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Abstract

Paleogene climate dynamics of Primory'e (Far East of Russia) are studied using the Coexistence Approach, for the first time applied on the large palaeobotanical records of this region. The palaeobotanical data for the reconstruction are based on the analysis of vast literature resources for 30 palynofloras and 24 leaf floras covering the early Paleocene (Danian) to late Oligocene (Chattian), i.e. a time-span of ca. 42 Myr, in total. The palaeobotanical records originate from continental deposits of 19 Cenozoic basins located on the territory of Primory'e. All palaeofloras considered were carefully re-evaluated regarding the validity of taxonomic identifications and their Nearest Living Relatives. Based on the three temperature and four precipitation variables, the climate data obtained are consistent with global trends, indicate major climate changes and demonstrate the general climate cooling during the Paleogene. The cooling is most striking regarding cold month mean temperature, while decline of mean annual temperature record was less distinct. Our data indicate that the Palaeogene climate of Primory'e was significantly warmer than present, in general, with warmest conditions prevailing throughout the Eocene and in the southeast of the study area. The observed flat Paleogene temperature gradients over Primory'e are related to the global pattern and specific regional aspects. The precipitation reconstruction points to conditions considerably wetter than at present. A distinct increase in mean annual precipitation is observed for the early Eocene and persisted throughout the Eocene and Oligocene. The regional rainfall pattern fundamentally differed from modern, and this holds for all studied variables. The inland region and the south of Primory'e were significantly more humid than today. The Paleogene pattern was possibly related to a monsoon type circulation and enhanced landward flow of humid air masses, due to an overall flatter morphology of the East Asian coastal areas.

Keywords	Coexistence Approach, temperature evolution, precipitation pattern, spatial gradients, temporal trends, climate seasonality.

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Dr. Howard Falcon-Lang
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"Palaeogeography, Palaeoclimatology, Palaeoecology"

Dear Dr. Howard Falcon-Lang,

As a corresponding author, I submitted the manuscript "Paleogene climate dynamics of Primory'e (Far East of Russia) – a reconstruction based on the palaeobotanical record" (the authors: O.V. Bondarenko, N.I. Blokhina, V. Mosbrugger, and T. Utescher) for a publication in the journal "Palaeogeography, Palaeoclimatology, Palaeoecology".

The paper includes: Highlights, Manuscript (including Figure Captions and Table Captions), 9 Figures, 4 Tables and 8 Supplements (Appendix Tables).
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Highlights

- Continental Paleogene climate of Primory'e is consistent with major global trends.
- Late Paleogene cooling trend is most striking regarding CMMT.
- Flat temperature gradients are related to the global pattern and specific regional aspects.
- Pattern of regional rainfall fundamentally differed from modern.
- Regional precipitation pattern was possibly related to a monsoon type circulation.

Paleogene climate dynamics of Primory'e (Far East of Russia) – a reconstruction based on the palaeobotanical record

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Abstract

Paleogene climate dynamics of Primory'e (Far East of Russia) are studied using the Coexistence Approach, for the first time applied on the large palaeobotanical records of this region. The palaeobotanical data for the reconstruction are based on the analysis of vast literature resources for 30 palynofloras and 24 leaf floras covering the early Paleocene (Danian) to late Oligocene (Chattian), i.e. a time-span of ca. 42 Myr, in total. The palaeobotanical records originate from continental deposits of 19 Cenozoic basins located on the territory of Primory'e. All palaeofloras considered were carefully re-evaluated regarding the validity of taxonomic identifications and their Nearest Living Relatives. Based on the three temperature and four precipitation variables, the climate data obtained are consistent with global trends, indicate major climate changes and demonstrate the general climate cooling during the Paleogene. The cooling is most striking regarding cold month mean temperature, while decline of mean annual temperature record was less distinct. Our data indicate that the Palaeogene climate of Primory'e was significantly warmer than present, in general, with warmest conditions prevailing throughout the Eocene and in the southeast of the study area. The observed flat Paleogene temperature gradients over Primory'e are related to the global pattern and specific regional aspects. The precipitation reconstruction points to conditions considerably wetter than at present. A distinct increase in mean annual precipitation is observed for the early Eocene and persisted throughout the Eocene and Oligocene. The regional rainfall pattern fundamentally differed from modern, and this holds for all studied variables. The inland region and the south of Primory'e were significantly more humid than today. The Paleogene pattern was possibly related to a monsoon type circulation and enhanced landward flow of humid air masses, due to an overall flatter morphology of the East Asian coastal areas.

Keywords: Coexistence Approach, temperature evolution, precipitation pattern, spatial gradients, temporal trends, climate seasonality.

1. Introduction

The Primory'e Region (or Primory'e) is located in the south of the Russian Far East (RFE), on the coast of the Sea of Japan, bordering the Eurasian continent and Pacific Ocean and constantly experiences its influence (Gerasimov, 1969). Most of Primory'e (4/5 of the territory) is occupied by the Sikhote-Alin Mountains stretching along the coast in southwest – northeast direction and also influencing the regional climate (Gorokhova, 2012). However, the location near the southern limit of the cool temperate climate zone is not so much crucial as its position at the edge of a vast continental area, which strongly cools in winter and heats up in summer. Moreover, the East Asian Monsoon (EAM) has a strong effect on Primory'e. At present, the climate of Primory'e is characterized as a temperate monsoon type climate (Borisov, 1967; Gerasimov, 1969; Svinukhov, 1983; Gorokhova, 2012; Gayko, 2016; Zhang and Wang, 2008), and coastal regions are under the influence of the ocean currents in the Sea of Japan, namely, the warm Tsushima current, and more importantly, the cold Primorsk current (Istoshin, 1959; Yurasov and Yarichin, 1991).

The study of the climate evolution of Primory'e in the geological past, in particular in the Paleogene, promotes the understanding of the formation of modern climate in this region. The Paleogene (65.5–23.03 Ma) was an interval of significant climatic and biotic reorganization. The knowledge of the climate evolution during this period 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 (Zachos et al*.*, 2008; Utescher et al*.*, 2009). Case studies of geological records offer direct evidence to explain the paleoclimatic changes. The evolution of Paleogene climates in eastern Eurasia in general and Primory'e in particular is tied to the history of the EAM and is complicated by tectonic events such as uplift of the Tibetan Plateau, and the Sea of Japan back-arc opening (e.g., An et al., 2001; Liu and Yin, 2002; Akhmetiev, 2004, 2015; Sato et al., 2006; Yamamoto and Hoang, 2009; Pavlutkin and Golozubov, 2010; Quan et al., 2012; Liu et al., 2015; Tada et al., 2016; Akhmetiev and Zaporozhets, 2017). Moreover, past climates of eastern Eurasia are supposed to reflect the varying intensity of the warm Kuroshio and cold subarctic currents (e.g., Gallagher et al., 2009; Matthiessen et al., 2009).

Paleogene regional climates can be reconstructed from the palaeobotanical records with a different degree of reliability, depending on the spatio-temporal resolution of palaeobotanical sites, and the taxonomic resolution of the studied plant organs (Akhmetiev, 2004). The evolution of continental Paleogene climates has been well studied on the basis of palaeobotanical data from Australia, Europe, and North America (Greenwood and Wing, 1995; Wilf, 2000; Wing and Harrington, 2001; Jolley and Widdowson, 2005; Mosbrugger et al., 2005; Wing et al., 2005; Utescher et al., 2007; Greenwood et al., 2010; Utescher et al., 2011; Quan et al., 2012) and marine proxy data from both hemispheres (Pearson et al., 2007; Zachos et al., 2008; Bijl et al., 2009). In East Asia, quantitative Paleogene climatic reconstructions on the basis of palaeobotanical data have been conducted on individual sites of China (e.g., He and Tao, 1997; Quan and Zhang, 2005; Su et al., 2009; Hao et al., 2010; Wang et al., 2010, Hoorn et al., 2012; Quan et al., 2012). Globally, the Paleogene was a period of climate changes from greenhouse to icehouse conditions in the so-called “doubthouse” times marked by climatic cooling, rapid growth of the Antarctic ice sheet, and a supposed drop in atmospheric CO_2 levels leading to the Eocene/Oligocene Transition (EOT) (Dupont-Nivet et al., 2007; Eldrett et al., 2009; Pearson et al., 2009; Xiao et al., 2010; Abels et al., 2011).

As regards the Paleogene climate evolution in the RFE in general and Primory'e, in particular, our knowledge is still very poor and fragmentary. Paleogene climatic reconstructions have been made by Budantsev (1997, 1999) for the northeastern part of the RFE, mostly for western Kamchatka. However, reconstructions of qualitative characteristics and quantitative parameters of the climate have been made using the Climate Leaf Analysis Multivariate Program (CLAMP), a method based on the morphological parameters of fossil leaves. Based on an example of the Irgirninskaya flora of western Kamchatka, Budantsev (1997, 1999) obtained quantitative characteristics of the late Eocene paleoclimate. The reconstructed conditions were compared to those of the modern climate of the Atlantic states of the USA, between 41–43 ° N and 73–75 ° W, characterized by cool summers and mild winters, and an uniform distribution of abundant rainfall typical of the temperate zone (Budantsev, 1997, 1999). For the northeastern part of the RFE Popova et al. (2012), using the Coexistence Approach (CA) document the transition from very warm and humid conditions in the late Oligocene via the Middle Miocene Climatic Optimum to a cool temperate climate during the Pliocene. For the southern part of Primory'e a first quantitative climate record was presented by Utescher et al., (2015) based on 14 floras and covering the time-span from the middle Eocene to early Pleistocene.

In the present detail study we use the exceptionally rich palaeobotanical heritage of Primory'e to reconstruct the Paleogene regional climate evolution in space and time, and to trace potentially monsoon-induced patterns. Based on a total of 54 reasonably well-dated pollen and leaf floras from 19 basins coherent climate maps are presented for the first time for seven stratigraphic levels covering climate evolution in a time-span of ca. 42 Myr, in total. All the climate data are reconstructed using a single approach applicable on every plant organ type (Coexistence Approach – CA). For the present application the taxonomical concept of the fossil materials and modern botanical affinity were carefully revised.

2. Study area and palaeogeographical settings

2.1 Study area

The palaeobotanical records of Primory'e studied herein with respect to palaeoclimate originate from 19 Cenozoic basins (Fig. 1). The Paleogene of Primory'e is represented by a series of volcanic and sedimentary deposits, unconformably lying on Mesozoic strata. The sedimentary facies includes fine to coarse-grained continental clastics and intercalated lignites excavated in several active open cast mines. For some of the basins, mainly generated by extensional tectonics (Pavlovskii, Pushkinskii and Maksimovskii Basins), intercalated volcanoclastic layers and tholeitic lava flows (Maksimovskii Basin, Takhobinskaya Fm. and Kuznetsovskaya Fm.) allow for radiometric dating of the strata (Table 1; Fig. 2). The sedimentary successions in the individual basins are characterized by numerous unconformities related to regional tectonics and phases of rifting and subsidence (Pavlutkin and Petrenko, 2010). When combining the strata of the individual basins a time-span of ca. 42 Myr can be covered.

The regional stratigraphic correlation chart for the basins is adapted from Pavlutkin and Petrenko (2010) (Fig. 2). The framework of this chart is based on a variety of stratigraphic data obtained from radiometric dating (volcanites), regional and inter-regional pollen zonation, as well as lithological, palaeobotanical and vertebrate fauna correlations (Akhmetiev, 1973; Varnavskii et al., 1988; Popov et al., 2005; Pavlutkin and Petrenko, 2010; Chatshin et al., 2013). The stratigraphic scheme has been tied to the International standard (Pavlutkin and Petrenko, 2010; Cohen et al., 2013) and at least allows for dating the flora-bearing horizons at the stage level (Fig. 2). For some of the floras stratigraphic ages are better constrained (cf. Table 1: radiometric datings for the Zanadvorovka, Gladkaja17, Kluch Stolbikova and Sobolevka floras).

2.2 Palaeogeographical setting

The geological situation of Primory'e and the adjacent territory of northeastern China, constitute a single continental area since the late Cretaceous, together with the inner zone of Japan and Korea, prior to the opening of the Sea of Japan (Maruyama et al., 1997). This opening, caused by intracontinental rifting, set on to the south of our study area. The initial rifting stage took place in the middle Eocene, while the major phase occurred considerably later, during the early to middle Miocene (Denisov, 1965; Golozubov, 2006). These geological settings fully confirm the conclusion drawn from paleobotany, regarding the commonality in the Mesozoic and earlier Paleogene phyto-history of this region (Kawai et al., 1962; Pavlyutkin and Golozubov, 2010). When taking into account these considerations we have to assume that the Paleogene geography fundamentally differed from modern conditions. Unlike today, the Pacific coast was located several hundred kilometers to the east of our study area, throughout the time-span regarded, and thus a direct maritime impact on the regional palaeoclimate probably did not exist (Fig. 3). To illustrate the palaeogeographical configuration of Primory'e in the middle Eocene (ca. 45 Ma), we used the OSDN plate reconstruction (hotspot reference frame) and palaeogeographic reconstructions by Maruyama et al. (1997) and Pavlyutkin and Golozubov (2010).

The Cenozoic sedimentary basins of southern Primory'e such as the Khasanskii, Shkotovskii and Zerkal'nenskii Basins are related to rifting and extensional tectonics. The subsidence of the basins was accompanied by volcanic activities. Though block tectonics may have caused minor level differences, a near sea-level elevation can be assumed for the palaeofloras recovered from these basins (Lebedeva, 1957; Denisov, 1965; Khudyakov et al., 1972).

