutjahr et al. 2017, Morgan et al. 2019, Jones et al. 2019). The PETM brought about noticeable biotic changes, such as extinction, appearance, blooming and / or diversification of various ocean and land-dwelling organisms. Besides, the late Paleocene – early Eocene (~56–51 Ma) interval was a critical phase in the history of the India–Asia convergence. This major tectonic event, the India–Asia collision, contributed to the uplift of the Tibetan Plateau, and the last has triggered the trend of decreasing atmospheric CO₂ concentration and major change in global climate in the Eocene (e.g. Clementz et al. 2011, Meng et al. 2012, Najman et al. 2017, Wang et al. 2018).

Globally, Paleocene climate was relatively stable, warm and moist. The Polar Regions were ice-free and covered with coniferous and deciduous forests (Willis & McElwain 2002). These Paleocene polar forests grew in winter darkness and mesothermal humid climate (Willard et al. 2019). Those were very low diversity forests with little habitat variation, very few climbers and more open structure (Collinson & Hooker 2003). The warm temperatures worldwide gave rise to thick tropical, subtropical and deciduous forest cover around the globe. Paleocene forests were probably denser than those of the Cretaceous. First angiosperms, seen in the Cretaceous, continued to develop and proliferate. In general, the Paleocene is marked by the development of modern plant species, cacti and palm trees appeared (Collinson 1990, 2000, 2001). Thus, Paleocene floras provide the potential for detailed interpretation of plant biomes and their response to global change such as warm climate thermal maxima and tectonic events, and the knowledge of the vegetation evolution during the Paleocene provides unique perspectives for the modeling of actual global changes and helps to probe into the integrated response of the Earth system to various driving forces (Utescher et al. 2009, Zachos et al. 2008).

Today, the Amur Region is located in the south of the Russian Far East (RFE) in the transition zone of continental and oceanic climates and its vegetation belongs to the con-

tinental-transition group of ecosystems with a monsoon climate (Naprasnikov et al. 1983). Due to the considerable remoteness from the Pacific Ocean (about 1200 km), the climate has pronounced features of continentality: large fluctuations of daily and annual temperatures, low winter and negative mean annual temperatures. In the cold season, air masses coming from Eastern Siberia, Mongolia, and from the Arctic Ocean dominate here while during summer winds blow from the Pacific Ocean bringing the major part of annual precipitation. Such distribution in the conditions of mountainous terrain, for example, the middle and upper parts of the Zeya River basin, causes river floods and often catastrophic flooding (Naprasnikov et al. 1983).

At present, a large part of the Amur Region is occupied by light coniferous taiga. Dark coniferous forests grow mainly in the east and northeast of the region. Zonal taiga forests are replaced in places by derivative birch forests. In the south of the region, various nemoral forests (the floral composition of nemoral vegetation formed in the Cenozoic (Turgai flora) from deciduous and coniferous species and herbaceous perennials) have remained representing an extremely depleted derivative of the Turgai flora. In the extreme southeast, nemoral vegetation is represented by cedar-broadleaved taiga with significant participation of relict “Tertiary” species (Starchenko 2009, Borisova & Starchenko 2018). The specifics of the flora and vegetation of the Amur Region are mainly associated with two factors: the belonging of the main part of the region to the Amur Basin and the location of the region on the border of the East Asian and Circum-Boreal floristic regions; the influence of the Pacific Ocean can be traced in the southern, central and eastern parts of the Amur Region (Starchenko 2009, Borisova & Starchenko 2018).

The evolution of the Paleogene (including Paleocene) climate and vegetation in East Eurasia in general and the Amur Region in particular is tied to global climate change, changes in regional palaeogeography and ocean currents, and the history of the East Asian monsoon (EAM), the emergence of which was promoted by the rise of the Tibetan Plateau (e.g., Akhmetiev 2004, 2015, Akhmetiev & Zaporozhets 2017, An et al. 2001, Liu & Yin 2002, Liu et al. 2015, Quan et al. 2012a, b, Sato et al. 2006, Tada et al. 2016, Yamamoto & Hoang 2009). Climate and vegetation in the Paleocene can be reconstructed from the palaeobotanical record. The Amur Region is one of the RFE regions, where large burials of Paleogene plants are concentrated, therefore the Paleogene (including Paleocene) floras of this region were subject to various taxonomic and stratigraphic studies the results of which were presented in the works of Akhmetiev (1973), Akhmetiev et al. (1969, 2002), Brattseva (1969), Kamaeva (1990), Kezina (2000, 2004, 2005), Kezina & Litvinenko (2007), Kezina & Ol'kin (2000), Krassilov (1976), Mamontova (1975, 1977), Varnavskii et al. (1988), Zaklinskaya et al. (1977), Ziva (1973), and others. However, these works are mainly devoted to the description of plant fossil remains, new fossil taxa, taxonomic diversity of plants, or palaeofloristic aspects. At the same time the knowledge on climate and vegetation dynamics in the Paleocene is still very poor and fragmentary.

For the RFE in general, our knowledge is mainly based on qualitative interpretations of macro- and microfloral successions, while quantitative studies were largely missing so far. Recently, quantitative palaeoclimate and vegetation studies were conducted on the Paleogene of the neighboring Primorye which unravelled major spatio-temporal changes (Bondarenko et al. 2019, 2020a, b) but revealed few details only as regards the evolution in the Paleocene.

Here we present a first higher-resolving time series for the climate and vegetation evolution of the Amur Region during the Paleocene. Our study is based on the investigation of 25 palynofloras sampled from a well that was cored through a complete Paleocene sedimentary sequence. We analyze changes in the taxonomic composition of the floras and the abundance of floral components and establish quantitative records to trace regional climate and vegetation dynamics at the time when first Cenozoic ecosystems became established. Moreover, we discuss potentially monsoon-induced patterns and how global signals manifested themselves in the Amur Region.

STUDY AREA

Sedimentary succession in the study area

The Erkovetskoe Brown Coal Field is located in the northwestern part of the Zeisko-Bureinskii Basin in the Amur Region of the RFE (Fig. 1A). The relief of the Coal Field is a flat plain, weakly dissected by a modern river system, with absolute heights of 190–250 m. The deposits are mapped by numerous cores (Fig. 1B).

The sediments of the Tsagayanskaya Formation, unconformably lying on older deposits of the Lower and Middle Cretaceous (Poyarkovskaya and Zavitsinskaya formations), have a wide regional extension. The total thickness of the formation exceeds 300 m. Lithologically, the Tsagayanskaya Formation is subdivided into three subformations: the Lower Tsagayanskaya, Middle Tsagayanskaya and Upper Tsagayanskaya subformations including the Kivdinskies layers (Fig. 1C).

The sediments of the Late Cretaceous Middle Tsagayanskaya subformation exposed in the Erkovetskoe Brown Coal Field are represented by dense clays composed of kaolin and montmorillonite, at places sandstones, sands, siltstones and layers of carbonaceous clays of greenish-gray and light gray color. Argillites are finely laminated and contain plant detritus. Interlayers and local brown coal lenses are found among clays and siltstones. The thickness varies from 20–35 to 170 m.

The early Paleocene Upper Tsagayanskaya subformation, which includes the late Paleocene Kivdinskies layers, is represented by a series of intermittent sand, siltstone and carbonaceous clay, overlying the sediments of the Middle Tsagayanskaya subformation without a visible discontinuity. The thickness of the subformation varies from 20 to 110 m. The upper part of the subformation includes a brown coal layer (6–9 m), its base smoothly dipping to the south. Palynologically, the Upper Tsagayanskaya subformation was studied by Kezina and Litvinenko (Kezina 2005, Kezina & Litvinenko 2007).

The lower part of the Upper Tsagayanskaya subforma-

tion is predominantly sandy. Its upper, coal-bearing part concordantly overlies the strata and that part has been denoted as Kivdinskies layers (Akhmetiev et al. 2002). The thickness of Kivdinskies layers usually attains 20–30, at some places 40–60 m. The brown coals of the Kivdinskies layers are overlain by homogeneous laminated clays, forming the topmost part of the Upper Tsagayanskaya subformation. Palynologically, the Kivdinskies layers were studied by Kezina and Litvinenko (Kezina 2005, Kezina & Litvinenko 2007).

In the central and northeastern parts of the sedimentary basin, the Kivdinskies layers are unconformably overlain by alluvial and lacustrine-alluvial sandy sediments of the early Eocene Raychikhinskaya Formation. In the Core 154, the Kivdinskies layers are covered by the Oligocene Mukhinskaya Formation.

Stratigraphy and dating

Biostratigraphic studies on the Tsagayanskaya Formation, which is the most renowned stratigraphic unit of the Amur Region, started more than a century ago. The problems concerning stratigraphy and nomenclature ranks of these Cretaceous to Paleogene deposits as well as the position of the Cretaceous–Paleogene boundary have been addressed in various studies (Yavorovsky 1911, Muzylev 1948, Fin'ko & Zaklinskaya 1958, Chemekov et al. 1960, Brattseva 1962, 1964, 1965, 1969, Kryshtofovich & Baikovskaya 1966, Ziva 1973, Krassilov 1976, Mamontova 1977, Zaklinskaya et al. 1977, Kamaeva 1990, Krasnyi et al. 1994, Bugdaeva et al. 2001, Akhmetiev et al. 2002, Sun et al. 2002, 2005, 2011, 2014, Markevich et al. 2004, 2011, Kezina 2005, 2011, Kezina & Litvinenko 2007, Herman et al. 2009, Hao et al. 2010, Moiseeva et al. 2018, and others). The formation of ideas about the structure and age of the Tsagayanskaya Formation and its subunits is exemplified in Fig. 2, based on selected works.

Recently, isotope dating was obtained for a rhyolitic tuff from the upper part of the Middle Tsagayanskaya subformation in the stratotype section of the Tsagayanskaya Formation (Ploskaya Mt.). Fission-track dating revealed an age of 61.7 ± 2.1 Ma (Suzuki 2004), whereas using U-Pb analysis, the age of this tuff layer was estimated as 66 ± 1 Ma (Knittel et al. 2013). Ages of 68.0 ± 0.96 Ma (U-Pb dating) were obtained from the same tuff layer at Ploskaya Mt. by Markevich et al. (2014). The isotope age of the rhyolitic tuff in the Baishantou section, exposed on the right bank of the Amur (Heilongjiang) River in China, according to Li et al. (2004), is 66 ± 1 Ma (U-Pb dating). Ages of 64.1 ± 0.7 Ma (U-Pb method) and 61.7 ± 1.8 Ma (fissiontrack dating) were obtained for the tuff layer in the lower part of Baishantou section by Suzuki et al. (2011).

Here we follow the stratigraphic concept of Moiseeva et al. (2018) (cf. Fig. 2).

