

Early Paleogene continental temperature patterns and gradients over eastern Eurasia

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ABSTRACT

Early Paleogene latitudinal continental temperature gradients along the Pacific coast of Eurasia are studied in time and space using the Coexistence Approach, for the first time applied on an extensive regional palaeobotanical record. The palaeobotanical data used in this reconstruction are compiled from literature resources on a total of 110 reasonably well-dated floras, including 79 palynofloras, 30 leaf floras and one carpoflora covering the early Paleocene (Danian) to early Eocene (Ypresian), i.e., a time-span of ca. 25 myr, in total. The palaeobotanical records originate from terrestrial deposits of 73 localities situated along the Pacific coast of Eurasia, including the Far East of Russia, Eastern Siberia, China, and Japan. Our results reveal very weak latitudinal temperature gradients during the early Paleogene. Nevertheless, based on mean values of mean annual temperature and cold month mean temperature, two different regional climatic zones can be distinguished in the Paleocene representing in each case the cooler and warmer (subtropical) part of warm temperate climate of the Koeppen-Geiger system. In the early Eocene, the gradient became more clearly pronounced and in addition, a cool temperate zone can be distinguished. The presence of mangroves in our early Eocene records, already known from previous studies, is largely in line with our climate reconstruction and possible can be related to hyperthermal events such as the PETM and ETM.

1. Introduction

Early Paleogene (Paleocene – early Eocene) climate is characterized as being in a generally warm and equable “greenhouse” state across the world, punctuated by brief hyperthermal phases (Abels et al., 2011; Dupont-Nivet et al., 2007; Pagani et al., 2005; Pearson et al., 2009; Westerhold et al., 2020; Xiao et al., 2010; Zachos et al., 2008). Marine archives indicate an overall warming during the late Paleocene – early Eocene, culminating in the Early Eocene Climatic Optimum (EECO), that has been identified as a global climatic event (Bijl et al., 2009; Zachos et al., 2008). The Paleocene–Eocene Thermal Maximum (PETM, 55.5 Ma) and subsequent ETM2 record the highest temperatures throughout the Cenozoic (Zachos et al., 2008). Model simulations of past greenhouse conditions in Earth's history have a considerable potential for validating climate prediction, while the hyperthermals of the early Paleogene are of particular interest (Bijl et al., 2009; Huber and Caballero, 2011; Shellito and Sloan, 2006; Sloan and Barron, 1992; Stap et al., 2010; Zachos et al., 2008). Hence, the knowledge of the Paleogene

climate evolution provides unique perspectives, also for the modeling of the actual global climate change, and helps to probe into the integrated response of the Earth system to various driving forces (Utescher et al., 2009; Zachos et al., 2008).

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; Greenwood et al., 2010; Jolley and Widdowson, 2005; Mosbrugger et al., 2005; Utescher et al., 2007, 2011; Wilf, 2000; Wing and Harrington, 2001; Wing et al., 2005), and marine proxy data from both hemispheres (Bijl et al., 2009; Pearson et al., 2007; Zachos et al., 2008). Very little is known from Asia because palaeoclimatic results have only been reported from particular geological intervals, on the basis of palaeobotanical data from individual sites of China (e.g., Hao et al., 2010; He and Tao, 1997; Hoorn et al., 2012; Quan and Zhang, 2005; Quan et al., 2011, 2012a, b; Su et al., 2009; Wang et al., 2010).

As regards the Paleogene climate evolution in the Russian Far East and Eastern Siberia, our knowledge is still very poor and fragmentary.