The Sikhote-Alin Range, located in the northeast of Primory'e represents a continental-margin range including late Cretaceous to Paleogene volcanites and intrusives (Parfenov et al., 2009). There is evidence for intensified uplift of this mountain range from the Eocene – Oligocene transition on. At the same time, older depressions subsided as intramontane basins, namely the Artemo-Tavrichanskii and Vanchinskii Basins in the south-west of Primory'e. It is largely unclear which elevation the Sikhote-Alin had attained in Paleogene times. However, palaeofloras reconstructed on the basis of fossil plant remains from the several Paleocene volcanic complexes allowed the suggestion that, within north-east Primory'e, the elevation of the Sikhote-Alin exceeded 500 m a.s.l. (Akhmetiev et al., 2009). From the second half of the Eocene to Miocene, there was an intensive uplift of this ridge (Parfenov et al., 2009). Oleinikov and Oleinikov (2005) estimate the elevation of the Sikhote-Alin Mountains in the central part of Primory'e in the late Miocene equal to 700–800 m a.s.l. The most recent uplift pulse of the Sikhote-Alin, however, occurred in the Pliocene and Quaternary, connected to basaltic eruptions. The elevation, which attains 1000–1400 m a.s.l. at the watershed of the Sikhote-Alin Mountains, created a modern mountainous relief with heights of up to 1856 m a.s.l. and co-occurred with increased subsidence in the neighboring part of the Sea of Japan and the Tatar Strait (Kropotkin and Shakhvarstova, 1965).

According to the available paleomagnetic data, the eastern part of Eurasia occupied a position close to the modern one, i.e. did not experience any significant displacements or rotations since the Late Jurassic (Lee et al., 1987; Zhu, 1993; Ushimura et al., 1996; Kolesov, 2003). At the same time, palaeomagnetic data for the pre-Cenozoic formations of Japan indicate that these rocks were formed much to the south of their present location (Hirooka, 1990). This is attributed to interactions with the relatively immobile Eurasia and the extremely mobile oceanic plate of Isanagi (Golozubov, 2006). According to Utescher et al. (2015), as regards plate tectonic movement, a southward displacement of Primory'e by ca. 2 degrees latitude occurred since the middle Eocene (Ocean Drilling Stratigraphic Network, GEOMAR plate reconstruction service using hotspot reference frame), thus decreasing the measured cooling signal.

3. Materials and methods

3.1 The floral record

The palaeobotanical record of Primory'e is diverse and has been the subject to extensive taxonomic studies (cf. Table 1 for references). For all that, all palaeofloras considered here were carefully re-evaluated regarding the validity of taxonomic identifications and the Nearest Living Relatives (NLRs) of the fossil taxa. In the present study, a total of 54 floras (30 PFs – palynofloras and 24 LF – leaf floras) are studied with respect to palaeoclimate at seven stratigraphic levels. The floras cover a total time-span of ca. 42 Myr, ranging from the early Paleocene (Danian) to late Oligocene (Chattian). The single floras are listed in Table 1, together with information on basin provenience, type of flora, stratigraphic age, method of dating, and references. The complete floral lists, assigned NLRs and their climatic requirements are given in the Electronic Supplements 1–7.

3.2. Quantitative palaeoclimate reconstruction – application of the Coexistence Approach (CA)

To reconstruct climate from the plant fossil record of Primory'e we use the 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 a detailed description of the method the reader is referred to the original papers describing the procedure (Mosbrugger and Utescher, 1997; Utescher et al., 2014). We use the Palaeoflora Database (Utescher and Mosbrugger, 2018) as source for climatic requirements of extant plant taxa. The database was complemented to meet the requirements of the presently used NLR concept. The database update includes ca. 80 new entries for fossil taxa and ca. 40 entries for modern plants. For the identification of climatic requirements of modern plants we used chorological information from Fang et al. (2009, 2011) and Sokolov et al. (1977, 1980, 1986) and climatological datasets from (Müller and Hennings, 2000; New et al., 2002). Climate data entries already available in the database were carefully checked for completeness. Floral lists with corresponding NLRs employed in this study and their climatic requirements are made available in the Electronic Supplements 1–7.

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). In the CA, at least 10 NLR taxa contributing with climate data are required to obtain reliable results (Mosbrugger and Utescher, 1997). Here, 9 to 148 taxa contribute to determining the climate data (Table 1). Except for the early Eocene Luchegorsk540, 541 flora (LF 33) with only nine taxa the palaeoflora are diverse enough to obtain reliable results. The precision of the CA results also depends on the taxonomical level of NLR identification (Mosbrugger and Utescher, 1997). Following Utescher et al. (2014, 2015), *Sciadopitys verticillata* (Thunb.) Siebold et Zucc., *Comptonia peregrina* (L.) Coult. and *Parrotia* C.A. Mey. are excluded from the analysis (Utescher et al., 2000). In addition, some taxa have not been considered in the calculations for various reasons. Cercidiphyllaceae Engl. were widespread in the Northern Hemisphere since the Late Cretaceous (Crane and DuVal, 2013). Today, the living fossils are restricted to more temperate climate (Palaeoflora Database: MAT < 17.8 °C; Fang et al. (2009, 2011): < 18.2 °C). We have to assume that the modern species do not reflect the full possible climatic range of the family and therefore exclude the taxon from climate reconstruction. Bombacaceae Kunth growing widely in tropics is a warm outlier in the analysis and is only present in two palynofloras. *Larix* Mill. represents a cold outlier in the analysis. The taxon is mainly present in pollen records and here interpreted as altitudinal element. To avoid interference in precipitation reconstruction, the taxon was excluded from the CA calculations. Its occurrence is discussed separately (see section *5.5.*).

To illustrate climate change in Primory'e during the Paleogene, the floras are allocated to seven time intervals. Time intervals are defined according to the international standard: early and late Paleocene, early, middle, and late Eocene, and early and late Oligocene. To visualize the results, a series of maps (cf. Figs. 4–6) is provided and discussed below showing the evolution of the six climate variables analyzed in seven Paleogene stages regarded. For the technical preparation of the maps ArcMAP 10.4 was used. Means of climate variables in each time interval obtained for Primory'e are given in Table 3 and shown as box plots (PAST software) (Fig. 7–8). The box plots for MATmean are shown next to the benthic oxygen isotope record after Zachos et al. (2008) (Fig. 7A and B).

3.3. Climate seasonality, monsoon intensity

In order to determine temperature seasonality of the Paleogene climate of Primory'e, the mean annual range of temperature (MART) was calculated as the difference of WMMT and CMMT for the time intervals studied (Table 3). To study precipitation seasonality, the mean annual range of precipitation (MARP – calculated as difference of MPwet and MPdry) was calculated for the time intervals (Table 3). In order to measure the EAM intensity during Paleogene we use the ratio of MPwet and MPdry on MAP (RMPwet and RMPdry) (Table 3). According to Jacques et al. (2011), the ratios of MPwet and MPdry of MAP are good indication of past monsoon intensity (summer – EASM and winter – EAWM respectively). To visualize the results, change of the MART and MARP, the RMPwet and RMPdry are taken as a measure of monsoon intensity and are shown as box plots in Figure 9.

4. Results

Climate data calculated for the 54 floras are given in the Electronic Supplement 8, complete lists of taxa for the localities, including their NLRs with climatic requirements, are provided in the Electronic Supplements 1–7.

To analyse the climate change of Primory'e during the Paleogene in space and time, paleoclimate data presently reconstructed for six different climate variables (MAT, CMMT, WMMT, MAP, MPwet and MPdry) are shown in the map series for seven time intervals in comparison with modern conditions. Gradients and patterns obtained for single climate variables are shown in Figures 4–6. Means of seven climate variables for each time interval and variables of climate seasonality and monsoon indices calculated from these means are given in Tables 2 and 3, and illustrated in Figures 7–9. Changing climate patterns can continuously be studied for the time-span from the early Paleocene to late Oligocene. The given figures in each case refer to means and CA intervals (Xmean/Xmin–Xmax).

4.1. Temperature

In the temperature evolution of Primory'e during the Paleocene (Table 2, Fig. 4F, G and 5F, G, M, N), the highest values in the early Paleocene for MAT (18.4/16–20.8 °C) and CMMT (9.7/9–10.4 °C) are indicated for the LF 38 (central part), WMMT (25.1/24–26.3 °C) for the LF 39 (northeast), and in the late Paleocene for the PF 37 (northeast) with MAT of 17.6/13.8–21.4 °C, CMMT of 10/6.1–13.9 °C and WMMT of 26.5/24.7–28.3 °C. Data obtained for the late Paleocene PF 37 indicate the warmest conditions observed in our data. In contrast, the lowest temperature results for the early Paleocene LF 39 (northeast) for MAT of 14.5/13.4–15.6 °C and CMMT of 8.5/6.6–10.4 °C, and for the late Paleocene LF 35 (central part) with MAT of 16.9/12.8–21.1 °C, CMMT of 3.8/−2.8–10.4 °C and WMMT of 25.3/22.5–28.1 °C. When comparing the means from MAT, CMMT, and WMMT, slightly cooler conditions are indicated during the early Paleocene (Table 3, Fig. 4F, G and 5F, G, M, N).

In the Eocene (Table 2, Fig. 4C–E, 5C–E and J–L), the highest values in the early Eocene for MAT (18.2/15.3–21.1 °C) are obtained for four floras: the PF 27, 28, 29 and 30 (southwest and central part), CMMT (9.6/6.6–12.6 °C) for the PF 27 (southwest), WMMT (27.3/26.6–28.1 °C) for the PF 26 (southwest), in the middle Eocene for MAT (18/16.7–19.4 °C) for the LF 22 (the most south flora), CMMT (9.7/7.7–11.8 °C) for the PF 22 (the most south flora), WMMT (27.3/26.6–28.1 °C) for the PF 21 (southwest), and in the late Eocene for MAT (18.2/15.3–21.1 °C) for the PF 16 (southwest), CMMT (10.2/−0.6–21.1 °C) for the PF 18 (central part), WMMT (27.3/26.6–28.1 °C) for the PF 13 and PF14 (southwest). The lowest values are indicated in the early Eocene for MAT (15.1/13.8–16.5 °C) and CMMT (3.9/3.1–4.8 °C) for the LF 34 (the most northeast flora), WMMT (24.2/19.6–28.8 °C) for the LF 33 (central part), in the middle Eocene for MAT (16.9/14.4–19.4 °C) for the PF 21 (southwest), CMMT (6.5/3.4–9.6 °C) for the PF 24 (southwest), and WMMT (25.2/23.6–26.8 °C) for the PF 22 (the most south flora), in the late Eocene for MAT (14.8/14.1–15.6 °C), CMMT (2.2/−0.1–4.6 °C) and WMMT (24.6/22.5–26.8 °C) for the LF 18 (central part). The mean values of MAT, CMMT, and WMMT reconstructed for the Eocene floras are generally indicated warm period with warm pick in the middle Eocene (Table 3, Fig. 4C–E, 5C–E and J–L).

The Oligocene data display a cooling trend (Table 3, Fig. 4A, B and 5A, B, H, I). The highest values are indicated in the early Oligocene for MAT (17.4/13.8–21.1 °C) and CMMT (8.2/3.8–12.6 °C) for the PF 7 (southwest), WMMT (27.4/26.6–28.2 °C) for the PF 6 (the most south flora), and in the late Oligocene for MAT (17.1/12.8–21.4 °C) and CMMT (6.6/−0.3–13.6 °C) for the PF 3 (southwest), WMMT (26.1/24.7–27.5 °C) for the LF 2 (southwest). The lowest values are indicated for the early Oligocene for MAT (14.8/14–15.6 °C) for the LF 8 (southwest), CMMT (4.3/3.5–5.1 °C) and WMMT (25.2/24.7–25.8 °C) for the LF 9 (northeast), and in the late Oligocene for MAT (14.4/13.3–15.5 °C) and CMMT (2.2/−0.1–4.5 °C) the LF 2 (southwest). The onset of pronounced cooling is quite evident from the late Oligocene temperature data, characterized by lower mean values of MAT, CMMT and WMMT (Table 3, Fig. 4A, B and 5A, B, H, I).

4.2. Precipitation

In the precipitation patterns of Primory'e during the Paleocene (Table 2, Fig. 4N, M and 6F, G, M, N), the highest values in the early Paleocene are indicated for the LF 39 (northeast) with MAP of 1293/1231–1355 mm, MPwet of 181/167–195 mm, MPdry of 40/37–43 mm and in the late Paleocene for MAP (1210/807–1613 mm) and MPdry (35/27–43 mm) for the LF 36 (northeast) and for MPwet (197/150–245 mm) for PF 37 (northeast). The lowest values are indicated for the early Paleocene LF 38 (central part) with MAP of 1045/735–1355 mm, MPwet of 162/88–237 mm, MPdry of 34/17–52 mm and for the late Paleocene LF 35 (central part) with MAP of 1045/735–1355 mm, MPwet of 176/116–237 mm and MPdry of 27/6–49 mm. MAPmean increased since the early Paleocene (Table 3, Fig. 4N, M and 6F, G, M, N).

In the Eocene (Table 2, Fig. 4J–L and 6C–D, J–L), the highest values are indicated for the early Eocene PF 28 (central part) with MAP of 1422/1231–1613 mm, for PF 30 (central part) with MPwet of 223/205–241 mm, for the PF 34 (northeast) with MPdry of 60/50–71 mm, in the middle Eocene for the PF 21 (southwest) with MAP of 1554/1531–1577 mm and MPdry of 54/45–64 mm, for the PF 25 (central part) with MPwet of 235/148–322 mm, in the late Eocene for the PF 18 (central part) with MAP of 1596/652–2540 mm and MPwet of 230/108–353 mm, and the LF 18 (central part) with MPdry of 55/28–83 mm. The lowest values are obtained for the early Eocene regarding MAP (1047/740–1355 mm) and MPwet (159/150–169 mm) for the LF 34 (northeast), MPdry (29/18–41 mm) for the PF 32 (central part), for the middle Eocene regarding MAP (1070/641–1500 mm) and MPwet (156/109–204 mm) for the PF 23 (southwest), MPdry (27/13–41 mm) for the PF 25 (central part), and in the late Eocene for MAP (1044/705–1383 mm) for the LF 17 (southwest), MP wet (172/170–174 mm) for the PF

19 (central part), MPdry (22/7–38 mm) for the LF 13 (southwest). In the Eocene the increasing trend of MAPmean continued. MPwetmean increased up to the middle Eocene and then decreased again, MPdrymean tended to increase during the Eocene (Table 3, Fig. 4J–L and 6C–D, J–L).