MATERIAL AND METHODS

Floral record

In the present study, microfloras (PFs) from 25 depth levels sampled from Core 154 ($50^{\circ}48'N$ $128^{\circ}43'E$) are analysed covering the Upper Tsagayanskaya subformation and Kivdinskies layers in the Erkovetskoe Brown Coal Field

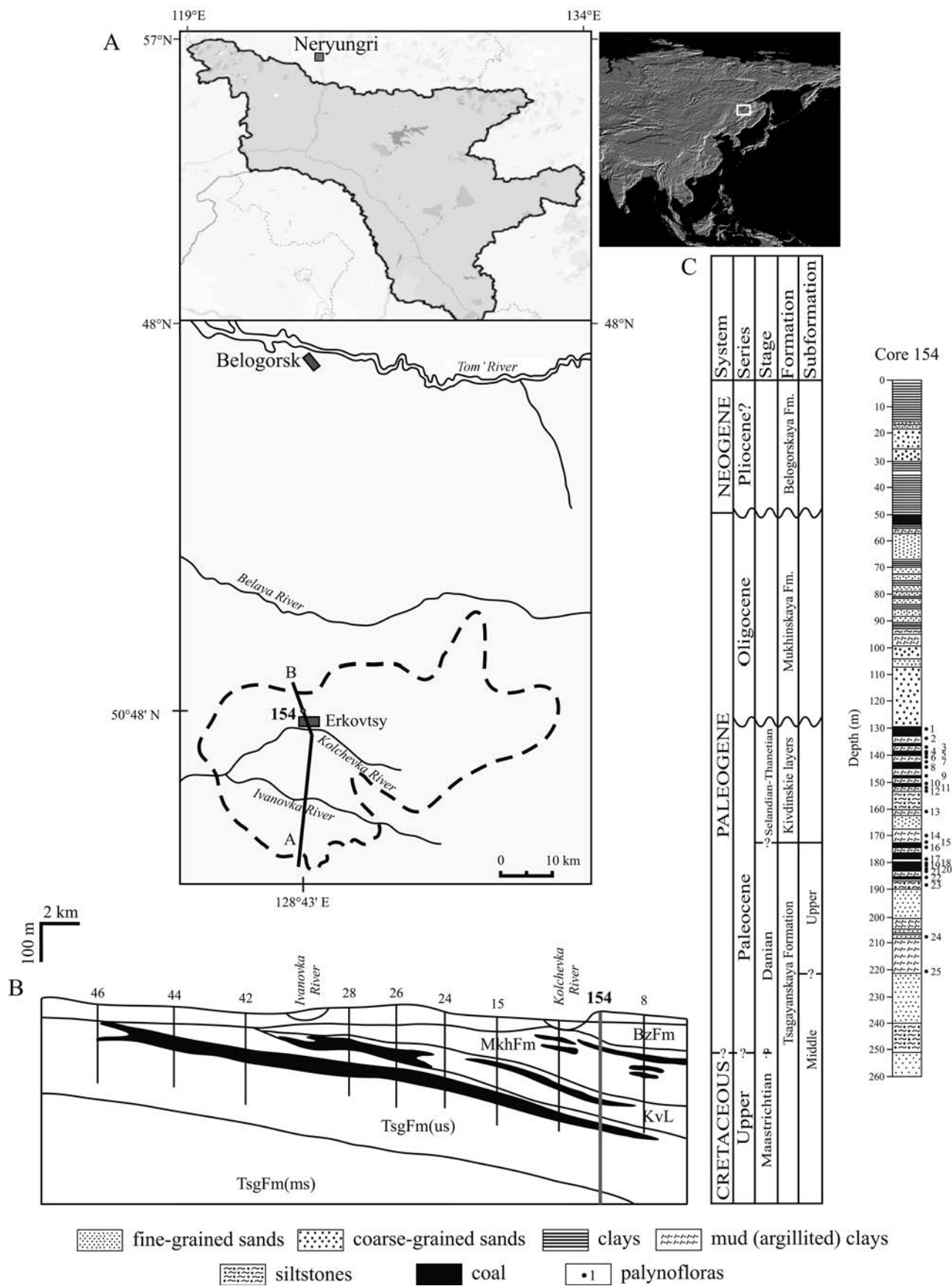


Figure 1 Map showing the location of the Amur Region and the location of the studied Core 154 (A), section of the sediments on the line A–B (B), lithological profile of the studied Core 154 and levels of palynofloras (C): Dotted line – contour of the Erkovetskii Brown Coal Field after Kezina (2005) and Kezina & Litvinenko (2007), TsgFm(ms) – Tsagayanskaya Formation (middle subformation), TsgFm(us) – Tsagayanskaya Formation (upper subformation), KvL – Kivdinskies layers, MkhFm – Mukhinskaya Formation, BzFm – Buzulinskaya Formation

(Fig. 1). All palynological data are taken from Kezina (2005) and Kezina & Litvinenko (2007). The microfloras yield evidence for a total of 90 different taxa (56 angiosperms, 16 gymnosperms and 18 pteridophytes) identified by Kezina (Kezina 2005, Kezina & Litvinenko 2007). As reported in the original studies, 350 pollen grains were counted per sample. The material was collected by and is stored in the Institute of Tectonics and Geophysics (ITG FEB RAS, Khabarovsk) in 1970s for conducting complex studies in the territory of the Zeisko-Bureinskii Basin.

Palynological method

The palynological data are represented in diagrams (Fig. 4) constructed with the TILIA program (Grimm 2011). The diagrams were divided into zones using Constrained Incremental Sums of Squares cluster analysis (CONISS) to formally estimate variations in the record. The percentage of each taxon and sub-sums were calculated based on the total sum of pollen and spores.

Quantitative palaeoclimate reconstruction: Coexistence Approach (CA)

To reconstruct climate from the palynomorph records we used the Coexistence Approach (CA) (Mosbrugger & 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 & Utescher 1997, Utescher et al. 2007, Bruch et al. 2011). For detailed description of the method the reader is referred to the original papers describing the procedure (Mosbrugger & Utescher 1997, Utescher et al. 2014). We use data sets from the Palaeoflora

Database (Utescher & Mosbrugger 2018). Floral lists with corresponding nearest living relatives (NLRs) employed in this study and their climatic requirements are made available in Supplementary electronic information 1.

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). Mean values of climatic parameters for each depth level are given in Table 1.

In the CA, at least 10 NLR taxa contributing with climate data are required to obtain reliable results (Mosbrugger & Utescher 1997). The climatic resolution of the CA results also depends on the taxonomical level of NLR identification (Mosbrugger & Utescher 1997). *Eucommia ulmoides* Oliver, *Ginkgo biloba* L. and *Sciadopitys verticillata* (Thunb.) Siebold et Zucc. were excluded from the analysis for being monotypic taxa. For Ericaceae Juss. and Rosaceae Juss. no data are at disposal. For the monotypic genera (but not monotypic families) we use climate data for families (for example, climate data of Myricaceae Blume were used for *Comptonia peregrina* (L.) Coult., Taxodiaceae Endl. ex K. Koch – for *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch and *Taxodium* Richard).

Climate seasonality, monsoon intensity

In order to determine temperature seasonality of the Paleocene climate of the Amur Region, the mean annual range of temperature (MART) was calculated as the difference of WMMT and CMMT for each level (Table 2,

Table 1. Mean values of climatic parameters for each depth level. Means by each depth level (calculated using coexistence interval means). MAT – mean annual temperature; CMMT – cold month mean temperature; WMMT – warm month mean temperature; 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.

Depth, m	Flora	Taxa with climate data	% of coexistence	MAT, °C	CMMT, °C	WMMT, °C	MAP, mm	MPwet, mm	MPdry, mm	MPwarm, mm
Late Paleocene										
130.2	PF1	18	100	18.8	11.7	26.0	1296	195	53	149
133.0	PF2	30	100	18.0	10.7	25.3	1296	247	42	158
136.6	PF3	33	99.6	18.1	10.3	25.5	1278	246	27	148
138.2	PF4	34	99.6	19.0	10.8	25.6	1296	197	42	158
138.6	PF5	28	99.5	19.0	11.8	25.6	1296	249	42	158
140.2	PF6	34	100	18.5	10.8	25.5	1407	251	38	158
142.2	PF7	36	99.6	18.4	10.3	25.7	1334	260	29	148
143.3	PF8	31	99.5	19.0	10.8	25.6	1296	197	42	158
146.4	PF9	24	100	19.0	11.8	25.6	1202	250	44	96
150.5	PF10	20	100	19.0	11.7	25.6	1740	270	37	171
151.4	PF11	35	99.6	18.1	10.3	25.5	1278	198	29	148
Early Paleocene										
152.6	PF12	31	99.5	17.8	10.9	25.2	1296	236	42	158
161.2	PF13	24	100	18.3	10.8	25.5	1296	235	42	158
170.0	PF14	26	99.4	17.0	10.3	25.2	1278	249	27	148
172.6	PF15	25	100	17.0	10.2	24.2	1176	262	27	134
174.3	PF16	24	100	16.5	10.3	23.8	1184	177	29	81
179.4	PF17	27	100	17.0	8.2	25.6	1115	219	27	126
180.2	PF18	18	100	17.2	7.5	25.0	1659	233	42	147
181.2	PF19	21	99.3	17.0	10.3	25.3	1278	197	27	148
183.1	PF20	16	100	16.5	10.3	25.1	1184	219	27	78
183.5	PF21	24	100	17.0	7.7	25.3	1278	197	27	148
185.5	PF22	21	100	17.0	6.8	25.4	1278	197	27	148
188.3	PF23	24	99.4	16.4	11.1	25.3	1352	249	39	155
207.4	PF24	25	99.4	18.4	10.3	25.3	1334	265	27	148
220.1	PF25	27	100	17.0	6.8	25.7	1278	246	27	148

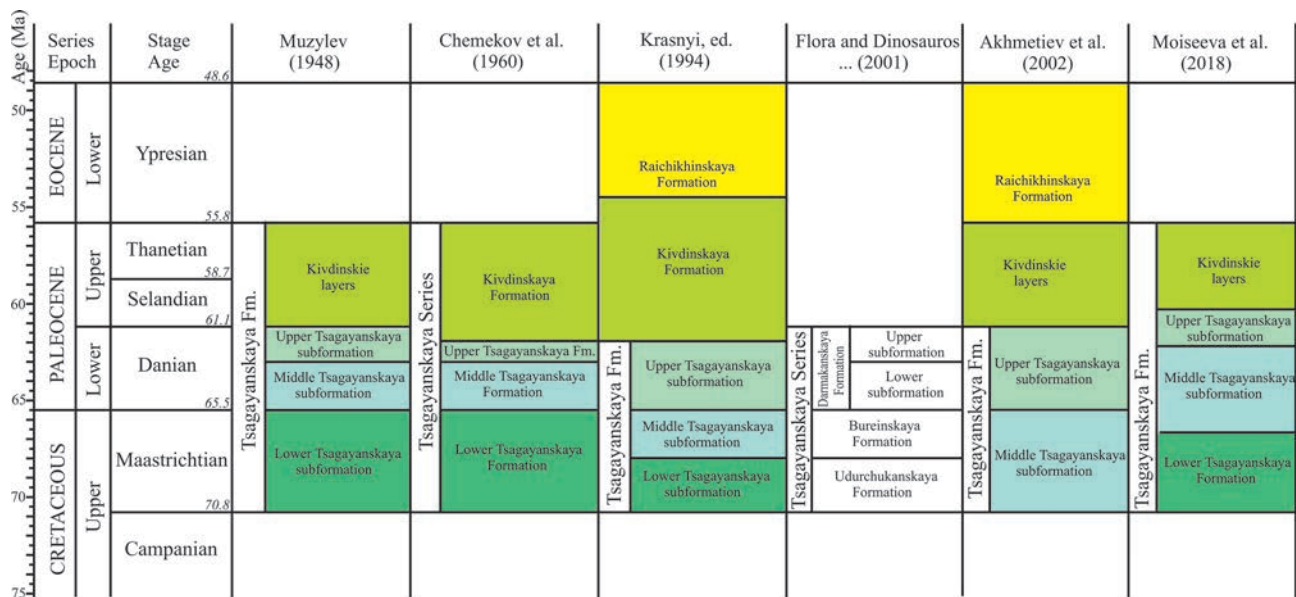


Figure 2 Chart with the formation names discussed in the text showing the different stratigraphic interpretations of the Tsagayanskaya Formation and its subunits