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There are essentially no regional studies on palaeoclimates, but individual remarks and considerations about the climatic conditions of the past or relatively sketchy qualitative characterizations of the climate are available for that time based on the study of a specific flora or several floras of a certain age and often for a limited area (cf. [Ablaev, 2000](#); [Ablaev and Vasiliev, 1998](#); [Akhmetiev, 1976, 1988](#); [Bolotnikova, 1979](#); [Fradkina, 1995](#); [Fradkina et al., 1979](#); [Kodrul, 1999](#); [Laukhin and Fradkina, 1984](#); [Laukhin et al., 1992](#); [Lopatina, 2004](#); [Pavlyutkin, 2007](#); [Zharikova, 1980](#); others). Quite recently, quantitative palaeoclimate studies have become more frequent. The Paleogene climatic dynamic has been studied based on palaeobotanical data mostly for the north-eastern part of Russia ([Akhmetiev, 2015](#); [Budantsev, 1997, 1999](#)). First progress in quantifying climate has been made recently and, in fact, there already are several quantitative studies on the Russian Far East and Eastern Siberia (cf. [Bondarenko et al., 2019](#); [2020a, b](#); [2021, 2022](#); [Bondarenko and Utescher, in press](#)). Such quantitative climate reconstructions are essential for comparison with data from other proxies or climate models. To date, extensive geological, geochemical, palaeobotanical, and palaeontological data have been compiled, requiring palaeoclimatic interpretation and generalization. This material, it seems to us, already makes it possible to start compiling survey palaeoclimatic maps, based on a quantitative assessment of the most important components of the palaeoclimate – temperature and atmospheric precipitation.

In order to quantitatively study latitudinal continental temperature gradients along the Pacific coast of Eurasia in space and time and to trace climate seasonality in the early Paleogene, we compiled published palaeobotanical sites from the Far East of Russia, Eastern Siberia, China, and Japan. Based on a total of 110 reasonably well-dated pollen and leaf floras of the Pacific side of Eurasia, coherent climatic data sets are presented for the first time for three stratigraphic levels, namely for the early Paleocene, late Paleocene, and early Eocene, covering the climate evolution over a time-span of ca. 25 myr, in total. All the climate data are reconstructed using a single approach (the Coexistence Approach – CA) applicable on every plant organ type. For the present application, the published flora lists and Nearest Living Relative (NLR) interpretations of the fossil record were revisited and homogenized.

2. Study area and palaeogeographical settings

2.1. Palaeogeographical setting

The early Paleogene palaeogeographic configuration of Asia fundamentally differed from modern (cf. [Scotese, 2013](#)). The Alpine orogenic phase had just started, elevations and relief in general were lower compared to modern, while the degree of its tectonic and erosional dissection sharply increased only during the Neogene and Quaternary periods ([Akhmetiev et al., 2012](#); [Utescher et al., 2015](#); [Wu et al., 2018](#); [Xiong et al., 2020](#)). During the Paleocene and Eocene, the Tethys with its E-W marine connection still existed, and in extratropical Central Eurasia the epicontinental Turgai Strait was established as a seaway link connecting the Tethys and Arctic oceans ([Akhmetiev et al., 2012](#)). Before the emergence of the latitudinal Alpine-Himalayan orogenic belt, the Tethys and its marginal seas to the north formed a continuous shelf area ([Akhmetiev et al., 2012](#)). The Tarim area and Siberian Platform also were covered by a shallow epicontinental sea ([Bosboom et al., 2014, 2015](#); [Volkova and Kuz'mina, 2005](#); [Zhang et al., 2007, 2012](#)) that reduced the width in latitude of the continental area by about one quarter compared to present. During the early Paleogene, the maximum extent of marine transgression occurred in the mid-latitudes of Central Eurasia, with over 60 % of the West Siberian Plate covered by the ([Akhmetiev et al., 2012](#); [Volkova and Kuz'mina, 2005](#)).

According to the available palaeomagnetic data, the eastern part of Eurasia occupied a position relatively close to the modern one, i.e., did not experience large displacements or rotations since the Late Jurassic ([Kolesov, 2003](#); [Lee et al., 1987](#); [Ushimura et al., 1996](#); [Zhu, 1993](#)). This

does not necessarily hold for the island arcs along the east margin of the Eurasian Plate. For instance, 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](#)).