In the Oligocene (Table 3, Fig. 4H, I and 6A, B, H, I), the highest values are indicated for the early Oligocene as regards MAP (1422/1231–1613 mm) and MPdry (54/45–64 mm) for the PF 8 (southwest), MPwet (236/178–295 mm) for the PF7 (southwest), in the late Oligocene for MAP (1278/979–1577 mm) for the PF 3 (southwest) and the PF 5 (central part), MPwet (235/148–322 mm) for the PF 3 (southwest), MPdry (49/43–55 mm) for the LF 2 (southwest). The lowest values are indicated for the early Oligocene LF 10 (northeast) with MAP of 1059/925–1194 mm, for the PF 6 (the most south flora) with MPwet of 151/150–153 mm, for the PF 7 (southwest) with MPdry of 29/18–41 mm, and for the late Oligocene PF 4 (central part) with MAP 1132/652–1613 mm, for the LF 2 (southwest) with MPwet of 171/152–191 mm and for the PF 3 (southwest) with MPdry of 27/13–41 mm. Beginning from the early Oligocene a decreasing trend of MAPmean is observed (Table 3, Fig. 4H, I).

4.3. Climate seasonality, monsoon intensity

Temperature (MART) and precipitation (MARP) seasonality parameters and the mean values of related climatic parameters for each time interval are given in Table 3 in comparison to the present-day values. The MART in the early Paleocene was 15.5 °C and gradually increased to 20.2 °C in the late Oligocene. The MARP in the early Paleocene was only 134 mm but gradually increased to 172 mm in the late Oligocene (Fig. 9A, B). The RMPwet gradually increased from 0.147 in the early Paleocene to

0.172 in the late Oligocene, while the RMPdry varied from 0.026 to 0.035 (Table 3, Fig. 9C, D).

5. Discussion

5.1. Differences in micro- and macro-based climate data

The integration of micro- and macrofloras in the present analysis allows for a couple of general considerations regarding resolution and quality of the obtained data thus providing clues about the integrity of the reconstruction. For the 30 microfloras, the number of taxa contributing with climate data ranged from 13 to 67 (mean 37.9, std. 12.2). The analysis of 24 macrofloras could be based on 9 to 148 (mean 42.6, std. 29.7) climate datasets of extant reference taxa. Hence, all results are considered reliable (>10 taxa; cf. Mosbrugger and Utescher, 1997), except for the early Eocene Luchegorsk540, 541 flora, but macrofloras better reflect past biodiversity.

Climatic requirements of 99.6 % of identified NLRs of the fossil taxa in microfloras and 99.4 % in macrofloras show overlapping. Generally, in 23 out of 54 cases, all NLRs can coexist, in all other cases over 96 % of taxa, indicating high significance level for the results (Mosbrugger and Utescher, 1997). The very high degree of overlapping in both micro- and macrofloras testifies the integrity of the NLR concepts used in each case. This is especially noteworthy when considering the fact that in a number of cases botanical affinity was identified at a sub-generic level. Occasionally multiple CA intervals occur at a close climatic range, possibly related to integration over differing floral horizons or caused by taphonomic effects (Utescher et al., 2014), were combined to one single interval (cf. Electronic Supplement 8).

As regards the MAT, the mean precision of the results, i.e. the mean width of the CA intervals for all floras amounts to 5.4 °C (std. 2.0 °C), and to 505 mm (std. 190 mm) for the MAP, respectively. When reconstructing MAT, CA intervals obtained from macrofloras are relatively narrow (mean width of CA intervals near 3.2 °C), in MAP reconstruction results are less precise (CA interval width around 415 mm at a mean). For microfloras owing to the commonly high taxonomic level of NLR assignment resulting CA ranges are comparatively wide and provide a poorer climatic resolution. For MAT the width of CA intervals is 6.5 °C at the mean (std. 3.1 °C). The resolution is reduced by ca. 50 % when compared to the macroflora. For MAP the width of CA intervals is also wider, 537 mm at the mean (std. 382 mm). According to Utescher et al. (2012), CA data obtained from microflora are easily capable of reflecting temporal trends due to more frequent occurrences of microfloras. However, in the majority of cases CA data based on microfloras do not allow for quantifying minor climatic changes (Utescher et al., 2012).

Apart from the fact that the highest values of all climatic parameters used are related to palynofloras, no regularities in the distribution of the parameters for different organ types have been found. LF and PF from the same site and the same time interval can have different or approximately equal values for one or several climatic parameters. For example, the MAT and CMMT are higher for the PF 2 and lower for the LF 2 but WMMT is significantly higher for the LF 2 and contrary to the MAT and CMMT is lower for the PF 6 but higher for the LF 6, whereas WMMT is approximately equal (Table 2). Higher means in the microfloras can be related to the fact that identifications at genus or even species level are not possible. The larger climate ranges of genera and families, in turn, shift the CA interval means to higher values. However, all the CA intervals obtained from micro- and macrofloras overlap when the floras come from the same locality. From 54 palaeofloras studied 15 microfloras originate from levels where macrofloras were found, and in all cases the reconstructed climate data are largely congruent. However, the overall narrower climate ranges obtained from the mainly local macroflora tend to cover the cooler and/or dryer ends of the broader ranges derived in the microflora-based reconstruction which has a lower climatic resolution and reflects regional rather than local climate. The fact that microflora-based data tend to indicate warmer conditions may be explained by a mainly northward aeolian transport of pollen grains during summer (cf. Bondarenko et al., 2013).

5.2. Spatial climatic gradients

The modern climate gradients of Primory'e reflect the superimposition of the continental scale atmospheric circulation pattern such as monsoonal circulation and regional forcings. The proximity of the northern Pacific combined with the existence of a coastal mountain range with a complex relief causes a highly variable regional climate with considerable gradients, even within the same physical and geographical area. The coastal mountain range of Primory'e, the Sikhote-Alin, presently attains an altitude from 500 up to 2000 m a.s.l. and plays a dual role in the distribution of both winter and summer temperatures on the northwestern and southeastern slopes (Khramtsova, 1966a). It serves as a barrier preventing the free flow of cold air masses from the continent to the Sea of Japan in winter and inland transport of moist Pacific air masses thus leading to more continental, drier climate conditions in the interior and eastern part of Primory'e.

When regarding the modern temperature distribution over Primory'e (Fig. 4A, 5A, B) it is shown that, apart from the reflected altitudinal pattern, isotherms follow about the northeast – southwest trending Pacific coast. Lowest MATs of ca. −1 °C are recorded in the northern part of the Sikhote-Alin Mountains while highest values of ca. 7 ° C occur on the south coast. Thus, a modern MAT gradient of ca. 8 °C results for the study area extending over about 6 ° latitude. This gradient includes a zonal component and, more importantly, an altitudinal gradient of ca. 400–450 meters (Kurentsova, 1968). The modern WMMT gradient equals ca. 5 °C (ca. 17–22 °C), with the lowest values in coastal regions of the Tatar Strait in northeast of Primory'e, while the highest values result for the western foothills of the Sikhote-Alin. CMMTs range from −8 to −14 ° C along the Pacific coast, and from −14 to −23 °C in the inland areas. Thus, modern CMMTs display a comparatively high zonal gradient of ca. 6–9 °C and CMMT increase from coast to inland areas and the border region with China in about the same order.

The Paleogene configuration (Fig. 4A–G, 5A–N) shows significantly higher temperature levels. While WMMT was higher by ca. 5–7 °C and MAT by over 15 °C, highest anomalies with respect to present result for CMMT, attaining more than 30 °C in inland areas of Primory'e. These high temperature anomalies, being most significant in the cold season, are in line with previous reconstructions of mid- to higher latitude continental temperature under the Paleogene greenhouse conditions, based on various proxies (e.g., Markwick, 1994; Greenwood and Wing, 1995; Utescher and Mosbrugger, 2007; Greenwood et al., 2010; Utescher et al., 2011; Inglis et al., 2017). Even for the Oligocene, having a lower atmospheric CO_2, MAT anomalies in the order of 10 °C were previously reported, based on floras of the European part of the Russian Federation and Western Siberia (Popova et al., 2012) and coincide with data from marine archives (e.g., Zachos et al., 2008; Evans et al., 2018). All reconstructed temperature patterns consistently indicate that the climate was warmest throughout the Eocene and in the southeast of the study area. As regards MAT and CMMT this feature coincides with the actual pattern. Inland sites in the 19 basins play a key role here in the comparison of past and present patterns. Unlike today, where a pointed seasonality characterizes the regional climate in this area, the Paleogene climate was equable and our palaeobotany-derived CMMT and WMMT data point to a very flat gradient of a few degrees only, close to or even beyond the resolution limit of the method employed. Flat Paleogene temperature gradients at the global or continental scale have been reported earlier (e.g., Greenwood and Wing, 1995). As regards the specific regional aspect our data indicate that (1) the Sikhote-Alin Range obviously did not act as a barrier hindering the inland flow of cool air masses from the Pacific and causing warm summers in the leeward area. Moreover there is evidence that (2) the distribution of air pressure system during the cold season over eastern Eurasia and the related winter monsoon, today causing very low CMMTs in the inland, fundamentally differed from modern throughout the Paleogene (Takaya and Nakamura, 2005; Utescher et al., 2015).

By its yearly amount of precipitation (550–920 mm) Primory'e belongs to a zone with sufficient moisture and rainfall for forest vegetation. The greatest amount of precipitation, up to 800–900 mm, falls on the west coast, in the Sikhote-Alin Mountains, on both the eastern and western slopes. In that area, MAP exceeds potential evaporation. Less humid, especially in spring and summer, are the areas of the Khanka Plain, where, with MAP at 500–600 mm, potential evaporation locally exceeds this amount. The modern MAP pattern in the study area shown a very distinct decline from coastal to inland areas (ca. 300 mm), very high MAP of >1000 mm are confined to altitudinal areas in the northeast. Rainfall patterns of MPwet, MPwarm and MPdry have a similar structure, with MPwet ranging from ca. 50–200 mm, MPwarm from 76–140 mm, and MPdry from almost 0–50 mm indicating seasonal drought for some inland areas (Khramtsova, 1966b).

The precipitation reconstruction points to conditions considerably wetter than at present. According to our results, a distinct MAP increase in the study area occurred in the early Eocene and persists throughout the Eocene and Oligocene. High Paleogene precipitation around the globe (i.e., North and South America, Australia, Antarctica, China) is consistent with high Eocene atmospheric humidity, which would have contributed significantly to polar, and global, Eocene warming (Greenwood and Huber, 2011). In the earlier Paleogene, monthly precipitation values in general are high when compared to modern conditions, broadly in accordance with the high temperatures (see above), and consistent with the general trend observed elsewhere in Eurasia from coeval records (e.g., Utescher et al., 2009; Bruch et al., 2011; Liu et al., 2011; Quan et al., 2011).

In the Paleogene of Primory'e, precipitation not only was at a higher level in general compared to present-day (Fig. 4H–N, 6A–N), the pattern of regional rainfall fundamentally differed, and this holds for all studied variables: MAP, MPwet, and MPdry. As far as data are available it is shown that the inland region (Kankha Plain) and the south of Primory'e were significantly more humid than today. In the early Eocene reconstruction it is shown that inland precipitation even exceeded the values obtained from the sites presently located on the Pacific coast and therefore receiving higher rainfall. Except for the early Paleocene (MAP, MPdry) and the late Paleocene (MAP, MPwet, MPdry), there is no evidence for raised precipitation caused by an orographic gradient in the area of the present Sikhote-Alin Range. Hence it can be concluded that in the Paleogene, elevation of this volcanic complex was considerably lower. Also it can be inferred from the observed rainfall patterns that the main flow direction of humid air masses was from the south and southwest where the Paleogene values are among the highest (early and late Eocene, early Oligocene). This Paleogene pattern was possibly related to a monsoonal type circulation and enhanced flow of humid air masses, due to an overall flatter morphology of the East Asian coastal areas. A direct impact of the Pacific on coastal areas of Primory'e as presently evident from the regional precipitation pattern is not visible in the Paleogene gradients. This is explained by the fact that the Paleogene coast line was located several hundred kilometers to the East (Fig. 3).

5.3. Time series

The Paleogene temperature evolution is best known from marine archives. Sea surface temperature (SST) levels in the Cenozoic were highest during the Paleocene–Eocene Thermal Maximum (PETM) and Eocene Thermal Maximum 2 (Wing et al., 2005; Zachos et al., 2008), and then decreased to a longer-lived climatic optimum in the middle Eocene (MECO), followed by an "ice-house" with small ephemeral ice-sheets in the early Oligocene (Zachos et al., 2008; Eldrett et al., 2009). For the continental realm, quantitative palaeoclimate reconstructions are scarce and do not cover the entire time-span (Mosbrugger et al., 2005; Roth-Nebelsick et al., 2004; Quan et al., 2012; Utescher et al., 2015).