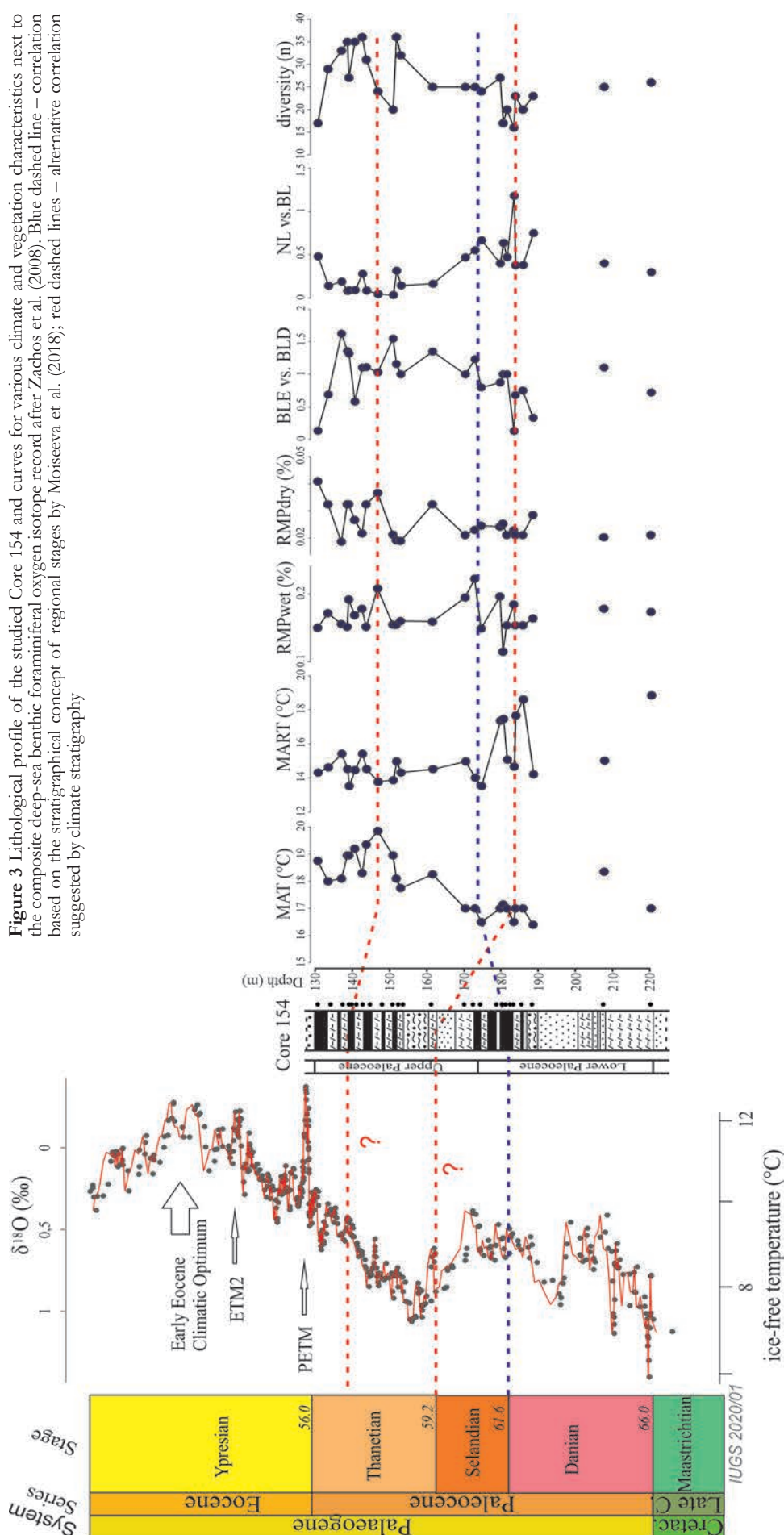
Fig. 3). To study precipitation seasonality, the mean annual range of precipitation (MAR_P – calculated as difference of MP_{wet} and MP_{dry}) was calculated (Table 2, Fig. 3). To obtain an estimate of the EAM intensity during Paleocene we use the ratio of MP_{wet} and MP_{dry} on MAP (RMP_{wet} and RMP_{dry}) (Table 2). According to Jacques et al. (2011), the

ratios of MP_{wet} and MP_{dry} of MAP provide a good indication of past monsoon intensity (summer – EASM and winter – EAWM respectively). The monsoon is a complex climatic phenomenon, nevertheless, in general increasing of RMP_{wet}, i.e. higher proportion of precipitation in the wet season, may indicate an intensification of EASM, while the

Table 2. Temperature and precipitation seasonality parameters and related values. Means by each depth level (calculated using coexistence interval means). MAT – mean annual temperature; CMMT – cold month mean temperature; WMMT – warm month mean temperature; MRAT – mean annual range of temperature (MART = WMMT – CMMT); MAP – mean annual precipitation; MP_{wet} – mean monthly precipitation of the wettest month; MP_{dry} – mean monthly precipitation of the driest month; MAR_P – mean annual range of precipitation (MAR_P = MP_{wet} – MP_{dry}); RMP_{wet} – ratio of MP_{wet} on MAP (RMP_{wet} = MP_{wet}/MAP*100); RMP_{dry} – ratio of MP_{dry} on MAP (RMP_{dry} = MP_{dry}/MAP*100).

Depth, m	Flora	MAT mean, °C	CMMT mean, °C	WMMT mean, °C	MART, °C	MAP mean, mm	MP wet mean, mm	MP dry mean, mm	MAR _P , mm	RMP wet, %	RMP dry, %
Modern											
–	–	0.3	-24.2	21.0	45.2	578	135	5	130	23.3	0.9
Late Paleocene											
130.2	PF 1	18.8	11.7	26.0	14.3	1296	195	53	142	15.0	4.1
133.0	PF 2	18.0	10.7	25.3	14.6	1296	247	42	205	19.0	3.2
136.6	PF 3	18.1	10.3	25.5	15.2	1278	246	27	219	19.2	2.1
138.2	PF 4	19.0	10.8	25.6	14.8	1296	197	42	155	15.2	3.2
138.6	PF 5	19.0	11.8	25.6	13.8	1296	249	42	207	19.2	3.2
140.2	PF 6	18.5	10.8	25.5	14.4	1407	251	38	213	17.8	2.7
142.2	PF 7	18.4	10.3	25.7	15.4	1334	260	29	231	19.5	2.2
143.3	PF 8	19.0	10.8	25.6	14.8	1296	197	42	155	15.2	3.2
146.4	PF 9	19.0	11.8	25.6	13.8	1202	250	44	206	20.8	3.7
150.5	PF 10	19.0	11.7	25.6	13.9	1740	270	37	233	15.5	2.1
151.4	PF 11	18.1	10.3	25.5	15.2	1278	198	29	169	15.5	2.3
Early Paleocene											
152.6	PF 12	17.8	10.9	25.2	14.3	1296	236	42	194	18.2	3.2
161.2	PF 13	18.3	10.8	25.5	14.7	1296	235	42	193	18.1	3.2
170.0	PF 14	17.0	10.3	25.2	14.9	1278	249	27	222	19.5	2.1
172.6	PF 15	17.0	10.2	24.2	14.0	1176	262	27	235	22.3	2.3
174.3	PF 16	16.5	10.3	23.8	13.5	1184	177	29	148	14.9	2.4
179.4	PF 17	17.0	8.2	25.5	17.3	1115	219	27	192	19.6	2.4
180.2	PF 18	17.2	7.5	25.0	17.5	1659	233	42	191	14.0	2.5
181.2	PF 19	17.0	10.3	25.3	15.0	1278	197	27	170	15.4	2.1
183.1	PF 20	16.5	10.3	25.1	14.8	1184	219	27	192	18.5	2.3
183.5	PF 21	17.0	7.7	25.3	17.6	1278	197	27	170	15.4	2.1
185.5	PF 22	17.0	6.8	25.4	18.6	1278	197	27	170	15.4	2.1
188.3	PF 23	16.4	11.1	25.3	14.2	1352	249	39	210	18.4	2.9
207.4	PF 24	18.4	10.3	25.3	15.0	1334	265	27	238	19.9	2.0
220.1	PF 25	17.0	6.8	25.7	18.9	1278	246	27	219	19.2	2.1

Figure 3 Lithological profile of the studied Core 154 and curves for various climate and vegetation characteristics next to the composite deep-sea benthic foraminiferal oxygen isotope record after Zachos et al. (2008). Blue dashed line – correlation based on the stratigraphical concept of regional stages by Moiseeva et al. (2018); red dashed lines – alternative correlation suggested by climate stratigraphy



decreasing of RMPdry, i.e. lower proportion of precipitation in the dry season, suggests an intensification of EAWM.

Vegetation reconstruction methods

In order to reconstruct palaeovegetation 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).

Quantitative palaeovegetation reconstruction: Plant Functional Type (PFT) approach

The Plant Functional Type (PFT) concept goes back to works of Prentice (e.g., Prentice et al. 1992, Prentice & Webb 1998) and has been widely used to describe vegetation cover in vegetation modeling. 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 palaeobotanical record was first introduced by Utescher et al. (2007). The present study employs an extended PFT classification scheme described in details 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 3). The allocation

Table 3. Plant functional type classification used for the present study (Popova et al. 2013).

PFT No.	PFT
Herbal	
1	C3 herbs (humid)
2	C3 herbs (dry)
3	C4 herbs
Shrubby	
4	Broadleaved summergreen arctic shrubs
5	Broadleaved summergreen boreal or temperate cold shrubs
6	Broadleaved summergreen temperate warm shrubs
7	Broadleaved evergreen boreal or temperate cold shrubs
8	Broadleaved evergreen temperate warm shrubs
9	Broadleaved evergreen xeric shrubs
10	Subdesertic shrubs
11	Tropical shrubs
Arboreal	
12	Needleleaved evergreen boreal or temperate cold trees
13	Needleleaved evergreen temperate cool trees
14	Needleleaved evergreen trees, drought-tolerant
15	Needleleaved evergreen trees, drought-tolerant, thermophilous
16	Needleleaved evergreen subtropical trees, drought-intolerant
17	Needleleaved summergreen boreal or temperate cold trees
18	Needleleaved summergreen subtropical swamp trees
19	Broadleaved evergreen trees, drought-tolerant
20	Broadleaved evergreen trees, drought-intolerant, thermophilous
21	Broadleaved evergreen subtropical trees, drought-intolerant
22	Broadleaved summergreen boreal or temperate cold trees
23	Broadleaved summergreen temperate cool trees
24	Broadleaved summergreen temperate warm trees
25	Broadleaved raingreen tropical trees
26	Broadleaved evergreen tropical trees
Aquatic	
27	Aquatic components

of fossil taxa to the single PFTs is based on interpretation of their NLRs (Supplementary electronic information 2), and follows the procedure described in Utescher & Mosbrugger (2007) and Utescher et al. (2007). Proportions of the different groups of PFTs are given in Table 4.