The orography in SW China was probably lower than today, because crustal thickening and uplift occurred later, as a consequence of the collision of the Indian Plate. Early Paleogene altitudes of the different tectonic units of the Tibetan Plateau still are under debate ([Hoorn et al., 2018](#); [Spicer et al., 2021](#); [Yuan et al., 2021](#)). Northeastern China and the adjacent Primorye Region constitute a joint continental area since the late Cretaceous, together with the inner zones of Japan and Korea, prior to the opening of the Sea of Japan in the middle Eocene ([Muryama et al., 1997](#)). Unlike today, the Pacific coast was located several hundred kilometers to the east, throughout the time-span regarded, and thus, sites presently having a coastal position probably were not under a proximate maritime impact. The Amur Region at the transition of the Late Cretaceous to Paleocene was a low-lying marshy area surrounded by an elevated hilly region with incised fluvial systems ([Beltenev and Varnavsky, 1977](#)). The major part of the Okhotsk Sea, in pre-Oligocene times, represented a semi-flooded peneplain, which on all sides, except for the south, was framed by a relatively narrow deep-water trough ([Semakin et al., 2016](#)). The final formation of the Okhotsk and Bering marginal seas occurred in the Eocene-Oligocene, connected to the onset of rifting processes ([Gladenkov et al., 2005](#)).

2.2. Study area

The palaeobotanical records of the Pacific coast of Eurasia studied herein originate from 73 localities ([Table 1](#), [Fig. 1](#), [Appendix 1](#)). The early Paleogene deposits of China are widely distributed and generally represent terrestrial facies conditions. The plant-bearing strata of eastern China are mainly of fluvial to lacustrine origin, while in central and western China, Paleogene deposits may contain red-beds and evaporites. The majority of these strata, however, lacks detailed geochronological investigations ([Li, 1984](#)). As a result, the ages of many of these floras were initially assigned only to a wide stratigraphical range, such as to an epoch or system level, based on floristic assemblages. This apparently reduces the resolution of palaeoclimatic results, or even casts doubt on their validity in palaeoclimatic modeling ([Quan et al., 2012a](#)). Fortunately, recent interdisciplinary studies significantly improve the age constraints in many localities (e.g., [Huang et al., 1998](#); [Miao et al., 2008](#); [Pei et al., 2009](#); [Shi et al., 2008](#); [Wang et al., 1999](#)). This provides opportunities to reconstruct palaeoclimates in a better resolution at the stage level ([Quan et al., 2012a](#)).

The early Paleogene deposits of Russian Far East (RFE) and Eastern Siberia are also widely distributed, and are dominated by non-marine facies. The strata of south RFE comprise volcanic and sedimentary deposits, unconformably overlying Mesozoic basement. The sedimentary facies include fine- to coarse-grained continental clastics and intercalated lignites excavated in several active opencast mines. For some of the basins, mainly generated by extensional tectonics (Maksimovskii, Pavlovskii and Pushkinskii Basins), intercalated volcanoclastic layers and tholeiitic lava flows (Maksimovskii Basin: Takhobinskaya and Kuznetsovskaya Formations) allow for radiometric dating of the strata. The sedimentary successions in the individual basins are characterized by numerous unconformities related to regional tectonics and phases of rifting and subsidence ([Pavlyutkin and Petrenko, 2010](#)). The early Paleogene deposits of Eastern Siberia and Northeast Russia are exposed in isolated Cenozoic coastal basins, superimposed on folded basement of the Siberian Platform of differing ages. These include tectonic structures adjacent to the Pacific Ocean (Murukta, Kharaulakh), depressions located in the lower reaches of the Lena River (Sogo, Kengdei, and Kunga Basins), sections of the Tastakh Lake area in the Yana–Indigirka interfluvium, sections of Ugol'naya Bay, Rarytkin Ridge, and Anadyr River

Table 1
List of selected early Paleogene fossil sites of Eurasian Pacific side.