The temperature evolution over Primory'e during the Paleogene in general reflects the global trend. The fossil floras studied indicate major climate change and demonstrate the general climate cooling during the Paleogene (Zachos et al., 2008). The high MAT obtained in the late Paleocene (17.3/13.1–21.4 °C) may be related to the globally high temperature level that existed at the time of the PETM while the high MAT recorded in the middle Eocene (17.4/14.7–20.2 °C) is connected to the MECO. The cooling in the late Eocene coincides with a coeval trend in the oxygen isotope record and the buildup of Antarctic ice sheets (Zachos et al., 2008). The cooling is most striking regarding CMMT, while the same trend from the MAT record is less distinct (Fig. 7A). Thus, the present temperature reconstruction based on a total of 39 sites confirms the results obtained by Utescher et al. (2015) based on five floras from southern Primory'e, for the time-span in which both records overlap (middle Eocene to late Oligocene). Compliance of the Primory'e temperature evolution since the middle Eocene and a coeval Atlantic continental record (Lusatian Basin, Lower Rhine Basin, Germany) was highlighted in Utescher et al. (2015). Another Paleogene temperature record, composed from floras recovered at Jiayin, Fushun, and Shulan, is available for northeast China and thus from the closer neighborhood of our study area (Quan et al., 2012). Features in common are the declining trend from the Paleocene to the early Eocene (CMMT), and a very warm late Eocene with subsequent distinct cooling (MAT, CMMT). The very warm late Eocene is not reflected in the global climate evolution and thus may represent a regional signal, possibly related to the initial opening of the Sea of Japan. A distinct cooling trend reported from the Fushun record (Quan et al., 2012) is not resolved in our data. According to Quan et al. (2012), among the estimated terrestrial temperature parameters, MAT slightly changed with an overall declining trend in the Eocene, from 15.6–21.1 °C, to 17–23.9 °C, followed by 15.7–18.6 °C. However, the winter temperature dramatically decreased from 12.6–13.3 °C in the middle Eocene to 7.7–8.1 °C in the late Eocene, while the summer temperature remained almost the same with the value of 24.7–28.1 °C, 26–27.9 °C, and 26.4–27.9

°C respectively in the early, middle, and late Eocene. All these data are within the range of our present reconstruction or slightly higher (CMMT), respectively, which coincides with the latitude of Fushun, lower by several degrees.

Given the fact that there is a strong correlation of temperature and rainfall (cf. section *5.2.*), precipitation evolution in the Paleogene of Primory'e about follows the temperature trends, with all precipitation variables showing a pointed increasing trend from the Paleocene towards the Eocene and, thereafter, minor decline in the Oligocene. The declining trend from the Lutetian to Chattian (~1300 to ~1200 mm) was already reported in Utescher et al. (2015) base on sites of southern Primory'e and can be confirmed here based on a larger set of palaeofloras, while the pointed decline of MPwet by over 50 mm in the time from the Priabonian to Chattian was apparently minor when analyzing a larger plant record. Precipitation data from the adjacent continental parts in northeast China, with MAP from 735 to 1362 mm, high MPwet (means from 126 to 226 mm) and low MPdry (means from 17 to 43 mm) (Quan et al., 2012) point to a comparable evolution.

The Eocene precipitation increase in Primory'e was possibly connected to the presence of first water bodies existing in the area of the later evolving Japanese back arc basin as evidenced from the existence of late Eocene to Oligocene marine sediments along the eastern coast of the Sea of Japan (Kano et al., 2007). Another possible explanation is a link to the onset of monsoon type circulation (cf. section *5.4.*).

5.4. Climate seasonality, monsoon intensity

Primory'e, presently is under the influence of the EAM (Zhang and Wang, 2008), The modern regime of temperature and humidification of the territory is characterized by a pronounced seasonality. Today, MART is at the very high level of 34.4 °C, at a mean, and MARP is around 135 mm. Summer and autumn precipitation account for about 70 % of the MAP, while rainfall in winter amounts to 10 % only (Khramtsova, 1966a, b). The modern RMPwet and RMPdry calculated based on the mean values using station data of Vladivostok (Müller and Hennings, 2000; New et al., 2002), are 0.201 and 0.014, respectively (Table 3).

As mentioned above, all our climatic data suggest a strong seasonal control of the Paleogene climate of Primory'e (Table 3). The higher past WMMT coupled with significantly higher CMMT indicate a lower than present seasonality of temperature during the Paleogene, however, MART gradually increased from ca 15 °C in the early Paleocene to ca. 20 °C the late Oligocene. It should be noted that the past WMMT was only slightly higher (3.7–5.3 °C) compared to the present-day value. At the same time, the past CMMT was significantly higher compared to the present-day value: 22.6 °C in the early Paleocene and 18.2 °C in the late Oligocene.

The pronounced seasonality of precipitation (MPwet 172–209 mm; MPdry as 30–45 mm) of the Paleogene climate of Primory'e gradually increased from ca. 130 mm in the early Paleocene to ca. 170 mm in the late Oligocene. Thus, the early Paleocene MARP was close to the modern but started to increase from the late Paleocene on, even attaining a higher-than-present level. However, the higher past MPwet coupled with distinctly higher MPdry indicate that, during the Paleogene, the climate of Primory'e was more humid, in general.

The calculated proportions of MPwet and MPdry to yearly precipitation (MPwet: 0.147 in the early Paleocene to 0.172 in the late Oligocene; MPdry: 0.026/0.035) are almost twice as high compared to present-day (Table 3) and suggest that both, EASM and EAWM were considerably weaker. Utescher et al. (2015) also suggest a seasonal control of precipitation in the Cenozoic climate of Primory'e, According to this reconstruction, the RMPwet stayed well below the modern value until the earlier part of the late Miocene. The high RMPwet obtained by Utescher et al. (2015) for the Messinian and Piacenzian levels point to a comparatively late increasing impact of the EAM on the study area, with the Calabrian date being an outlier in this trend, indicating lower monsoon intensity at that time (Bondarenko et al., 2013).

There are vast 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 and Wang, 2005), and paleoenvironmental 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 and Goldner, 2012; Hoorn et al., 2012; Quan et al., 2012, 2014; Wang et al., 2013; Licht et al., 2014; Bosboom et al., 2015). The seasonal precipitation patterns we reconstruct support the assumption of a Paleogene monsoon. The strong pulse observed in RMPwet values of our late Oligocene samples is possibly related to coeval tectonic deformation and rapid exhumation in the northwestern Tibetan Plateau and the Pamir Plateau, starting in the late Oligocene (Tada et al., 2016).

5.5. Paleogene Larix record – evidence for altitudinal vegetation zones?

As mentioned above, *Larix* was excluded from climatic calculations for the Paleogene of Primory'e, because it formed a cold outlier when present in the fossil record, but fossil evidence for this genus may provide valuable clues about the regional Paleogene topogaphy. At present, larch grows in boreal, cold temperate regions of the Northern Hemisphere, including Europe, Asia, and North America (Kharkevich, 1989; FNA Editorial Committee, 1993; Wu and Raven, 1999) and thus, ist presence in the warm temperate phytocoenoses existing in the Palaeogene of Primory´e is in need of further considerations. At present, larch occurs from the Pacific coast of Primory'e to the tree line at higher altitudes, however, in the southwest of the study area the genus is less common, whereas in the northeast it is one of the major forest-forming trees (Kharkevich, 1989). Larch grows at the (0)300–4300(4600) m a.s.l., mainly in mountains, hills, slopes, rare in swamps, valleys and lowland subarctic plains (Kharkevich, 1989; FNA Editorial Committee, 1993; Wu and Raven, 1999).

Paleogene floras of Primory'e containing larch remains are listed in the Table 4. While *Larix* was absent from the early Paleocene floras the earliest records of *Larix* pollen are known from the late Paleocene floras in the northeast of the territory. In the Eocene, *Larix* pollen and even macro-remains are reported from various sites located in the north and northeast of the study area while for the middle Eocene *Larix* pollen are also described from several localities of the southwest.

The concentration of *Larix* records in the northeast of the study area was probably related to uplift processes in the area of the present-day Sikhote-Alin Range (Fig. 3) that were connected with coeval volcanic activities. The elevation may have exceeded 500 m a.s.l. (Akhmetiev et al., 2009), and it is assumed that this was already sufficient for the manifestation of altitudinal vegetation zones (Blokhina, 1987). Thus, it may be assumed, that in the Paleogene, the larch was, most likely, an element of intrazonal altitudinal vegetation. Since the early Oligocene and in the Neogene (cf. Bobrov, 1972; Blokhina, 1999, 2012), *Larix* became more abundant and widespread in the pollen record of Primory´e, probably linked to the observed general cooling trend and/or uplift processes.

6. Conclusions

The exceptionally rich palaeobotanical record of Primory'e holds the key for reconstructing the detailed Paleogene regional climate evolution in space and time, and to trace potentially monsoon-induced patterns. The high diversity of the palaeofloras and up-to-date taxonomy result in useful climatic interpretations. Our climate maps for the first time allow quantifying climate change in space and time on the Pacific side of Eurasia over the past 42 Myr. The climate curves of Primory'e are consistent with major global trends, indicate major climate changes and demonstrate the general climate cooling during the Paleogene. The cooling is most striking regarding CMMT, the same trend from the MAT record is less distinct. Our temperature reconstruction for the Palaeogene of Primory'e points to significantly warmer conditions than at present. All inferred temperature patterns consistently indicate that the climate was warmest throughout the Eocene and in the southeast of the study area. The high temperature anomalies, being most distinct as regards the cold season, are in line with previous reconstructions of mid- to higher latitude continental temperature under the Paleogene greenhouse conditions based on various proxies. At the same time, flat Paleogene temperature gradients of Primory'e have been related to the specific regional aspects (1) the Sikhote-Alin Range obviously did not act as a barrier hindering the landward flow of cool air masses from the Pacific and causing warm summers in the leeward area and (2) the distribution of air pressure system during the cold season over eastern Eurasia and the related winter monsoon fundamentally differed from modern in the throughout Paleogene. The precipitation reconstruction points to conditions considerably wetter than at present. According to our results, a distinct increase in MAP is observed in the early Eocene and persists throughout the Eocene and Oligocene. Moreover, in the Paleogene of Primory'e, precipitation not only was at a higher level in general compared to present-day, the pattern of regional rainfall fundamentally differed, and this holds for all studied variable and shows that the inland region (Khanka Plain) and the south of Primory'e were significantly more humid than today. There is no evidence for raised precipitation caused by the modern orographic gradient of the Sikhote-Alin Range. It can be concluded that in the Paleogene, elevation of this volcanic complex was considerably lower and be inferred from the observed rainfall patterns that the main flow direction of humid air masses was from the south and southwest where the Paleogene values are among the highest. This Paleogene pattern was possibly related to a monsoon type circulation and enhanced flow of humid air masses, due to an overall flatter morphology of the East Asian coastal areas.

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Figure captions

Figure 1. Map over Primory'e showing the location of the studied Cenozoic basins. Dotted line: contours of the basins after Pavlutkin and Petrenko (2010). 1 – Khasanskii, 2 – Ambinskii, 3 – Artemo-Tavrichanskii, 4 – Shkotovskii, 5 – Pushkinskii, 6 – Vanchinskii, 7 – Ivanovskii, 8 – Pavlovskii, 9 – Snegurovskii, 10 – Chernyshevskii, 11 – Zerkal'nenskii, 12 – Tur'erogskii, 13 – Krylovskii, 14 – Kemskii, 15 – Nizhnebikinskii, 16 – Amginskii, 17 – Maksimovskii, 18 – Svetlovodnenskii, 19 – Ozero Toni.

Figure 2. Regional stratigraphic chart for the Paleogene sediments of some Cenozoic basins of Primory'e considered in this study (modified from Pavlutkin and Petrenko, 2010), tied to the international standard (Cohen et al., 2013). Details on the palaeofloras are given in Table 1. BgFm – Bogopol'skaya Formation, TkhFm – Takhobinskaya Formation, TdFm – Tadushinskaya Formation, SuFm – Suvorovskaya Formation, KzFm – Kuznetsovskaya Formation, UgFm – Uglovskaya Formation, TjFm – Tujanovskaya Formation, NdFm – Nadezhdinskaya Formation, KhFm – Khasanskaya Formation, UdFm – Ust'-davydovskaya Formation, SvFm – Svetlinskaya Formation, SbFm – Salibezskaya Formation, FtFm – Fatashinskaya Formation, PvFm – Pavlovskaya Formation, VzFm – Voznovskaya Formation, MsFm – Maksimovskaya Formation.

Figure 3. Palaeogeographic reconstruction of Primory'e for 45 Ma. PP – Pacific Plate, OP – Okhotsk Plate, EASM – East Asian Summer Monsoon, EAWM – East Asian Winter Monsoon.

Figure 4. MAT (A) and MAP (B) in the Paleogene of Primory'e in comparison with modern: a – late Oligocene, b – early Oligocene, c – late Eocene, d – middle Eocene, e – early Eocene, f – late Paleocene, g – early Paleocene.