To exclude unlikely PFTs we use the likelihood procedure according to François et al. (2011) and Henrot et al. (2017). This methodology is similar to the CA used in palaeoclimate reconstructions from the palaeobotanical 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 plant types present at the site by suppressing extreme end members, such as cold boreal/temperate and tropical PFTs. The 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 (Supplementary electronic information 2).

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.

Plant biome reconstruction: Integrated Plant Record (IPR) vegetation analysis

The Integrated Plant Record (IPR) vegetation analysis is a semi-quantitative method first introduced by Kovar-Eder & Kvaček (2003) to assess zonal vegetation based on the fossil plant record (leaf, fruit, and pollen assemblages). In order to employ the IPR, 13 basic taxonomic-physiognomic groups, termed components, defined to reflect key ecological characteristics of an assemblage (Kovar-Eder & Kvaček 2003, 2007,

Table 4. Proportions of the different groups of PFTs for each depth level. References and complete flora lists including Nearest Living Relatives used for vegetation analysis are given in Supplementary electronic information 2.

Depth, m	Flora	Number of fossil taxa allocated to PFTs	Number of scores before likelihood procedure	Number of scores after likelihood procedure	Plant functional types							
					Aquatic (PFT 27)	Terrestrial (1-26)	Herbaceous (1-3)	Shrubby (4-11)	Arboreal (12-26)	Coniferous (12-18)	Deciduous (4-6, 22-25)	Evergreen (7-9, 19-21, 26)
Late Paleocene												
130.2	PF 1	18	48	40	2.4	97.6	4.9	26.8	65.9	29.3	53.7	7.3
133.0	PF 2	31	112	96	2.1	97.9	3.1	27.1	67.7	11.5	46.9	32.3
136.6	PF 3	34	104	77	2.6	97.4	3.9	23.4	70.1	15.6	29.9	45.5
138.2	PF 4	37	119	88	3.4	96.6	8.0	28.4	60.2	6.8	36.4	43.2
138.6	PF 5	33	104	75	4.0	96.0	6.7	25.3	64.0	8.0	36.0	44.0
140.2	PF 6	39	121	99	4.0	96.0	6.1	27.3	62.6	8.1	52.5	26.3
142.2	PF 7	39	112	83	4.8	95.2	4.8	22.9	67.5	20.5	33.7	33.7
143.3	PF 8	35	95	72	4.2	95.8	11.1	30.6	54.2	6.9	38.9	36.1
146.4	PF 9	27	91	67	3.0	97.0	3.0	29.9	64.2	4.5	44.8	41.8
150.5	PF 10	21	74	59	5.1	94.9	1.7	28.8	64.4	3.4	35.6	50.8
151.4	PF 11	37	102	77	3.9	96.1	6.5	23.4	66.2	22.1	31.2	32.5
Early Paleocene												
152.6	PF 12	34	108	84	2.4	97.6	7.1	32.1	58.3	10.7	39.3	36.9
161.2	PF 13	26	86	65	3.1	96.9	4.6	24.6	67.7	13.8	33.8	41.5
170.0	PF 14	24	78	57	1.8	98.2	8.8	24.6	64.9	28.1	29.8	29.8
172.6	PF 15	27	76	57	1.8	98.2	15.8	14.0	68.4	28.1	22.8	28.1
174.3	PF 16	25	77	66	1.5	98.5	4.5	19.7	74.2	36.4	30.3	24.2
179.4	PF 17	30	100	71	0	100	8.5	25.4	66.2	25.4	33.8	29.6
180.2	PF 18	19	57	42	0	100	9.5	28.6	61.9	33.3	26.2	26.2
181.2	PF 19	22	76	58	0	100	3.4	32.8	63.8	29.3	31.0	31.0
183.1	PF 20	18	51	44	2.3	97.7	11.4	20.5	65.9	45.5	34.1	4.5
183.5	PF 21	28	79	61	1.6	98.4	9.8	31.1	57.4	23.0	36.1	24.6
185.5	PF 22	25	81	67	1.5	98.5	4.5	41.8	52.2	23.9	35.8	26.9
188.3	PF 23	26	79	55	1.8	98.2	7.3	27.3	63.6	38.2	38.2	12.7
207.4	PF 24	25	78	60	0	100	1.7	25.0	73.3	26.7	31.7	35.0
220.1	PF 25	29	97	72	0	100	5.6	33.3	61.1	20.8	40.3	29.2

Kovar-Eder et al. 2008, Teodoridis et al. 2011) are used: conifer (CONIF), broadleaved deciduous (BLD), broadleaved evergreen (BLE), sclerophyllous (SCL), legume-like (LEG), zonal palm component (ZONPALM), arborescent fern (ARBFERN), dry herbaceous (D-HERB), mesophytic herbaceous (M-HERB). Azonal components, i.e. azonal woody component (AZW), azonal non-woody component (AZNW) and aquatic component (AQUA). The component PROBLEMATIC TAXA 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 Supplementary electronic information 3. The number of taxa assigned to the components for each flora is given in Table 5.

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 number of zonal taxa preserved. Ten zonal taxa are regarded as a minimum to perform this method (Kovar-Eder et al. 2008). Recently, Kovar-Eder & 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 5.

Based on relative proportions of the components the following six zonal vegetation types are distinguished (Kovar-Eder & Kvaček 2007, Kovar-Eder et al. 2008): zonal temperate to warm temperate broadleaved deciduous fo-

Table 5. IPR scores, component proportions, and IPR vegetation types for each depth level. References and complete flora lists including Nearest Living Relatives used for vegetation analysis are given in Supplementary electronic information 3.

Depth, m	Flora	ZONAL VEGETATION TYPE										Total	BLD prop, %	BLE prop, %	SCL+LEG prop, %	ZONAL HERB prop, %	Vegetation type
		CONIF	BLD	BLE	SCL	LEG	ZON PALM	ARB FERN	D-HERB	M-HERB							
Late Paleocene																	
130.2	PF1	1.5	5.98	1.49	0.99	0	0	0	0.33	1.16	11.45	70.7	17.6	11.7	13.0	MMF	
133.0	PF2	2	12.06	4.65	1.66	0	0	0	1.33	1.41	23.11	65.7	25.3	9.0	11.9	MMF	
136.6	PF3	4	11.9	5.57	2.16	0	0.5	1	0.91	1.91	27.62	57.2	25.2	10.4	10.2	MMF	
138.2	PF4	3.5	12.06	5.73	2.16	0	0	0	1.91	3.24	28.27	61.5	27.5	11.0	18.2	MMF	
138.6	PF5	2.5	11.98	4.65	2.16	0	0	0	0.33	3.16	24.45	64.9	23.4	11.7	14.3	MMF	
140.2	PF6	1	14.68	5.85	2.11	1	0	0	1.78	4.61	30.7	63.0	23.7	13.3	20.8	MMF	
142.2	PF7	6	12.82	5.24	1.91	0	0.5	0	1.66	2.91	30.71	63.7	24.4	9.5	14.9	MMF	
143.3	PF8	2.5	11.9	4.9	1.08	0	0	0	1.66	5.49	27.2	67.8	26.0	6.2	26.3	MMF	
146.4	PF9	1.5	10.65	4.07	1.91	0	0.5	0	0	2.58	20.88	63.4	22.3	11.4	12.4	MMF	
150.5	PF10	0.5	7.57	4.57	1.08	1	0.5	0	0.33	0.66	15.88	52.6	29.3	14.5	6.2	MMF	
151.4	PF11	7	10.52	5.27	1.28	0	0	1	0.86	3.94	29.54	59.3	27.8	7.2	16.2	MMF	
152.6	PF12	2.5	8.6	5.52	1.03	0	0	1	0.53	4.61	23.79	53.3	34.2	6.4	21.6	MMF/BLEF	
161.2	PF13	2	7.85	4.77	1.61	0	0	0	0.53	2.61	19.04	56.5	31.9	11.6	16.5	MMF/BLEF	
170.0	PF14	5	5.99	3.16	0.83	0	0	1	1.66	1.66	19.3	54.6	28.8	7.6	17.2	MMF	
172.6	PF15	4.5	5.99	2.91	0.58	0	0	2	0.66	6.24	22.88	52.2	25.3	5.1	30.2	MMF	
Early Paleocene																	
174.3	PF16	7	4.74	2.16	1.33	0	0	0	0.33	2.91	18.47	57.6	26.2	16.2	17.5	MMF	
179.4	PF17	6.5	8.85	2.61	1.44	0	0	0	0.86	3.61	23.87	68.6	20.2	11.2	18.7	MMF	
180.2	PF18	4	3.24	1.91	0.58	0	0	0	0.33	3.33	13.39	56.5	33.3	10.1	27.3	MMF/BLEF	
181.2	PF19	6	5.32	2.74	0.58	0	0	0	0.33	0.58	15.55	61.6	31.7	6.7	5.9	MMF/BLEF	
183.1	PF20	5	3.86	0.53	0.53	0	0	0	0.86	3.36	14.14	78.5	10.8	10.8	29.8	BLDF/MMF	
183.5	PF21	4.5	6.69	2.61	1.08	0	0	0	0.66	3.61	19.15	64.5	25.1	10.4	22.3	MMF	
185.5	PF22	5	5.94	2.69	0	1	0	0	0.33	2.28	17.24	61.7	27.9	10.4	15.1	MMF	
188.3	PF23	5	7.24	1.41	1.08	0	0	0	0.33	1.83	16.89	74.4	14.5	11.1	12.8	MMF	
207.4	PF24	5	7.85	4.44	1.11	0	0	0	0.53	0.78	19.71	58.6	33.1	8.3	6.6	MMF/BLEF	
220.1	PF25	4.5	10.48	3.07	0.91	0	0	0	0.33	2.08	21.37	72.5	21.2	6.3	11.3	MMF	

rests (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 & Teodoridis (2018) defined ecotone between the MMF/ShSF.

RESULTS

Palynological data

Based on the works of Kezina (2005) and Kezina & Litvinenko (2007), 90 taxa in total (56 angiosperms, 16 gymnosperms and 18 pteridophytes) were identified. Most taxa belong to groups which nowadays comprise trees and shrubs. Sporomorphs deriving from herbs were generally rare. Cluster analysis performed with the TILIA software yields 4 palynozones (Fig. 4).

Zone I ranges from 220 to 187 m in depth (Fig. 4). Angiosperm pollen dominates (up to 75.8 %), with mostly *Myrica* sp., *Corylopsis* sp., *Comptonia* sp., *Triporopollenites plectosus* And., *Triatriopollenites* sp., and *Triporopollenites* sp. Gymnosperm taxa account for up to 32.5 %, dominated by Cupressaceae Gray and Pinaceae Lindl. Pteridophytes are relatively rare (4.7 to 11.9 %), and are mainly represented by Polypodiaceae Bercht. et J. Presl.

Zone II ranges from 187 to 174 m in depth (Fig. 4). Gymnosperms (29.7 to 62.4 %) and Pteridophytes (10.0 to 55.1 %) alternately dominate the assemblages. The gymnosperms are dominated by Taxodioideae (including *Taxodium*) – up to 65 %. Pteridophytes represented by Polypodiaceae (up to 40.6 %) and *Onoclea* (up to 14.0 %) spores. Angiosperm palynomorphs (up to 27.6 %) occur at a lower frequency than in Zone I, and include abundant *Alnus* sp., *Myrica* sp., *Cuprianipillis* sp., *Sparganium* sp. and *Triporopollenites plectosus*.

Zone III ranges from 174 to 153 m in depth (Fig. 4). Angiosperm pollen dominates and reaches 92.7 %. Angiosperms are represented mainly by *Ulmoideipites tricostratus* And. (up to 71.2 %) and *Sparganium* sp. (up to 23.9 %). Pteridophytes (up to 35.3 %) are dominated by *Onoclea* sp. (up to 23.9 %) and Polypodiaceae (up to 15.4 %). Gymnosperm taxa occur at a lower frequency (4.0 to 13.7 %).

Zone IV ranges from 153 to 130 m in depth (Fig. 4). Angiosperm pollen predominates (48.1 to 94.0 %) with mostly *Triporopollenites plectosus*, *Myrica* sp., Moraceae Link, *Pandanus* sp., *Platyacarya* sp., *Anacolosidites* sp., Fagaceae Dumort. (including *Quercus gracilis* Boitz. and *Quercus* sp.), Hamamelidaceae R. Brown. *Corylopsis* pollen is very frequent (53.2 %) in topmost part of this zone, with a relatively low proportion of *Fothergilla* sp. (0.9 %). Gymnosperms (0.9 to 41.8 %) and Pteridophytes (2.0 to 46.2 %) alternately dominate the assemblages. The Gymnosperm taxa are dominated by Taxodioideae (up to 41.8 % from a depth of 136.6 cm). *Azolla* sp. (up to 24.7 %) and *Salvinia* sp. (up to 18.3 %) are dominate among Pteridophytes in the lower part of this zone.

Paleoclimate reconstruction

The analysis of 25 microfloras is based on 16 to 36 (mean 26.24) climate datasets of extant reference taxa. In 25 out of 14 cases, all NLRs can coexist, in all other cases over 99 % of taxa attributing high significance. 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. 8.4°C at the mean (varies from 6.1°C to 10.6°C).

The mean values of MAT show a general smooth cooling trend in the lower part and warming trend in upper part of the well (Table 1, Fig. 5). The highest MAT values are indicated in the early Paleocene for the PF 24 at 207.4 m – 18.4°C (15.3–21.4°C), in the late Paleocene for five floras at 138.2–138.6 m and 143.3–150.5 m – 19.0°C (14.8–23.1°C). The lowest MAT values are indicated in the early Paleocene for the PF 23 – 16.4°C (11.1–21.7°C), in the late Paleocene for the PF 4 and PF 14 and 15 – 17.0°C (12.6–21.4°C). For the other floras of the early Paleocene the MAT mean values vary in the range of 16.5–17.2°C, while of the late Paleocene – from 17.8 to 18.5°C.

For the CMMT means demonstrate a general warming trend throughout the Paleocene (Table 1, Fig. 5). The highest values of CMMT are indicated in the early Paleocene for the PF 23 – 11.1°C (6.6–15.6°C) and in the late Paleocene for the PF 5 and 9 – 11.8°C (6.6–17.0°C). The lowest CMMT values are obtained in the early Paleocene for the PF 22 and 25 – 6.8°C (-0.3–13.9°C), in the late Paleocene for the PF 15 – 10.2°C (6.4–13.9°C). For the other floras of the early Paleocene the mean values of MAT vary from 7.5 to 10.3°C, of the late Paleocene – from 10.3 to 11.7°C.

WMMT means vary slightly during the Paleocene (Table 1, Fig. 5). The highest WMMT values are indicated in the early Paleocene for the PF 25 – 25.7°C (23.0–28.3°C), while in the late Paleocene for the PF 1 – 26.0°C (23.6–28.4°C). The lowest values of WMMT are obtained in the early Paleocene for the PF 16 – 23.8°C (19.4–28.1°C), in the late Paleocene for the PF 15 – 24.2°C (20.2–28.1°C). For the other floras of the early Paleocene the mean values of WMMT vary from 24.9 to 25.6°C, of the late Paleocene – from 25.2 to 25.7°C.

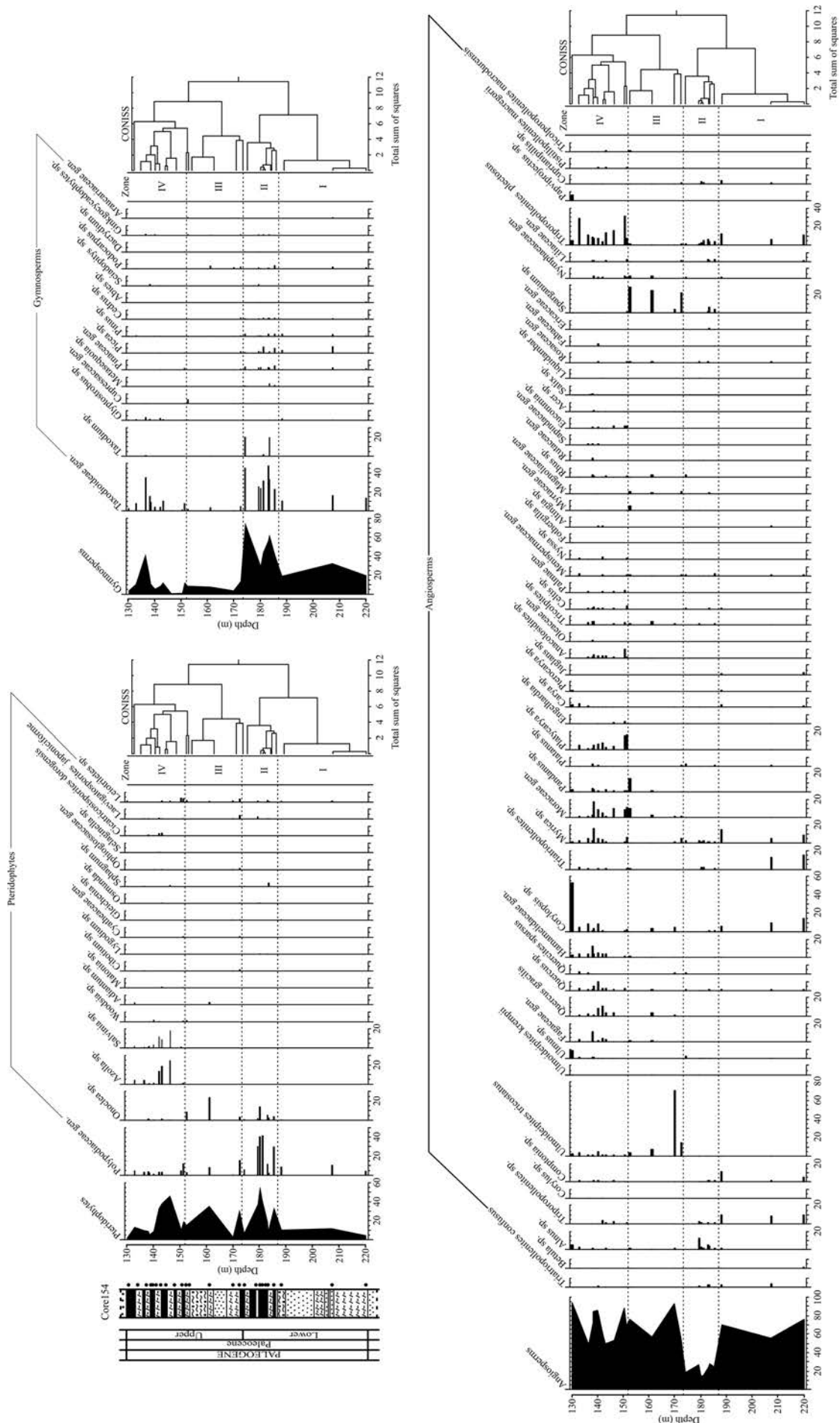
MAP shows a general decrease from 1200–1350 mm in the lower part of the early Paleocene to 1100–1200 mm in the upper part of the early Paleocene (Table 1, Fig. 5). The highest Paleocene values of MAP are indicated in the early Paleocene for the PF 18 – 1659 mm (703–2615 mm) and in the late Paleocene for the PF 10 – 1740 mm (979–2500 mm). Other floras indicate a MAP of at least 1200 mm.

MPdry means in the Paleocene of the Amur Region were at ca. 27–53 mm (Table 1, Fig. 5).

The mean values of MPwet attain very high values (177–270 mm) throughout the Paleocene (Table 1, Fig. 5).

Climate seasonality, monsoon intensity

Temperature (MART) and precipitation (MARP) seasonality parameters and the mean values of related climatic parameters for each flora are given in Table 2 in comparison to the present-day values. The MART ranges in 13.5–18.9°C in the early Paleocene and up to 15.4°C in the late