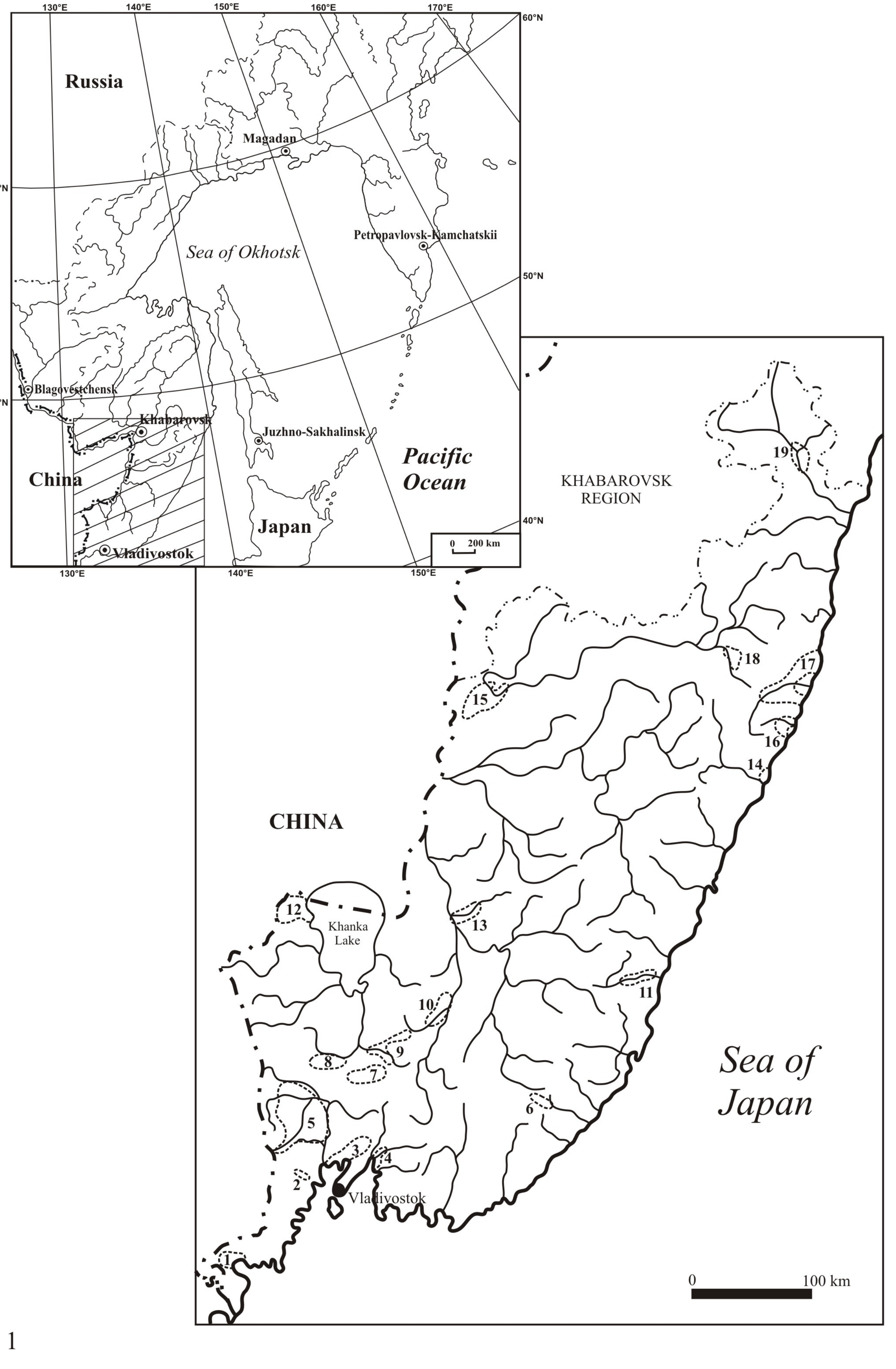
Figure 5. CMMT (A) and WMMP (B) in the Paleogene of Primory'e in comparison with modern: a – late Oligocene, b – early Oligocene, c – late Eocene, d – middle Eocene, e – early Eocene, f – late Paleocene, g – early Paleocene.

Figure 6. MPwet (A) and MPdry (B) in the Paleogene of Primory'e in comparison with modern: a – late Oligocene, b – early Oligocene, c – late Eocene, d – middle Eocene, e – early Eocene, f – late Paleocene, g – early Paleocene.

Figure 7. MAT records (A) next to the composite deep-sea benthic foraminiferal oxygen isotope record after Zachos et al. (2008) (B), CMMT (C) and WMMT (D) records based on means of CA intervals for all palaeofloras studied.

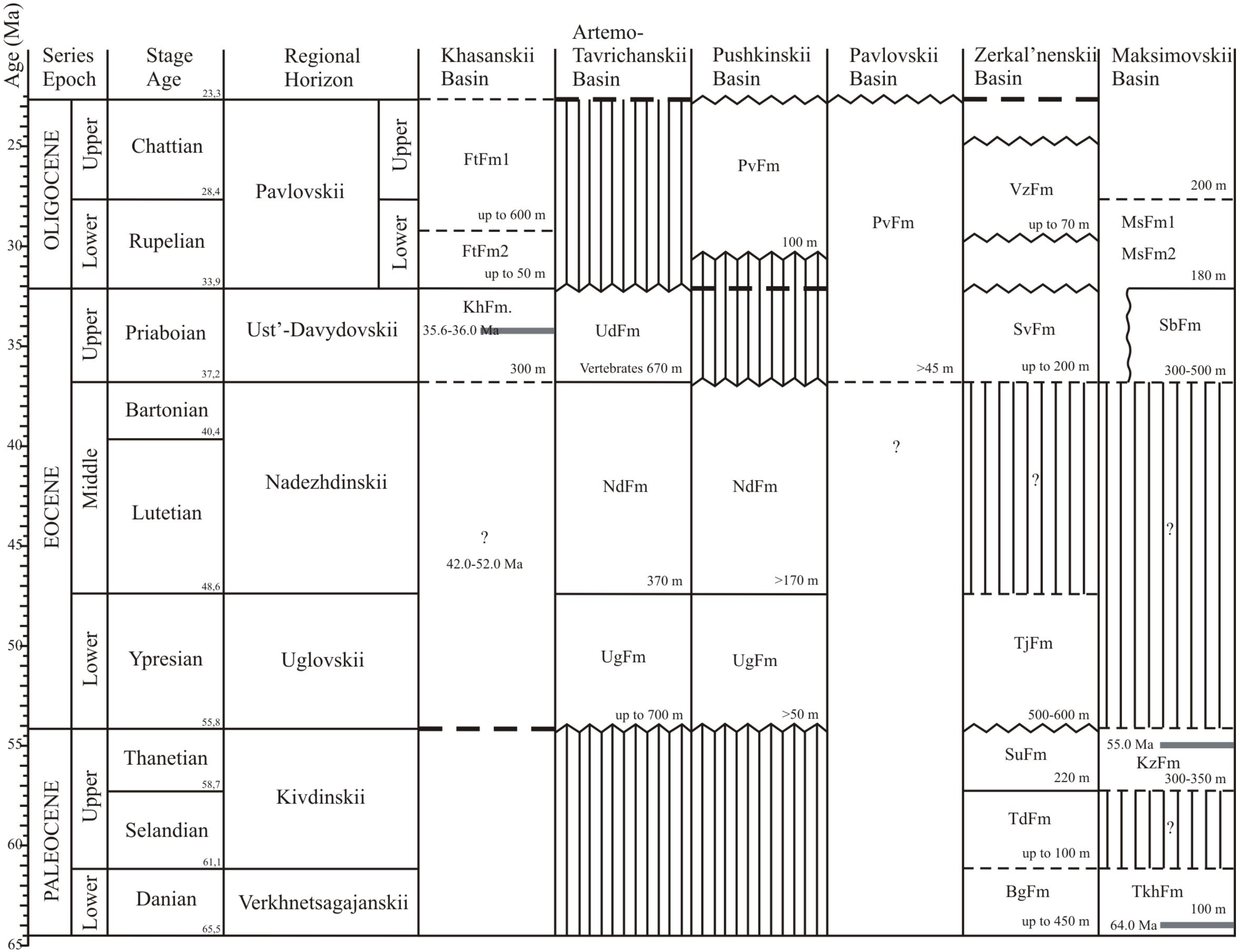
Figure 8. MAP (A), MPdry (B), MPwet (C) and MPwarm (D) records based on means of CA intervals for all palaeofloras studied (cf. Fig. 7 for legend).

Figure 9. MART (A), MARP (B), RMPwet (C) and RMPdry (D) records based on means of CA intervals for all palaeofloras studied (cf. Fig. 7 for legend).



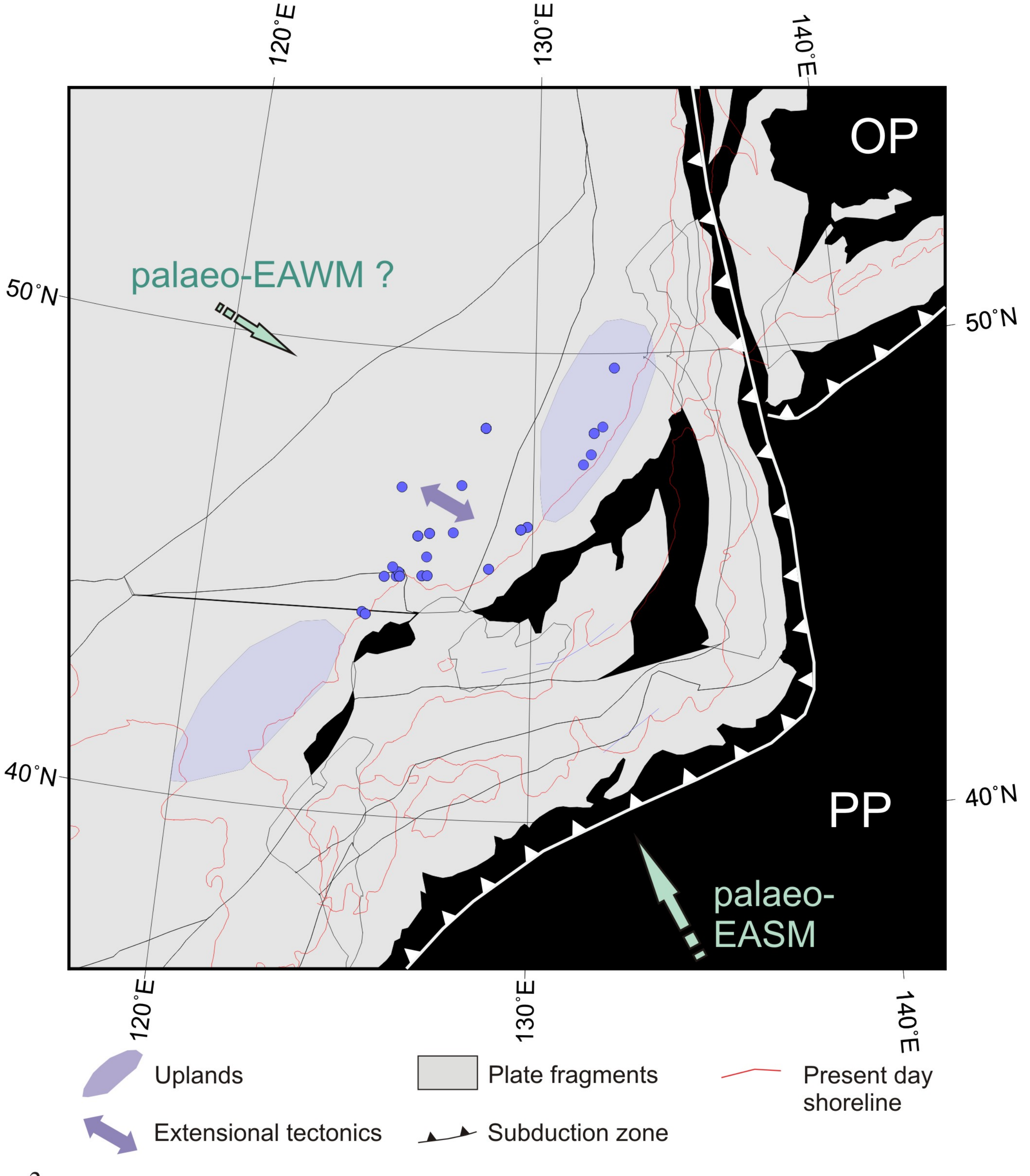
130°E
140°E
150°E
160°E
170°E
60°N
Russia
Magadan
60°N
Sea of Okhotsk
Petropavlovsk-Kamchatskii
50°N
Blagovestchensk
50°N
Khabarovsk
Juzhno-Sakhalinsk
Pacific Ocean
China
Japan
40°N
Vladivostok
0 200 km
130°E
140°E
150°E
KHABAROVSK REGION
19
18
17
15
16
14
CHINA
12
Khanka Lake
13
11
10
9
8
7
Sea of Japan
6
5
3
4
2
Vladivostok
1
0
100 km

1

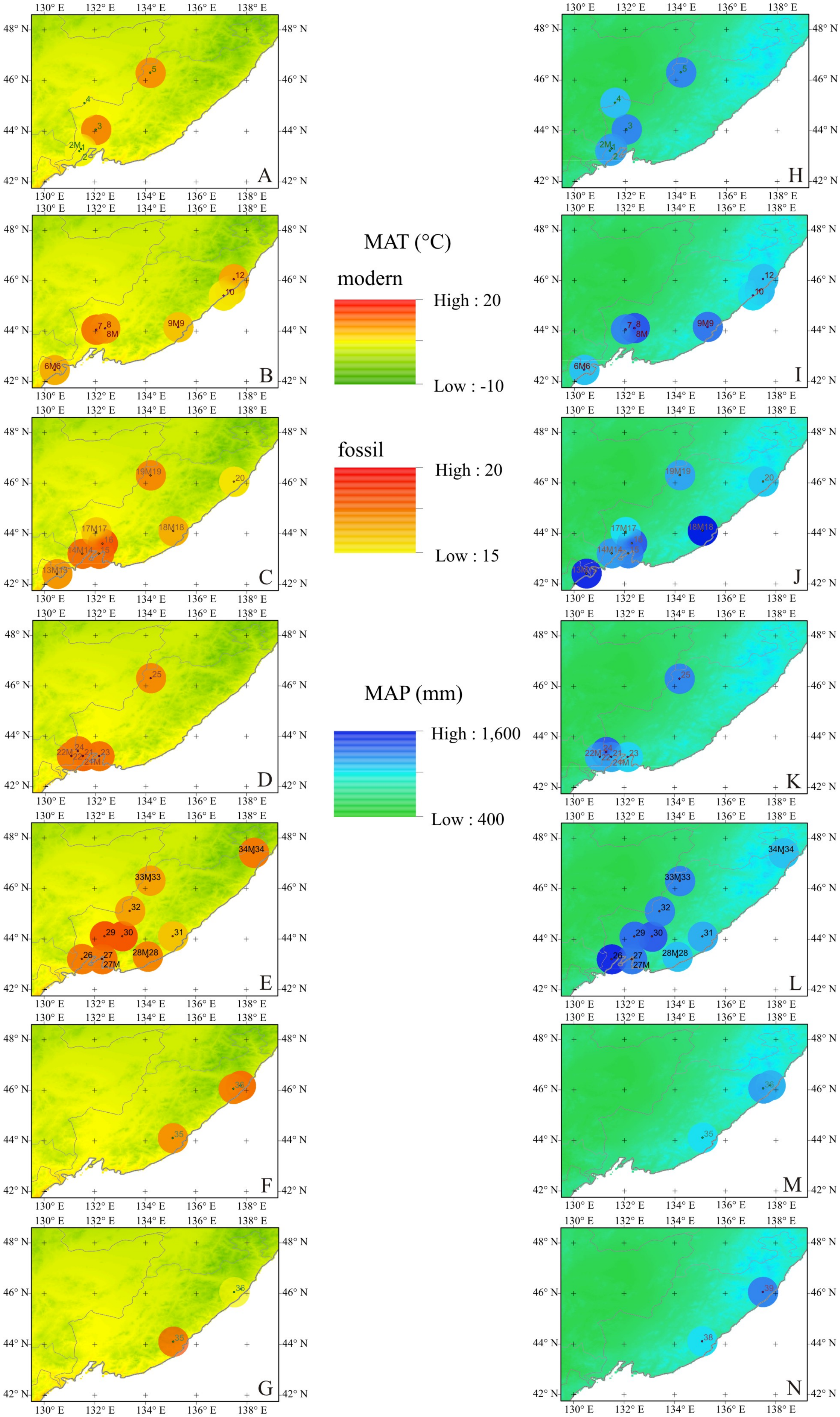


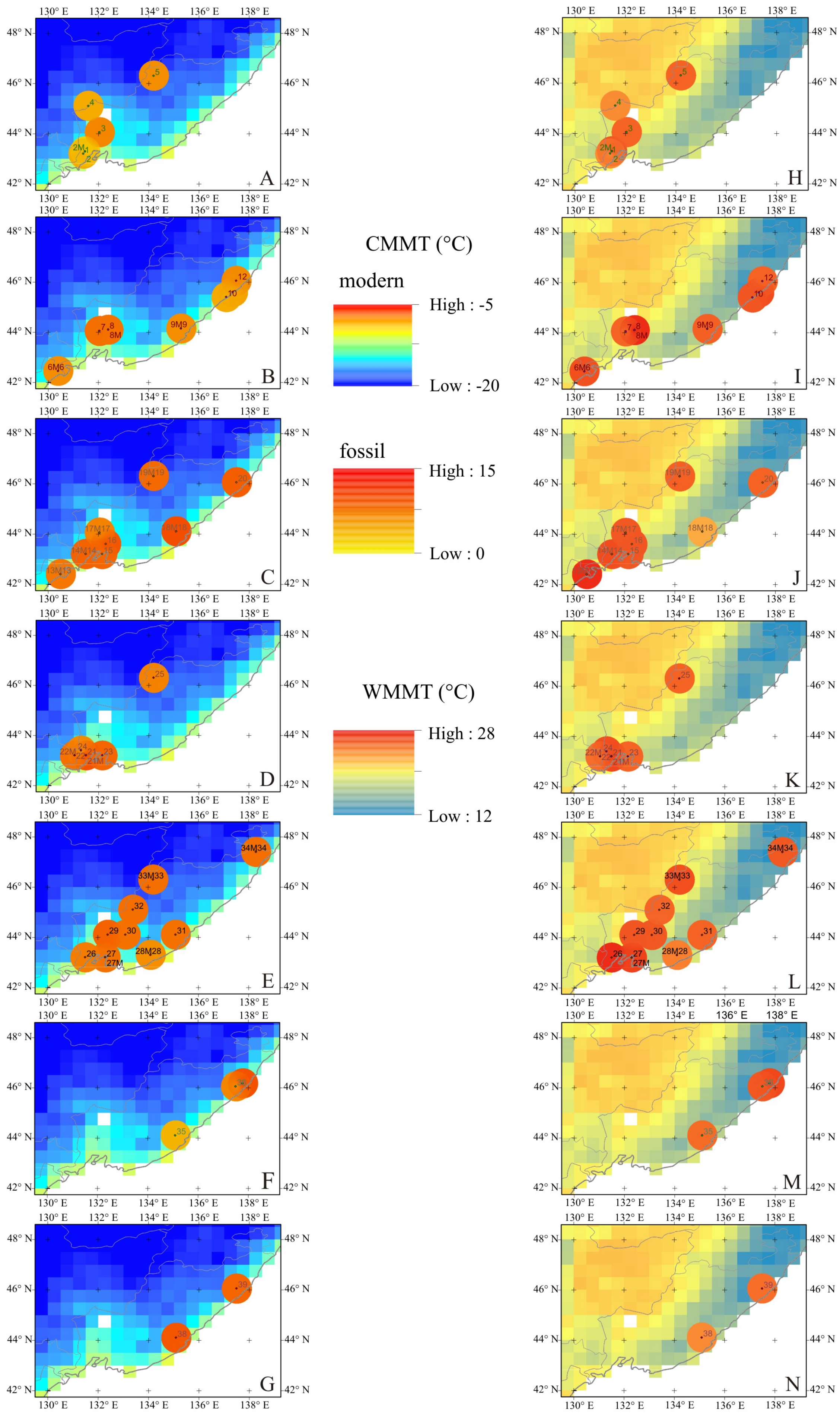
Age (Ma)
Series Epoch
Stage Age
Regional Horizon
Khasanskii Basin
Artemo-Tavrichanskii Basin
Pushkinskii Basin
Pavlovskii Basin
Zerkal'nenskii Basin
Maksimovskii Basin
OLIGOCENE
EOCENE
PALEOCENE
Upper
Lower
Middle
Chattian
Rupelian
Priaboian
Bartonian
Lutetian
Ypresian
Thanetian
Selandian
Danian
23,3
28,4
33,9
37,2
40,4
48,6
55,8
58,7
61,1
65,5
Pavlovskii
Ust'-Davydovskii
Nadezhdinskii
Uglovskii
Kivdinskii
Verkhnetsagajanskii
FtFm1
up to 600 m
FtFm2
up to 50 m
KhFm.
35.6-36.0 Ma
300 m
?
42.0-52.0 Ma
UdFm
Vertebrates 670 m
NdFm
370 m
UgFm
up to 700 m
PvFm
100 m
NdFm
>170 m
UgFm
>50 m
PvFm
>45 m
?
VzFm
up to 70 m
SvFm
up to 200 m
?
TjFm
500-600 m
SuFm
220 m
TdFm
up to 100 m
BgFm
up to 450 m
200 m
MsFm1
MsFm2
180 m
SbFm
300-500 m
?
55.0 Ma
KzFm
300-350 m
?
TkhFm
100 m
64.0 Ma
25
30
35
40
45
50
55
60
65

2


120°E
130°E
140°E
OP
50°N
palaeo-EAWM ?
40°N
PP
palaeo-
EASM
Uplands
Extensional tectonics
Plate fragments
Subduction zone
Present day
shoreline

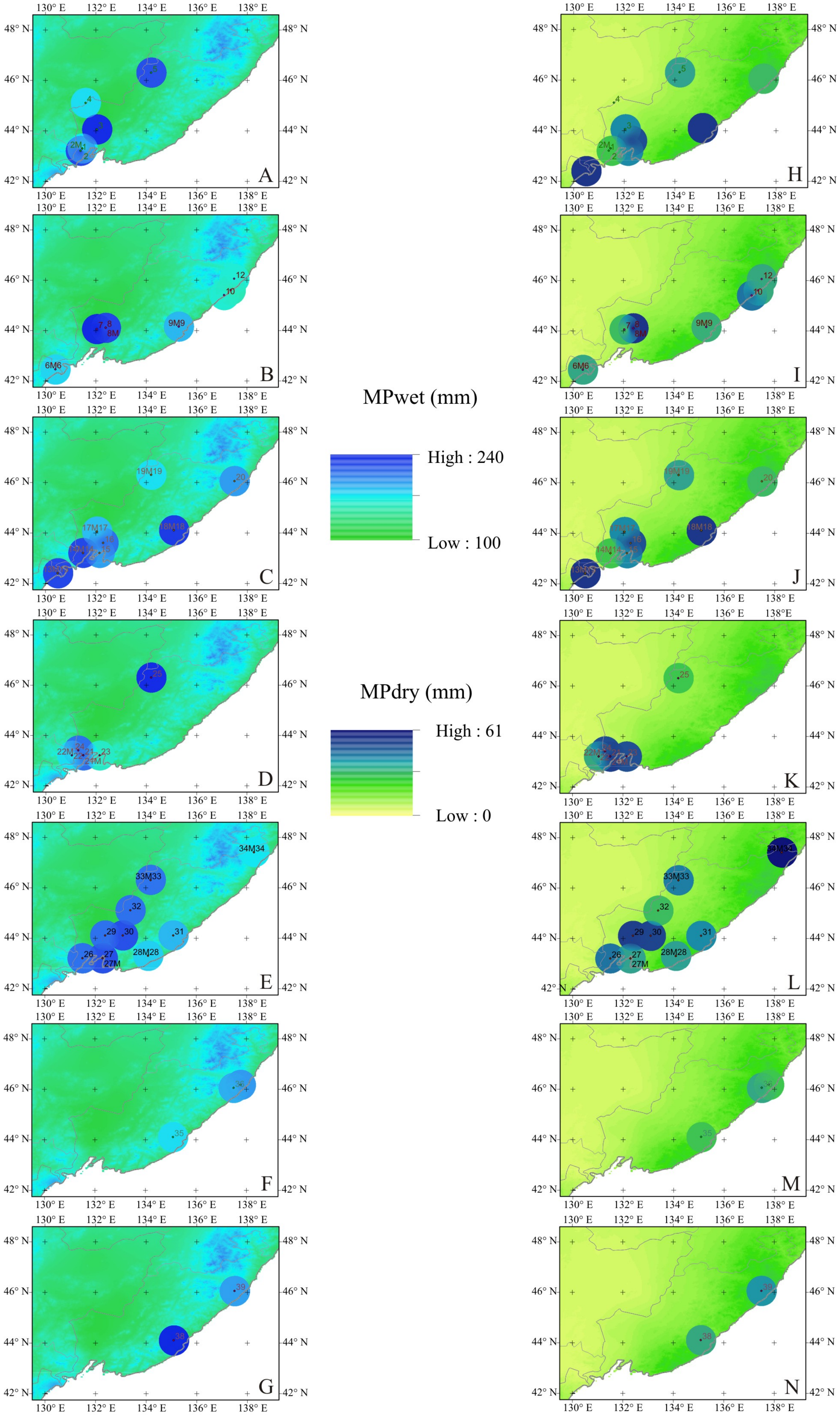
3

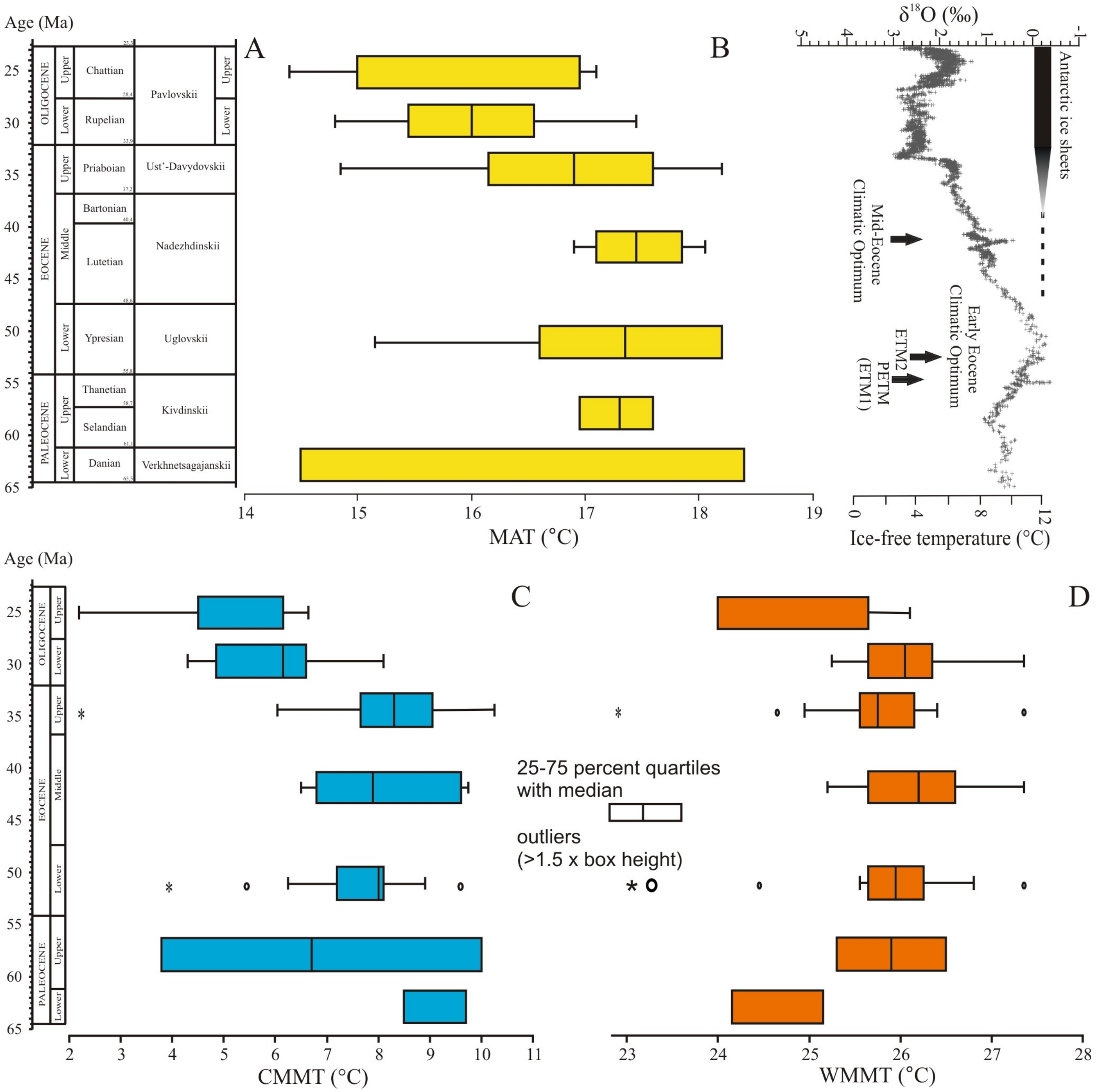

MAT (°C)
modern
High : 20
Low : -10
fossil
High : 20
Low : 15
MAP (mm)
High : 1,600
Low : 400
A
B
C
D
E
F
G
H
I
J
K
L
M
N