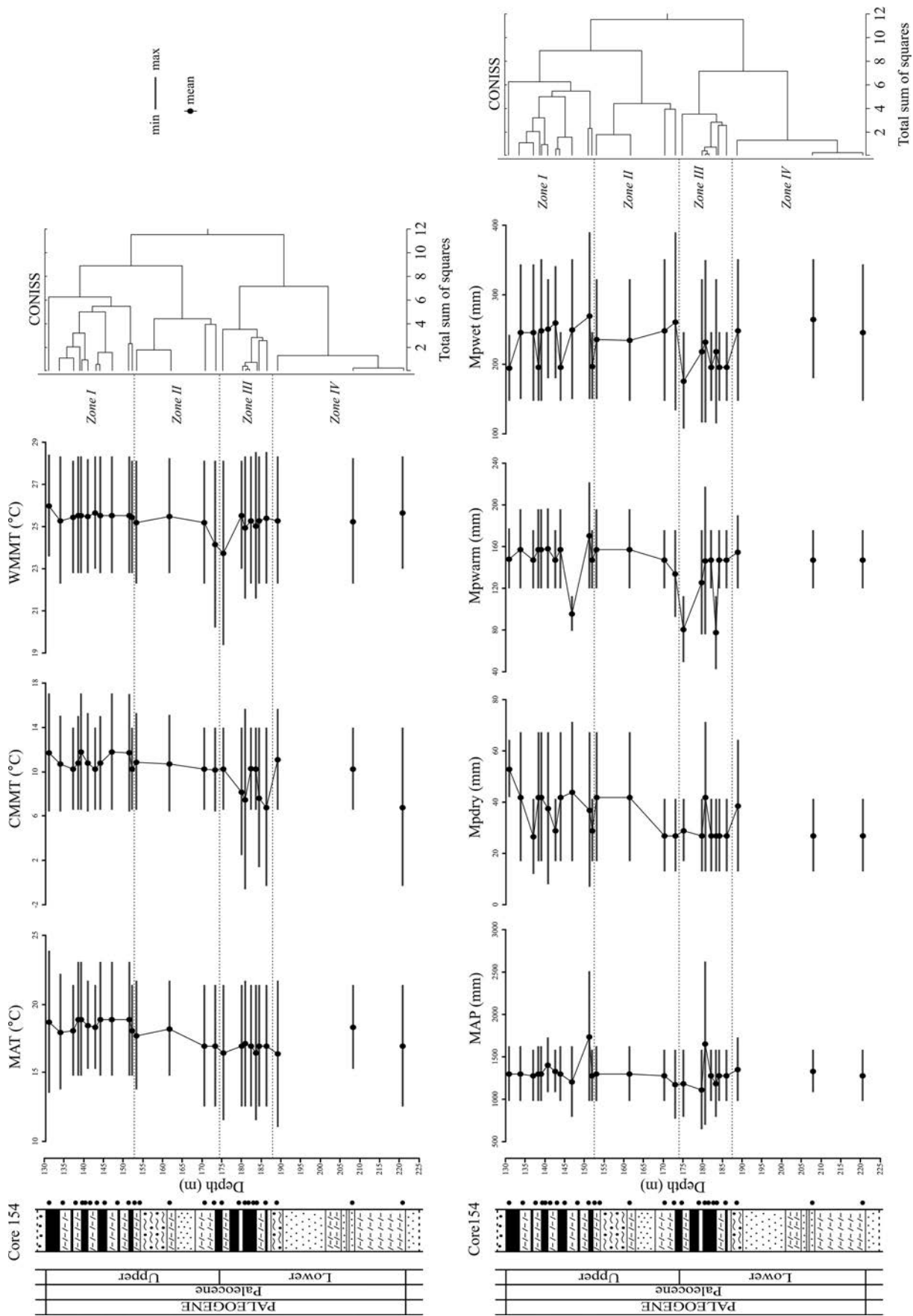


Figure 5 Temperature and precipitation variables: MAT – mean annual temperature, CMMT – cold month mean temperature, WMMT – warm month mean temperature, MAP – mean annual precipitation, MPwet – mean monthly precipitation of the wettest month, MPdry – mean monthly precipitation of the driest month, MPwarm – mean monthly precipitation of the warmest month

Paleocene. The MARP varies from 148 to 238 mm in the early Paleocene and from 142 to 235 mm in the late Paleocene. The RMP_{wet} fluctuates within 14.0–20.4 % in the early Paleocene and from 15.0 to 22.3 % in the late Paleocene, while the RMP_{dry} varied from 2.0 to 2.9 % in the early Paleocene and from 2.1 to 4.1 % in the late Paleocene (Table 2).

Vegetation: PFT approach

Using the PFT approach, palaeovegetation data of the Amur Region were obtained for 25 palynofloras. The number of fossil taxa in each sample is lower than the number of encountered PFTs (Table 4), therefore we consider that our results are meaningful. Aquatic plants (PFT 27) are presented in 20 palynofloras. The proportion of aquatic plants varies from 0 to 2.3 % in the early Paleocene and from 1.8 to 4.6 % in the late Paleocene (Table 4, Fig. 6). Herbaceous plants (PFTs 1–3) are presented in all floras. The diversity of herbaceous PFTs varies from 1.7 to 11.4 % of total diversity of the flora in the early Paleocene and from 1.5 to 15.8 % in the late Paleocene (Table 4, Fig. 6 and 7). Shrubs (PFTs 4–11) are presented in all floras studied: 19.7–41.8 and 14.03–32.9 % in the early and late Paleocene correspondently (Table 4, Fig. 6). After applying the likelihood procedure, arboreal plants (PFTs 12–26) are presented in all floras studied. Arboreal PFTs content 52.2–74.2 in the early Paleocene floras and 53.9–68.4 % in the late Paleocene floras (Table 4, Fig. 6 and 7). Needleleaved (PFTs 12–18) are presented in all floras. In the early Paleocene floras the proportion of coniferous varies within the range of 20.8–45.5 %, in the late Paleocene floras – 3.1–29.3 % of total diversity of the flora (Table 4, Fig. 6 and 7). Broadleaved deciduous plants (PFTs 4–6, 22–25) are present in all floras. The diversity of deciduous PFTs in the early Paleocene varies from 26.2 to 40.3 %, in the late Paleocene floras – from 22.8 to 53.7 % of total diversity of the flora (Table 4). Broadleaved evergreens (PFTs 7–9, 19–21, 26) are present in all floras. The proportion of broadleaved evergreens varies from 4.5 to 35.0 % in the early Paleocene floras and from 7.3 to 52.3 % of total diversity of the flora in the late Paleocene floras (Table 4, Fig. 6 and 7).

When regarding the diversity spectra of the Paleocene floras analyzed (Fig. 6), it is shown that broadleaved summergreen shrubs and trees (PFTs 5, 6, and 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). Needleleaved summergreen boreal trees (PFT 17) and needleleaved evergreen boreal or temperate cold trees (PFT 12) are completely absent in the spectra after the likelihood procedure. Needleleaved summergreen subtropical swamp trees (PFT 18) are presented in all floras (Fig. 6). Herbaceous plants in the Paleocene floras of the Amur Region are mainly represented by humid herbs (PFT 1).

In general, the diversity spectra of the floras are characterized by high diversities of broadleaved summergreen (22.8–52.5 %), broadleaved evergreen (12.7–50.8 %) and needleleaved PFTs (3.4–36.4 %), with the exception of PF 1 characterized by highest diversities of broadleaved summergreen (53.7 %) and very low diversities of evergreen PFTs

(7.3 %) and PF 20 characterized by highest diversities of needleleaved (45.5 %) and lowest diversities of broadleaved evergreen PFTs (4.5 %).

IPR vegetation analysis

To apply IPR-vegetation analysis, 25 microfloras were analyzed. Based on the relative proportions of the components, one zonal vegetation type and two ecotones between them were revealed for the Paleocene of the Amur Region (Table 5, Fig. 6 and 7). The zonal vegetation type of warm temperate to subtropical mixed mesophytic forest (= mixed mesophytic forest, MMF) was revealed for most floras (18 out of 25), but mainly (12 floras) in the late Paleocene. The floras assigned to this zonal vegetation type are characterized by proportions of the BLD component from 52 to 74 %, BLE component – 14–30 %, SCL+LEG component – 5–16 %, and 10–30 % of herbs. The ecotones (MMF/BLEF and BLDF/MMF) are characterized by the transitional (intermediate) proportions of components in comparison with the corresponding zonal vegetation types (Table 5, Fig. 6 and 7). The ecotone MMF/BLEF was revealed for floras (6 out of 25) in the Early Paleocene and is characterized by 51–62 % of BLD, 31–34 % of BLE, 6–14 % of SCL+LEG, and 6–22 % of herbs. The ecotone BLDF/MMF was revealed only for the flora (PF 20) at the level 183.1 m in the Early Paleocene and is characterized by 78 % of BLD, 11 % of BLE, 11 % of SCL+LEG, and 30 % of herbaceous components.

DISCUSSION

Paleocene climate evolution

For all known uncertainties and delimited climatic resolution primarily caused by uncertainties in NLR identification and their high taxonomical rank basic conclusions on the Paleocene climate of the mid-latitudinal Amur Region can be drawn. Given the scarcity of continental quantitative palaeoclimate data for the Paleocene in general, also rough estimated may provide valuable information. With MAT of at least ca. 15°C and CMMT ca. 6°C in the warmer parts of the record and ca. 12.5°C / 0°C in the coolest part, a warm temperate or possibly also nearly cool temperate climate persisted throughout the deposition of the strata. The climate was overall humid, with high MAP rates of at least ca. 1000 mm in the warmer phases and over ca. 750 mm during the cooler phases. The above lower limits coincide with most results obtained from coeval macro- and microfloras in the coastal area of neighboring Primorye (Bondarenko et al. 2019), except for the early Paleocene Ustinovka leaf flora indicating somewhat warmer conditions (MAT ca. 16–21°C; CMT ca. 9–10 °C). Further CA-based data come from several well-dated sites of NE China (e.g., Fushun Mine). These data tend to have somewhat warmer cool limits of CA intervals, with MAT_{min} ca. 17–18°C, and CMMT_{min} > 7°C (Quan et al. 2012b), possibly referable to a minor latitudinal gradient.

When assessing the Paleocene temperature level in respect to the early Paleogene evolution in general there is evidence for overall cooler conditions compared to the Eocene. A warming trend from the late Paleocene to the

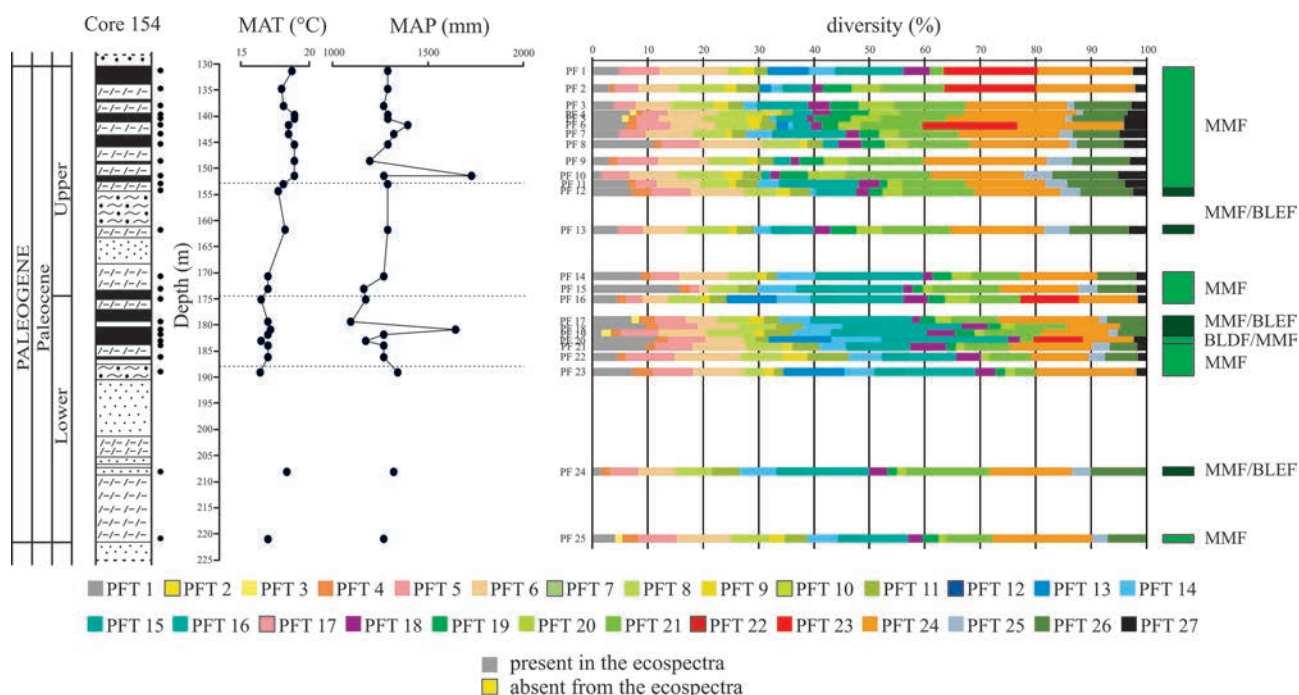


Figure 6 Ecospectra of PFT diversity and vegetation types next to lithological profile of the studied Core 154 and curves of MAT and MAP: MAT – mean annual temperature, MAP – mean annual precipitation, MMF – mixed mesophytic forest, MMF/BLEF – ecotone between mixed mesophytic forest and broadleaved evergreen forest, BLDF/MMF – ecotone between broadleaved deciduous forest and mixed mesophytic forest

early Eocene has been reported from various mid-latitude continental parts of the Northern Hemisphere such as Kazakhstan (Akhmetiev 2010), Bighorn Basin (Wilf 2000, Fricke & Wing 2004), the NW German Cenozoic (Inglis et al. 2017). In North America and Europe, the early to middle Eocene warmth led to almost tropical climate conditions, with MATs well over 20°C in the mid-latitudes (e.g., Wilf 2000, Woodburne et al. 2009, Mosbrugger et al. 2005), partly exceeding the maximum values of CA intervals obtained in our reconstruction. For the mid-latitudes of East Asia, however, it has been suggested that the Eocene continental warmth was less pronounced (based on Chinese localities: MAT < 20°C; CMMT < 12.5°C) (Zhang et al. 2016), also data from Primorye point to a lower Eocene temperature level compared to the Atlantic Eurasian area at the same latitude (Utescher et al. 2015).

The above described 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 & Speijer 2008). Hence, this warming trend represents a global pattern that appears to be at odds with the generally declining atmospheric CO₂ reported for that time-span (Zachos et al. 2008, Huber & Caballero 2011). However, stomatal-based proxies suggest time intervals with pCO₂ as low as 300 ppmv during the Paleocene (Beerling & Royer 2011, Steinthorsdottir et al. 2016).

Apart from information on the general Paleocene temperature level in the study area our data provide the first more detailed time series possibly spanning most of the Paleocene. For the lower part of Core 154 only two productive samples are available and hence no clear temporal trends are revealed. However, from depth level 190 m upwards

means of CA intervals obtained for MAT display a distinct overall warming trend coinciding with the declining trend in d¹⁸O values in the global isotope stack throughout the later Paleocene (Zachos et al. 2008). At the same time there is a trend to more equable climates as evident from declining MART (Fig. 3). In this context it is noteworthy that globally cooler conditions as evident from comparatively high d¹⁸O values near the K–T boundary possibly correlate with the highest seasonality of temperature in our record (MART ca. 19°C at depth level 220 m).

According to the palynostratigraphical constraints outlined in the next Section, this warming would comprise the late Danian to Thanetian while the warm peak in the Selandian would not be recorded in the continental data. Considering shorter-term variability our MAT record suggests an alternative stratigraphic solution in which the positive isotope shift in the earliest Thanetian correlates with a cool phase observed near the base of the lower brown coal unit in the core (at depth level 183 m). Moreover, the intermittent cooling setting on at depth level 138 m might mirror the short-term cooling in the global isotope record pre-dating the PETM (Zachos et al. 2008).

As is shown in Fig. 3, our Paleocene data suggest a strong impact of climate change and variability on vegetation composition in the Amur Region. This is mainly evident from changes in the ratio of broadleaved evergreen versus deciduous PFTs that largely co-varies with MAT exemplifying the affinity of evergreens to warmer climates.

Paleocene vegetation change: general aspects of the evolution of Paleocene palynomorph complexes in the Amur Region

According to the data of Kezina (2005) and Kezina & Litvinenko (2007), the prevalence of angiosperms (up to

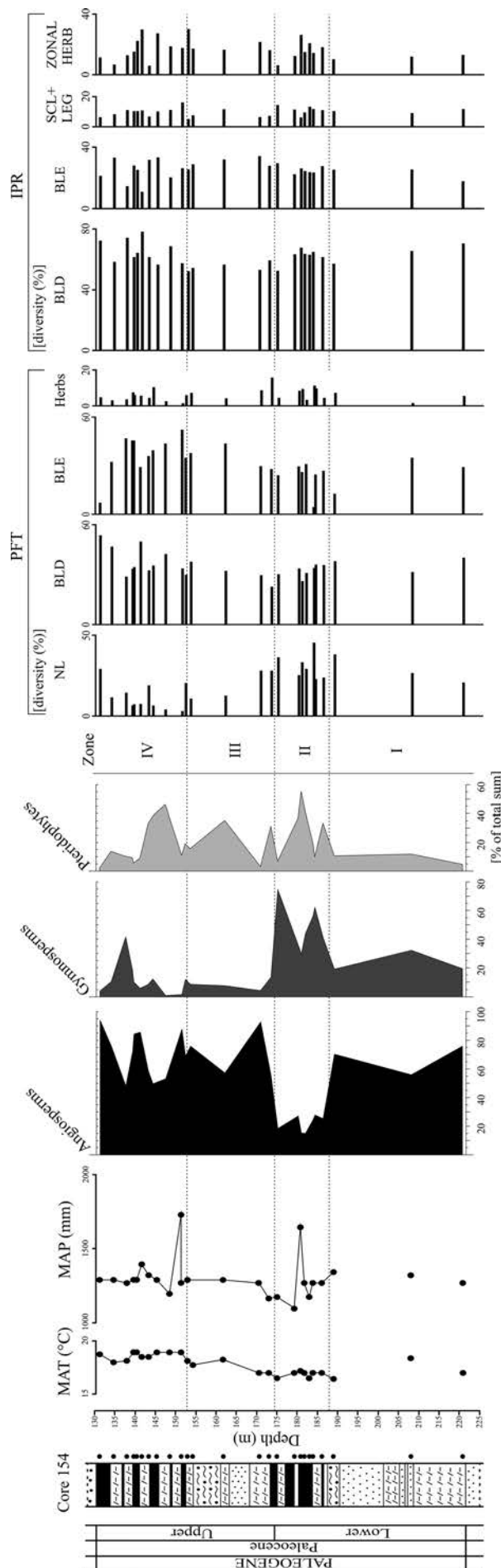


Figure 7 Quantitative characteristics of plants according to palynology, PFT, and IPR methods next to lithological profile of the studied Core 154 and curves of MAT and MAP: MAT – mean annual temperature, MAP – mean annual precipitation, NL – needleleaved evergreen plants, BLE – broadleaved deciduous plants, BLD – broadleaved evergreen plants, SCL+LEG – sclerophyllous and legume-like plants

60 %) is typical for the Middle Tsagayanskaya subformation, while the prevalence of spores and angiosperms is typical for the Upper Tsagayanskaya subformation. The Kivdinskii layers are characterized by the absolute dominance of Taxodiaceae (up to 66–83 %). Based on formally estimating of variations in the record, our data suggest four zones differing in proportions of pteridophytes, gymnosperms and angiosperms. Thus, angiosperms prevail at depths from 220 to 187 m, from 174 to 153 m and from 153 to 130 m, while spore plants and gymnosperms dominated at depths from 187 to 174 m. Taxodiaceae prevail at depths from 153 to 130 m. Ziva (1973) and Kezina (2005) placed the early/late Paleocene boundary at the level of 174 m. Later, Kezina & Litvinenko (2007) moved this boundary to 130 m. According to our data, the early/late Paleocene (Danian/Selandian) boundary corresponds to the boundary between the Zones II and III at the level of 174 m.

The prevalence of Ulmaceae pollen in the complex of the lower, predominantly sandy, part of the Upper Tsagayanskaya subformation, as well as the presence of Betulaceae Gray, Fagaceae, Hamamelidaceae, Juglandaceae A. Richard ex Kunth, and triplicate morphotypes with unclear botanical affinity (*Triporopollenites plicoides* Zakl., *Triatriopollenites confusus* Zakl., *Triatriopollenites* sp., *Tricolpites* sp., *Tricolporopollenites* sp., etc.) with accessory Cretaceous relics (*Parviprojectus* sp., *Anacolodites* sp., etc.), brings this complex closer to the Upper Tsagayanskaya complex of the Arkharo-Boguchanskii Brown Coal Field and the complex of the flora-bearing stratotypes of the Belaya Mountain (Kezina 2005, Kezina & Litvinenko 2007). In terms of taxon composition, this palynocomplex is likewise close to the Danian palynocomplexes of the Zeisko-Bureinskii Basin (Khlonova 1969). Based on its characteristic taxonomic composition, namely the dominance of angiosperms with a variety of spores and a small number of gymnosperms, and presence of spores typical of the Late Cretaceous palynoflora this complex is also comparable with the early Paleocene palynocomplex of the Tsagayanskaya Formation (upper subformation) of the Ushumunskii (Mamontova 1975) and Amuro-Zeiskii Basins (Brattseva 1969). Moreover, this palynocomplex is similar to the late Maastrichtian and Danian complexes of marine and continental sediments of Sakhalin (Budrin & Gromova 1973). A similar complex is described in Primorye (Markevich 1995), whose age is determined in the interval of late Maastrichtian – early Danian. In general, according to Kezina (2005), the palynocomplex characterizes the flora of the transitional interval, when individual Cretaceous relics were still present in the flora, but elements of the boreal flora (*Betula* L., *Alnus* Mill., Ericaceae, etc.), that later widely spread throughout the Cenozoic, already had appeared and diversified.

A similar composition of the palynocomplex of the coal-bearing part of the Upper Tsagayanskaya subformation (= Kivdinskii layers) has been established for

other cores in the Erkovetskii Brown Coal Field (Mal'tseva & Kezina 1985). The palynocomplex has a general systematic composition and an association of taxa (*Ulmoideipites tricolatus*, *Quercites sparsus* (Mart.) Samoil., *Triatriopollenites confusus*, *Myrica* sp., *Comptonia* sp., *Pterocarya* sp., etc.) considered characteristic of the "Kivdinskaya Formation" (Danian – Paleocene) as established by Brattseva (1969) for sections of the Raichikhinskii Brown Coal Field. However, the spectrum of the uppermost flora (PF 1) is somewhat different in composition from the rest of the floras (PFs 2–15) attributed to the Kivdinsk layers of the Upper Tsagayanskaya subformation by the appearance of *Fothergilla* sp. The same situation is reported by Kezina (2005) in the Raichikhinskii Brown Coal Field, where the spectrum of the uppermost flora from the Kivdinsk layers differs in composition from the underlying floras by the appearance of *Fothergilla* sp., *Rhus* sp., *Araliaceae* Juss., *Ericaceae*, and higher abundance of *Betulaceae*, etc. According to Kezina (2005), this is the evidence of the late Paleocene age close to the Eocene (e.g., end of the Thanetian). In addition, it should be noted that *Fothergilla* sp., along with others, is one of the leading taxa for Eocene sediments of Siberia (Kul'kova 1973) and the Far East (Brattseva 1969).

Vegetation change

Using PFT diversity spectra as proxies for vegetation type (Table 4, Fig. 6 and 7), the vegetation of the Amur Region in the Paleocene mainly was of mixed evergreen-deciduous type, except for the mixed deciduous-conifer forest with some evergreens at 130.2 m and the mixed conifer-deciduous forest with some evergreens at depth level 183.1 m. The results obtained from the PFT approach are in accordance with our data obtained from IPR approach. Based on IPR, the MMF zonal vegetation type dominated in the Amur Region during the Paleocene, especially in the upper part. The warmest vegetation type, representing by the ecotone MMF/BLEF, was obtained in the lower part at depth levels 152.6–161.2, 180.2–181.2, and 207.4 m. The coldest vegetation type, representing by the ecotone BLDF/MMF, was revealed only for the PF 20 at the 183.1 m (Table 5, Fig. 6 and 7). In both cases zonal forest biomes have a warm temperate character.