CMMT (°C)
modern
High : -5
Low : -20
fossil
High : 15
Low : 0
WMMT (°C)
High : 28
Low : 12
130° E
132° E
134° E
136° E
138° E
42° N
44° N
46° N
48° N
A
B
C
D
E
F
G
H
I
J
K
L
M
N

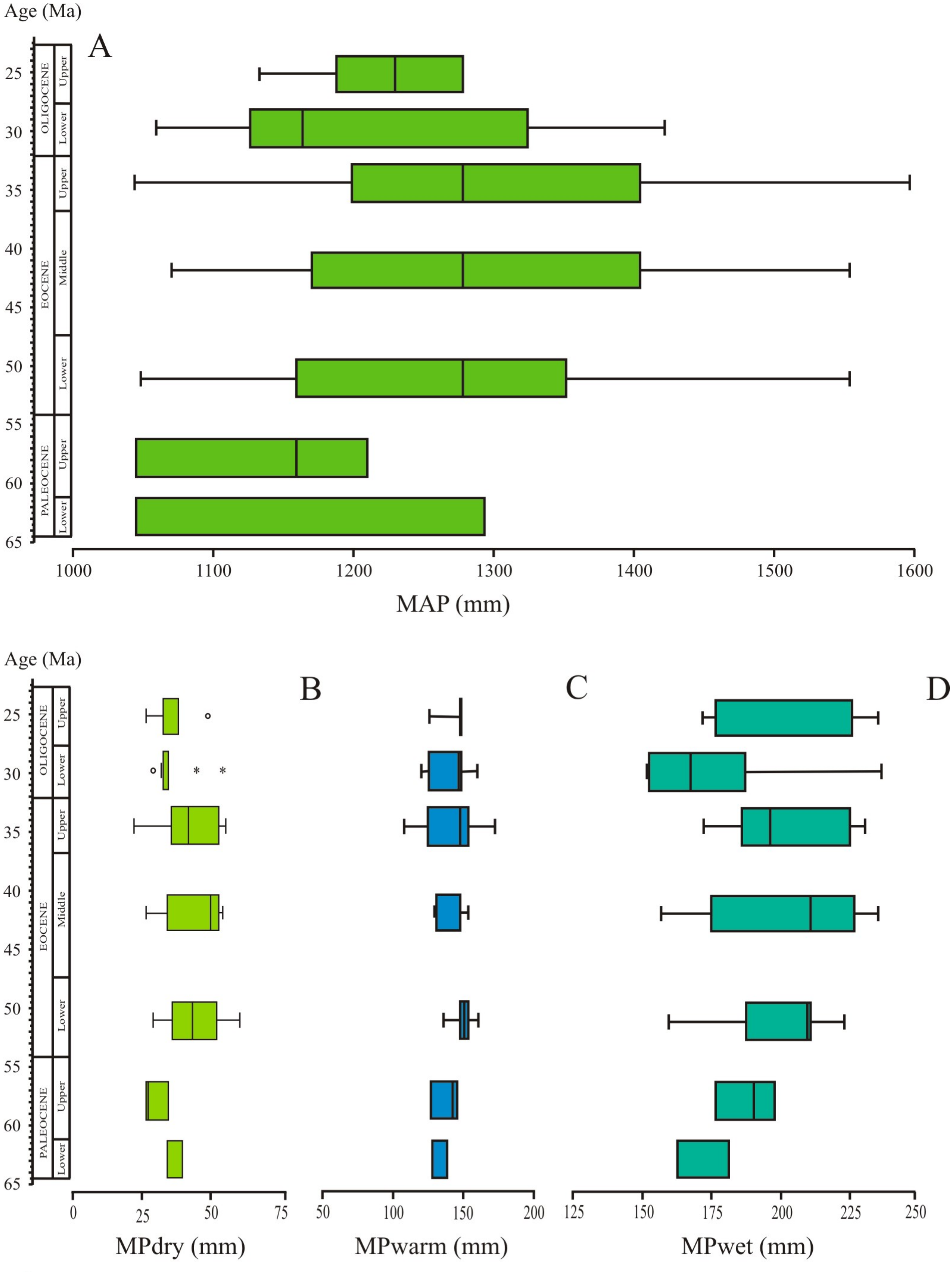
5


MPwet (mm)
High : 240
Low : 100
MPdry (mm)
High : 61
Low : 0
130° E
132° E
134° E
136° E
138° E
42° N
44° N
46° N
48° N
A
B
C
D
E
F
G
H
I
J
K
L
M
N

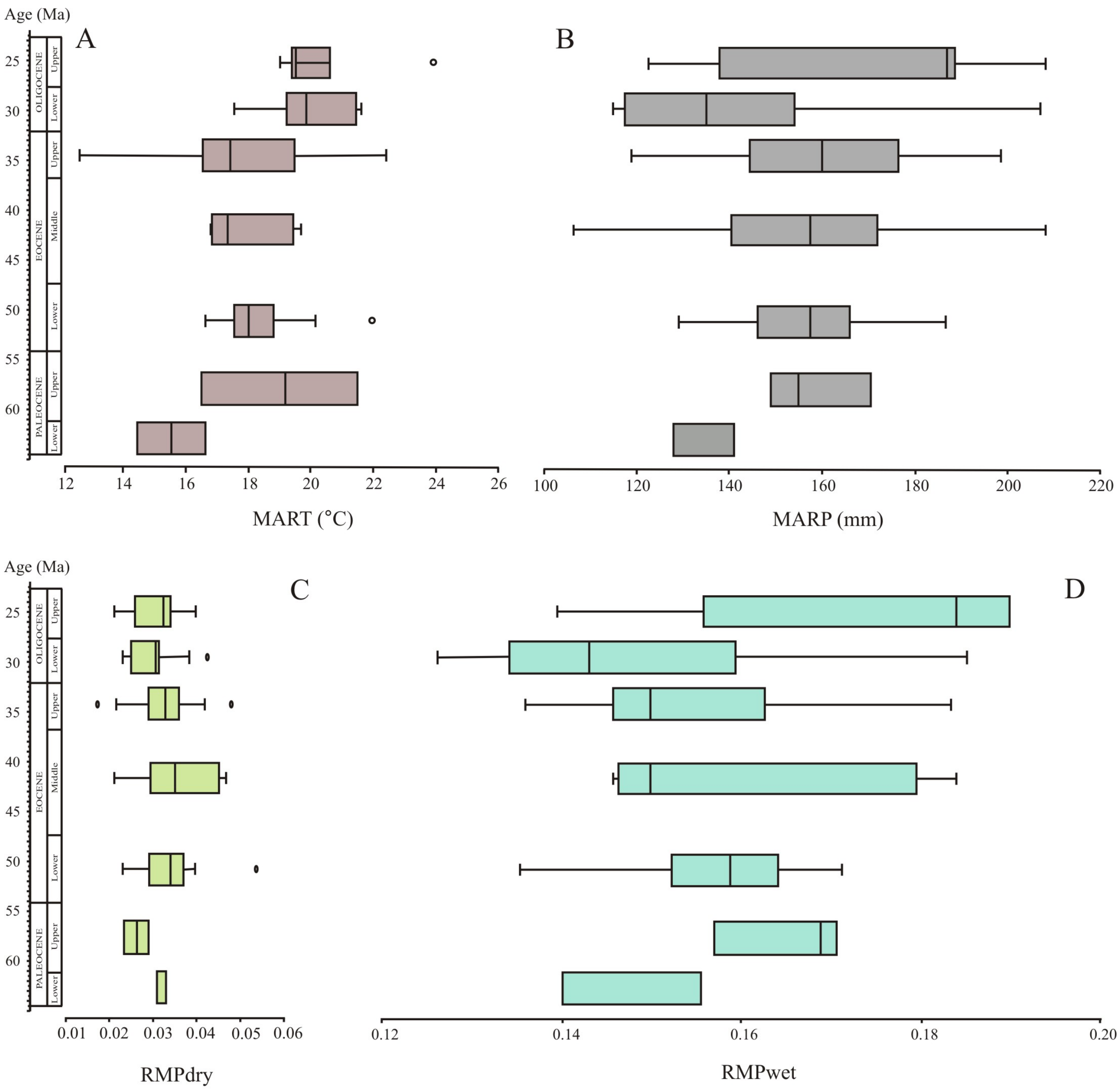


Age (Ma)
A
B
C
D
OLIGOCENE
EOCENE
PALEOCENE
Upper
Middle
Lower
Chattian
Rupelian
Priaboian
Bartonian
Lutetian
Ypresian
Thanetian
Selandian
Danian
Pavlovskii
Ust'-Davydovskii
Nadezhdinskii
Uglovskii
Kivdinskii
Verkhnetsagajanskii
MAT (°C)
δ18O (‰)
Antarctic ice sheets
Mid-Eocene Climatic Optimum
Early Eocene Climatic Optimum
ETM2
PETM (ETM1)
Ice-free temperature (°C)
25-75 percent quartiles with median
outliers (>1.5 x box height)
CMMT (°C)
WMMT (°C)

7


Age (Ma)
A
OLIGOCENE
EOCENE
PALEOCENE
Upper
Lower
Middle
25
30
35
40
45
50
55
60
65
1000
1100
1200
1300
1400
1500
1600
MAP (mm)
B
C
D
0
25
50
75
100
150
200
125
175
225
250
MPdry (mm)
MPwarm (mm)
MPwet (mm)

8


Age (Ma)
A
B
C
D
OLIGOCENE
EOCENE
PALEOCENE
Upper
Lower
Middle
25
30
35
40
45
50
55
60
12 14 16 18 20 22 24 26
MART (°C)
100 120 140 160 180 200 220
MARP (mm)
0.01 0.02 0.03 0.04 0.05 0.06
RMPdry
0.12 0.14 0.16 0.18 0.20
RMPwet

9

Table 1. Palaeofloras studied. P: palynofloras; L: leaf flora.

Stratigraphic level	Locality name	Lon	Lat	Type of flora	Fossil taxa / taxa with climate data	Basin, formation	Age, method of dating	References
1. Late Oligocene	1. Zanadvorovka	131.4	43.2	P	30/28	Ambinskii, analog of Pavlovskaya	Chattian, K/Ar dating (24.0 ± 3.0 Ma), palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010; Popov et al., 2007
	2. Pushkinskii9180	131.5	43.3	P L	30/28 28/26	Pushkinskii, Pavlovskaya	Chattian, palaeobotany (inter-regional correlation)	Pavlutkin et al., 2012
	3. Pavlovka9035-D	132.05	44.05	P	35/32	Pavlovskii, Pavlovskaya	Chattian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
	4. Turii Rog8	131.6	45.1	P	32/30	Tur'erogskii, analog of Pavlovskaya	Chattian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
	5. Luchegorsk6212	134.2	46.3	P	32/30	Nizhnebikinskii, Upper Coal	Chattian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
2. Early Oligocene	6. Kraskino9182, 9196	130.4	42.45	P L	71/63 161/148	Khasanskii, Nizhnefatashinskaya	Rupelian, palaeobotany (inter-regional correlation)	Pavlutkin et al., 2014
	7. Pavlovka9035-D	132.05	44.05	P	37/34	Pavlovskii, Pavlovskaya	Rupelian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
	8. Rettikhovka	132.4	44.1	P L	36/33 48/43	Snegurovskii, analog of Pavlovskaya	Rupelian, palaeobotany (inter-regional correlation)	Ablaev, 1977; Akhmetiev et al., 1973; Klimova et al., 1977; Pavlutkin, Petrenko, 1994, 2010
	9. Voznovo9206	135.3	44.15	P L	79/67 80/67	Zerkal'nenskii, Voznovskaya	Rupelian, palaeobotany (inter-regional correlation)	Pavlutkin et al., 2014
	10. Tikhii Kluch	137.1	45.4	L	49/39	Kemskii, Kizinskaya	Rupelian, palaeobotany (inter-regional correlation)	Akhmetiev, 1988; Rybalko et al., 1980; Varnavskii et al., 1988
	11. Amgu9302	137.36	45.6	L	62/57	Amginskii, Granatnenskaya	Rupelian, palaeobotany (inter-regional correlation)	Akhmetiev, 1988; Akhmetiev, Shyvareva, 1989; Klimova, 1981, 1988; Pavlutkin et al., 2014
	12. Maksimovka	137.5	46.05	L	81/71	Maksimovskii, Maksimovskaya	Rupelian, palaeobotany (inter-regional correlation)	Akhmetiev, 1988; Rybalko et al., 1980; Varnavskii et al., 1988
3. Late Eocene	13. Gladkaja17	130.5	42.4	P L	41/36 33/28	Khasanskii, Khasanskaya (= Nazimovskaya)	Priabonian, K/Ar dating (35.6-36.0 Ma), palaeobotany (inter-regional correlation)	Chatshin et al., 2013; Gromova, 1980; Pavlutkin, Petrenko, 1997, 2010; Pavlutkin et al., 2006; 2014
	14. Tavrichanka9142	131.5	43.2	P L	46/40 75/70	Artemo-Tavrichanskii, Ust'-davydovskaya	Priabonian, vertebrate fauna, palaeobotany (inter-regional correlation)	Flerov et al., 1974; Pavlutkin, 2007; Pavlutkin, Petrenko, 1993, 2010; Pavlutkin et al., 2006; Yanovskaya, 1954
	15. Shkotovo	132.15	43.2	P	26/22	Shkotovskii, Upper Coal Fm.	Priabonian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
	16. Ivanovka610	132.3	43.6	P	50/44	Ivanovskii, analog of Pavlovskaya	Priabonian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010