It is known that vegetation changes are often induced by climate change. The observed vegetation patterns and their changes through the Paleocene in many cases can be correlated with warm temperate climate patterns and the overall continental palaeoclimate evolution as reconstructed from the palaeobotanical record. The change in the proportion of some groups of PFTs (needleleaved vs. broadleaved, broadleaved deciduous vs. broadleaved evergreen) throughout the Paleocene also reflects changes in some climatic parameters (Fig. 3). The constant presence of PFT 18 in all studied floras throughout the Paleocene suggests a high humidity in general, and agrees with the precipitation reconstruction demonstrating considerably wetter conditions than at present. PFT 18 is also indicative for the existence of swamps at places and intrazonal swamp forest communities and thus points to the presence of inundated areas throughout the studied time-span. The constant

presence of humid herbs (PFT 1) as well coincides with the mentioned above high humidity throughout the Paleocene.

The tropical PFTs (PFT 25 and 26) are present in many floras but in the low proportion (up to 11.9 %, 1.9–6.3 % at mean). Nevertheless, many taxa scoring for tropical PFTs may represent temperate types (for example, *Hamelidaceae*, *Magnoliaceae* Juss., *Minispermaceae* Juss., *Ulmaceae* Mirb., etc.). However, the warmest IPR vegetation types are observed in the Danian part while PFT analysis point to higher broadleaved evergreen diversity in the upper part (which agrees with the inferred climate evolution).

There is evidence from our data that Paleocene mid-latitude vegetation of the Amur Region was basically warm temperate mixed forest. In contrast to the Amur Region, zonal temperate to warm temperate broadleaved deciduous forest (BLDF) was reconstructed for the Paleocene of Primorye using IPR (Bondarenko et al. 2019), and broadleaved deciduous forest was reconstructed based on PFT (Bondarenko et al. 2020a). Moreover, in the Paleocene of Primorye, all tropical PFTs are excluded when applying the likelihood procedure. The absence of tropical PFTs in the Paleocene of Primorye makes sense when considering the latitudinal position of the study area and the reconstructed palaeoclimate which does not support the occurrence of tropical plants (Bondarenko et al. 2020a), but it is in contrast with Bolotnikova (1979) and Lopatina (2004) suggesting the presence of tropical vegetation. There is evidence that in the RFE, thermophilous vegetation persisted even in the Neogene. From early Neogene carpofores of the eastern RFE, Popova et al. (2013) reconstructed a high diversity (40–50 %) of warm temperate woody plants, including evergreen broadleaved trees.

In contrast to the Amur Region and Primorye, according to Collinson (1990, 2000, 2001), a thick tropical, subtropical and deciduous forest cover existed in the Paleocene around the globe. Graham (1999: 162–169) and Brea et al. (2011) indicated tropical and subtropical forests worldwide, mainly populated by conifers and broadleaved trees. Willis & McElwain (2002) show that in the Paleocene even the Polar Regions were covered with coniferous and deciduous forests. In the North Dakota, floras include the same floral families have characterized South American rainforests and the American Western Interior since the Paleocene (Wing et al. 2009, Brea et al. 2011). Most likely, these differences can be explained by different approaches to the reconstruction of vegetation and interpretation of the results.

The middle part of the succession, from depth levels 187 to 174 m (Fig. 4), is characterized by high diversity of conifers, dominated by *Taxodioideae*. This phase correlates with an overall lower temperature level. Forests with high proportion of *Taxodium* refer to brown coal facies and may represent azonal vegetation connected to increased extension of peat bog facies.

Diversity evolution in our record testifies an already relatively high level for the earliest Paleocene, however, diversity significantly increased in the warmest phases of the late Paleocene. Elsewhere, forests of the Paleocene were characterized as generally species-poor while their diversity did not fully recover until the end of the Paleocene (Johnson

& Ellis 2002, Wilf & Johnson 2004), a trend which is also reflected in our reconstruction. This diversity increase throughout the Paleocene is also related to a diversification or first appearance of modern plant species (Collinson 1990, 2000, 2001).

Today, the Amur Region, heterogeneous in terms of topography, climate, and soil, has a very heterogeneous vegetation cover (Starchenko 2009, Borisova & Starchenko 2018). It includes taiga, coniferous-deciduous forests and forest-steppes, representing the subarctic, cool temperate to warm temperate zones while forests cover about 70 % of this region. Part of the forest zone is occupied by surface waters and swamps. According to our results the Paleocene vegetation cover in the study area fundamentally differed from modern. Based on the low proportion of herbaceous PFTs (0–15.8 %), our data indicate that the Amur Region was entirely covered by forest vegetation during the Paleocene. Comparable conditions were reconstructed for the Paleocene Primorye (Bondarenko et al. 2020a). The results obtained from the PFT approach again are in accordance with data obtained from IPR approach. According to Kovar-Eder et al. (2008) and Teodoridis et al. (2011), with zonal herb proportions ranging from 5.9 to 29.8 %, no open woodland is reconstructed for the Amur Region throughout the Paleocene based on the IPR-vegetation analysis. Thus, a closed forest cover likely existed in the Amur Region throughout the Paleocene. Popova et al. (2013) point out a steep declining trend of the arboreal component in Western Siberia but not before the end of the Eocene. Densely forested areas were also reported from other continental parts such as Northern America where little evidence of wide-open plains has been obtained (Graham 1999: 162–169). In this context it has been assumed that the extinction of large herbivorous dinosaurs may have allowed the forests to grow quite dense (Williams et al. 2009).

Seasonality and monsoon

The Amur Region presently is under the influence of the EAM (Zhang & Wang 2008). The modern regime of temperature and humidity of this region is characterized by a pronounced seasonality. Today, MART is at the very high level of 45.2°C, at a mean, and MARP is around 130 mm. Summer precipitation account for up to 70 % of the MAP, while rainfall in winter amounts to 8 % only (Naprasnikov et al. 1983). The modern RMPwet and RMPdry calculated based on the mean values using station data of Blagoveshchensk (Müller & Hennings 2000, New et al. 2002), are 23.3 % and 0.9 %, respectively (Table 2).

All our climatic data suggest a relatively strong seasonal control of the Paleocene climate of the Amur Region (Table 2). The slightly higher-than-present Paleocene WMMTs in combination with significantly higher-than-present CMMTs indicate a lower-than-present seasonality of temperature during the Paleocene, however, MART gradually decreased from ca 18.9–14.2 °C in the lower part (at depth levels 179.4–220.1 m) to ca. 13.5–15.4°C in the upper part of the well (at depth levels 130.2–174.3 m).

The pronounced seasonality of precipitation (MPwet 177–270 mm; MPdry as 27–53 mm) of the Paleocene cli-

mate of the Amur Region significantly fluctuated during the Paleocene but does not show distinct increasing/decreasing trend. The Paleocene MARP was at a higher-than-present level. However, the higher past MPwet coupled with distinctly higher MPdry indicate that, during the Paleocene, the climate of the Amur Region was more humid, in general. The calculated proportions of MPwet and MPdry to yearly precipitation (MPwet: 14.0–22.3 %; MPdry: 2.0–4.1 %) are almost twice as high compared to present-day (Table 2) and suggest that both, EASM and EAWM were considerably weaker.

Bondarenko et al. (2020b) indicated also pronounced seasonality of climate of Primorye throughout the Paleogene. Utescher et al. (2015) suggested a seasonal control of precipitation in the Cenozoic climate of Primorye. According to this reconstruction, the ratio of the wet month precipitation of the total amount of annual precipitation (RMPwet) used as a proxy for EAM intensity (Jacques et al. 2011) stayed well below the modern value until the earlier part of the late Miocene.

There are extensive literature resources discussing the timing of establishment of the EAM and prevalence of arid climates in the continental interior of Asia, based on various proxies that partly lead to controversial results and conclusions. For example, studies based on thick eolian deposits in northern China (Guo et al. 2002, Qiang et al. 2011), pollen records (Sun & Wang 2005), and palaeoenvironmental patterns based on geological and geo-biological evidence (Guo et al. 2008, Wang et al. 2014b) constrained the time of the formation of the EAM to 22–25 Ma, i.e. to the Oligocene-Miocene transition. An et al. (2001) suggested that the evolution of the EAM was coupled with phased uplift of the Tibetan Plateau since the late Miocene, while others have claimed that proto-Tibetan highlands already existed throughout the Paleogene (e.g., Wang et al. 2014a, Spicer 2017), and that a monsoon type circulation was already operational during most of the Paleogene (Huber & Goldner 2012, Hoorn et al. 2012, Quan et al. 2012b, 2014, Wang et al. 2013, Licht et al. 2014, Bosboom et al. 2015). The seasonal precipitation patterns we reconstruct support the assumption of a (considerably weaker-than-present) Paleogene proto-monsoon.

CONCLUSION

Our data provide the first detailed time series for the early Paleogene climate evolution of the RFE, possibly spanning most of the Paleocene. As a result, the climate of the Amur Region during the Paleocene in general was overall humid, warm temperate in the warmer parts and cool temperate in the coolest part of the studied time-period. The MAT record reconstructed for Core 154 displays a distinct warming trend for the upper part of the succession, most probably coinciding with the declining trend in the global oxygen isotope record throughout the late Paleocene. At the same time there is a trend to more equable climates as evident from declining MART. Palynostratigraphical constraints in our record support the concept of a late Paleocene age for this warming. Shorter-term variability in our MAT record suggests intermittent cooler phases in the earliest

Thanetian and in the latest Paleocene, possibly correlated with the positive oxygen isotope shift in the global record pre-dating the PETM. The globally cooler conditions near the K–T boundary correlate with the highest seasonality of temperature observed in our record. All our climate data suggest relatively strong temperature seasonality and pronounced precipitation seasonality for the Paleocene climate of the Amur Region.

The application of cluster analysis on the palynological dataset reveals a total of four pollen zones that are characterized by differing palynomorph percentages. These zones allow for inter-regional stratigraphic correlations and support the stratigraphical concept suggested by Moiseeva et al. (2018). Diversity evolution in the record testifies an already relatively high level for the earliest Paleocene, however, diversity significantly increased in the warmest phases of the late Paleocene.

Quantitative data obtained from the application of the PFT and IPR approaches allow for tracing vegetation evolution in the Amur Region throughout the early Paleogene. Both methods prove the prevalence of mixed evergreen-deciduous forest of mainly warm temperate character having a diverse shrub layer throughout the studied time-span (IPR types: MMF, MMF/BLEF; rarely BLDF/MMF). Herbaceous components are constantly present but attain moderate diversities only (<10 %). Hence, our vegetation data in general indicate more forested conditions within the studied territory during the Paleocene than at present. The ratio of broadleaved evergreen vs. deciduous PFTs largely co-varies with the MAT record, thus exemplifying the affinity of evergreens to the warmer climate phases. The phase with high diversity of conifer PFTs in the middle part of the succession correlates with an overall lower temperature level. Forests with diverse conifers may represent azonal vegetation connected to increased extension of peat bog facies. The persistent occurrence of PFTs indicative for humid conditions such as mesic herbs and swamp trees (PFTs 1, 18) coincides with the assumption of humid climate conditions in the Paleocene Amur Region.

All our data suggest a relatively strong seasonal control of the precipitation in the Paleocene Amur Region pointing to the existence of a proto-monsoon. When taking RMPwet and RMPdry as proxies for estimating monsoon intensity it is shown that the values were almost twice as high compared to present-day suggesting considerably weaker EASM and EAWM.

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