	17. Pavlovka9035-D	132.05	44.05	P L	50/43 25/21	Pavlovskii, Pavlovskaya	Priabonian, palaeobotany (inter-regional correlation)	Bolotnikova, 1993, 1994; Pavlutkin, Petrenko, 2010; Varnavskii et al., 1988
	18. Svetlyi	135.1	44.1	P L	14/13 22/16	Zerkal'nenskii, Svetlinskaya	Priabonian, palaeobotany (inter-regional correlation)	Mikhailov et al., 1989; Pavlutkin, Petrenko, 2010
	19. Luchegorsk	134.2	46.3	P L	61/48 56/47	Nizhnebikinskii, Bikinskaya	Priabonian, palaeobotany (inter-regional correlation)	Ablaev et al., 2006; Bolotnikova, Sedykh, 1987; Koshman, 1964; Kundyshev, Verkhovskaya, 1989
	20. Salibeza	137.5	46.05	L	48/38	Svetlovodnenskii, Salibezskaya	Priabonian, palaeobotany (inter-regional correlation)	Klimova, Tsar'ko, 1989; Varnavskii et al., 1988
4. Middle Eocene	21. Vol'no-Nadezhdinskoe	131.5	43.2	P L	59/49 25/20	Artemo-Tavrichanskii, Nadezhdinskaya	Bartonian, palaeobotany (inter-regional correlation)	Akhmetiev et al., 1978; Pavlutkin, 2007; Pavlutkin, Petrenko, 1993, 2010
	22. Bolotnaja	131.05	43.2	P L	45/41 75/70	Artemo-Tavrichanskii, Nadezhdinskaya	Lutetian, palaeobotany (inter-regional correlation)	Ablaev, 2000; Ablaev, Akhmetiev, 1977; Akhmetiev, 1993; Kundyshev, Petrenko, 1987; Pavlutkin, 2007; Pavlutkin, Petrenko, 2010
	23. Shkotovo	132.15	43.2	P	31/27	Shkotovskii, Nadezhdinskaya	Middle Eocene, palaeobotany (inter-regional correlation)	Baskakova, Gromova, 1982
	24. Terekhovka	131.3	43.4	P	44/39	Pushkinskii, Nadezhdinskaya	Middle Eocene, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
	25. Luchegorsk540, 541	134.2	46.3	P	33/29	Nizhnebikinskii, Luchegorskaya	Middle Eocene, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
5. Early Eocene	26. Tavrichanka9142	131.5	43.2	P	58/48	Artemo-Tavrichanskii, Uglovskaya	Ypresian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
	27. Smolyaninovo	132.3	43.2	P L	56/48 42/39	Shkotovskii, Uglovskaya	Ypresian, palaeobotany (inter-regional correlation)	Baskakova, Gromova, 1979, 1984; Pavlutkin, Petrenko, 2010; Tatshi et al., 1996; Varnavskii et al., 1988; Verkhovskaya, Kundyshev, 1989
	28. Kluch Ugolnyi	134.1	43.3	P L	19/16 20/15	Vanchinskii, analog of Uglovskaya	Ypresian, palaeobotany (inter-regional correlation)	Chekryzhov et al., 2010; Pavlutkin, Petrenko, 2010
	29. Rettikhovka	132.4	44.1	P	56/46	Snegurovskii, analog of Uglovskaya	Ypresian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
	30. Arsen'evka	133.1	44.1	P	57/44	Chernyshevskii, analog of Uglovskaya	Ypresian, palaeobotany (inter-regional correlation)	Bolotnikova, 1988
	31. Kluch Tujanov	135.1	44.1	L	62/52	Zerkal'nenskii, Tujanovskaya	Ypresian, palaeobotany (inter-regional correlation)	Baskakova, Lepekhina, 1990; Varnavskii et al., 1988

	32. Krylovskii524	133.4	45.1	P	59/51	Krylovskii, Uglovskaya	Ypresian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
	33. Luchegorsk540, 541	134.2	46.3	P L	58/45 12/9	Nizhnebikinskii, Lower Coal Fm.	Ypresian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
	34. Ozero Toni	138.3	47.4	P L	32/30 44/36	Ozero Toni, Kizinskaya	Early Eocene, palaeobotany (inter-regional correlation)	Oleinikov, Klimova, 1977; Varnavskii et al., 1988
6. Late Paleocene	35. Ustinovka	135.1	44.1	L	25/22	Zerkal'nenskii, Tadushinskaya	Selandian, palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010
	36. Kluch Stolbikova	137.5	46.05	L	14/10	Maksimovskii, Kuznetsovskaya	Thanetian, K/Ar dating (55.0 Ma), palaeobotany (inter-regional correlation)	Pavlutkin, Petrenko, 2010; Varnavskii et al., 1988
	37. Kluch Kedrovyi	137.78	46.17	P	37/34	Maksimovskii, Kedrovskaya	Thanetian, palaeobotany (inter-regional correlation)	Varnavskii et al., 1988
7. Early Paleocene	38. Ustinovka	135.1	44.1	L	31/26	Zerkal'nenskii, Bogopol'skaya	Danian, palaeobotany (inter-regional correlation)	Ablaev et al., 2005; Krasilov, 1989
	39. Sobolevka	137.5	46.05	L	64/56	Maksimovskii, Takhobinskaya	Danian, K/Ar dating (64.0 Ma), palaeobotany (inter-regional correlation)	Akhmetiev, 1973, 1988; Borsuk, 1952

References and complete flora lists including Nearest Living Relatives used for climate calculations are given in Electronic Supplements 1-7.

Table 2. Mean values of climatic parameters for each palaeoflora and stratigraphic level.

Stratigraphic level	Locality name	Type of flora	MAT, °C	CMMT, °C	WMMT, °C	MAP, mm	MPwet, mm	MPdry, mm	MPwarm, mm
1. Late Oligocene	1. Zanadvorovka	P	15	4.5	24	1188	225	38	148
	2. Pushkinskii9180	P	15	4.5	24	1188	225	38	148
		L	14.4	2.2	26.1	1229	171	49	126
	3. Pavlovka9035-D	P	17.1	6.6	25.6	1278	235	27	147
	4. Turii Rog8	P	15	4.5	24	1132	176	38	148
	5. Luchegorsk6212	P	16.9	6.1	25.6	1278	221	33	147
	mean		**15.6**	**4.7**	**24.9**	**1216**	**209**	**37**	**144**
2. Early Oligocene	6. Kraskino9182, 9196	P	16.9	6.1	27.4	1163	151	35	125
		L	16.3	6.1	26.2	1118	179	35	125
	7. Pavlovka9035-D	P	17.4	8.2	25.6	1278	236	29	147
	8. Rettikhovka	P	16.9	7.9	27.3	1422	226	54	148
		L	14.8	8	25.8	1329	167	32	158
	9. Voznovo9206	P	16	6.1	27.3	1323	187	33	120
		L	15.4	4.3	25.2	1134	152	35	160
	10. Tikhii Kluch	L	15.2	4.4	26	1059	160	45	130
	11. Amgu9302	L	15.4	4.8	26.3	1137	152	34	146
	12. Maksimovka	L	16.5	7.8	25.6	1126	161	34	137
	mean		**16.1**	**6.4**	**26.3**	**1209**	**177**	**37**	**140**
3. Late Eocene	13. Gladkaja17	P	16.9	7.6	27.3	1554	226	54	147
		L	17.6	9.3	25.6	1307	212	22	154
	14. Tavrichanka9142	P	16.9	7.9	27.3	1554	226	45	147
		L	17.6	8.9	26.4	1227	225	26	147
	15. Shkotovo	P	17.6	8.5	25.9	1278	195	42	147
	16. Ivanovka610	P	18.2	9.6	26.1	1404	210	50	153
	17. Pavlovka9035-D	P	16.5	8.3	24.9	1373	187	40	160
		L	17.1	8.3	25.9	1044	186	41	108
	18. Svetlyi	P	16.3	10.2	22.9	1596	230	54	172
		L	14.8	2.2	24.6	1158	180	55	125
	19. Luchegorsk	P	16.1	6	25.5	1265	172	53	120
		L	17.2	8.3	25.7	1198	175	36	119

	20. Salibeza	L	17.5	9	25.6	1095	196	30	142
	mean		**17**	**8**	**25.7**	**1312**	**202**	**42**	**142**
4. Middle Eocene	21. Vol'no-Nadezhdinskoe	P	16.9	7.9	27.3	1554	226	54	147
		L	17.8	9.7	26.6	1172	210	53	134
	22. Bolotnaja	P	17.4	7.8	25.2	1170	175	34	153
		L	18	9.6	26.4	1284	199	43	134
	23. Shkotovo	P	17.5	8.6	25.6	1070	156	50	129
	24. Terekhovka	P	17.3	6.5	26.2	1404	210	50	147
	25. Luchegorsk540, 541	P	17.1	6.8	25.6	1278	235	27	147
	mean		**17.4**	**8.1**	**26.1**	**1276**	**202**	**45**	**142**
5. Early Eocene	26. Tavrichanka9142	P	17.3	7.2	27.3	1554	210	45	147
	27. Smolyaninovo	P	18.2	9.6	26.2	1295	192	44	153
		L	17.5	7.9	26.8	1315	222	36	148
	28. Kluch Ugolnyi	P	18.2	8	26	1422	210	56	148
		L	17.2	6.2	24.4	1122	180	37	136
	29. Rettikhovka	P	18.2	8.9	26.1	1351	210	53	154
	30. Arsen'evka	P	18.2	8	25.9	1404	223	52	153
	31. Kluch Tujanov	L	15.9	9	25.6	1170	187	41	160
	32. Krylovskii524	P	16.6	8.1	25.5	1278	211	29	153
	33. Luchegorsk540, 541	P	16.6	8.1	26.2	1278	209	43	147
		L	15.2	5.4	24.2	1159	198	36	150
	34. Ozero Toni	P	17.4	8.2	25.9	1126	173	60	136
		L	15.1	3.9	25.9	1047	159	30	152
	mean		**17.1**	**7.6**	**25.9**	**1271**	**199**	**43**	**149**
6. Late Paleocene	35. Ustinovka	L	16.9	3.8	25.3	1045	176	27	142
	36. Kluch Stolbikova	L	17.3	6.7	25.9	1210	190	35	145
	37. Kluch Kedrovyi	P	17.6	10	26.5	1158	197	27	127
	mean		**17.3**	**6.8**	**25.9**	**1138**	**188**	**30**	**138**
7. Early Paleocene	38. Ustinovka	L	18.4	9.7	24.1	1045	162	34	138
	39. Sobolevka	L	14.5	8.5	25.1	1293	181	40	128
	mean		**16.4**	**9.1**	**24.6**	**1169**	**172**	**37**	**133**

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.

Table 3. Temperature and precipitation seasonality parameters and related values.

Stratigraphic level	MATmean, °C	CMMTmean, °C	WMMTmean, °C	MART, °C	MAPmean, mm	MPwetmean, mm	MPdrymean, mm	MARP, mm	RMPwet	RMPdry
Modern	4.9	-13.5	20.9	34.4	721	145	10	135	0.201	0.014
Late Oligocene	15.6	4.7	24.9	20.2	1216	209	37	172	0.172	0.030
Early Oligocene	16.1	6.4	26.3	19.9	1209	177	37	140	0.146	0.031
Late Eocene	17	8	25.7	17.7	1312	202	42	160	0.154	0.032
Middle Eocene	17.4	8.1	26.1	18	1276	202	45	157	0.158	0.035
Early Eocene	17.1	7.6	25.9	18.3	1271	199	43	156	0.157	0.034
Late Paleocene	17.3	6.8	25.9	19.1	1138	188	30	158	0.165	0.026
Early Paleocene	16.4	9.1	24.6	15.5	1169	172	37	135	0.147	0.032

Means by stratigraphic level (calculated using coexistence interval means).

Table 4. Location of the Paleogene floras containing Larix in Primory'e.

Stratigraphic level	Locality name	Lon	Lat	Type of flora	References
1. Late Oligocene	Pavlovka9035-D	132.05	44.05	PF	Pavlutkin, Petrenko, 2010
2. Early Oligocene	Pavlovka9035-D	132.05	44.05	PF	Pavlutkin, Petrenko, 2010
	Rettikhovka	132.4	44.1	LF	Klimova et al., 1977
	Voznovo9206	135.3	44.15	PF, LF	Pavlutkin et al., 2014
	Tikhii Kluch	137.1	45.4	LF	Varnavskii et al., 1988
	Maksimovka	137.5	46.05	LF	Varnavskii et al., 1988
3. Late Eocene	Luchegorsk	134.2	46.3	PF	Bolotnikova, Sedykh, 1987
4. Middle Eocene	Bolotnaja	131.05	43.2	PF	Kundyshev, Petrenko, 1987
5. Early Eocene	Smolyaninovo	132.3	43.2	PF	Pavlutkin, Petrenko, 2010
	Arsen'evka	133.1	44.1	PF	Bolotnikova, 1988
	Luchegorsk540, 541	134.2	46.3	PF	Pavlutkin, Petrenko, 2010
	Ozero Toni	138.3	47.4	LF	Varnavskii et al., 1988
6. Late Paleocene	Kluch Kedrovyi	137.78	46.17	PF	Varnavskii et al., 1988
7. Early Paleocene	-	-	-	-	-