Site	Location	Coordinate		Age control	PA	Formation/group (member)	Age	Fossil type	References
		Lat	Lon						
1	Novosibirskie Islands, Republic of Sakha, Russia	75,53	143,91	IRC, D, GD	1	Anzhuisкая	EE	P, C	Fradkina (1995), Fradkina et al. (1979), Grinenko et al. (1989, 1997), Kulkova (1973), Suan et al. (2017)
2	Bykovskaya Channel, Republic of Sakha, Russia	72, 20	127,90	IRC, D	2	Kengdeiskaya	EE	P, L	Budantsev (1983), Fradkina (1995), Grinenko and Kiseleva (1971), Grinenko et al. (1989, 1997)
3	Kengdei, Republic of Sakha, Russia	71,79	124,98	IRC, Mo	3	Kengdeiskaya	EE	P, L	Fradkina (1995), Grinenko et al. (1989, 1997)
4	Sogo, Republic of Sakha, Russia	71,50	128,90	IRC	4	Soginskaya (upper part)	LP	P	Fradkina (1995), Grinenko et al. (1989, 1997)
				IRC	5	Soginskaya (lower part)	LP	P	Fradkina (1995), Grinenko and Fradkina (1988), Grinenko et al. (1989, 1997)
5	Kunga, Republic of Sakha, Russia	71,28	128,99	IRC, D	6	Kengdeiskaya	EE	P, L	Fradkina (1995), Grinenko et al. (1989, 1997), Laukhin et al. (1988)
6	Kunga, Republic of Sakha, Russia	71,28	128,99	IRC	7	Emgend'enskaya	EE	P	Fradkina (1995), Grinenko et al. (1989, 1997)
7	Tastakh, Republic of Sakha, Russia	70,90	145,60	IRC	8	Tastakhskaya	EE	P, L	Budantsev (1983), Fradkina (1995), Kryshofovich (1958), Kulkova (1971, 1973)
8	Kolyma1, Republic of Sakha, Russia	68,70	158,50	IRC, SC	9	Timkinskaya	LP	P	Fradkina (1985, 1995), Fradkina and Laukhin (1984), Grinenko et al. (1989, 1997), Zharikova et al. (1982)
9	Yarovaya91, Chukotka Autonomous Region, Russia	67,80	161,20	IRC	10	Khetachanskaya (interval 84,0–160,8 m)	LP	P	Belaya and Litvinenko (1989), Fradkina (1995), Grinenko et al. (1997)
10	Diring-Yuryue15, Republic of Sakha, Russia	67,18	135,07	IRC, SC	11	Dirinskaya (interval 383–418 m)	EE	P	Fradkina (1995), Grinenko et al. (1989, 1997)
				IRC, SC	12	Yantarninskaya	LP	P	Fradkina (1995), Grinenko et al. (1989, 1997)
11	Sakan'ya272-1, Republic of Sakha, Russia	67,06	145,20	IRC	13	Sakan'inskaya (interval 832–1075 m)	EP	P	Fradkina (1995), Grinenko et al. (1997)
12	Slezovka15, Republic of Sakha, Russia	67,01	153,60	IRC, SC	14	Iryumasskaya	LP	P	Fradkina (1995), Grinenko et al. (1997)
				IRC	15	Afononskaya	EP	P	Fradkina (1995), Grinenko et al. (1997)
13	Koluchinskaya guba, Chukotka Autonomous Region, Russia	66,60	174,00	IRC	16	Ukvyveemskaya	EP	P	Fradkina (1995), Grinenko et al. (1997), Kisterova et al. (1979), Volobueva et al. (1988)
14	Shamanikha, Republic of Sakha, Russia	65,70	153,40	IRC, SC	17	Shamanikhovskaya (upper part)	EE	P	Fradkina (1995), Grinenko et al. (1989), Zharikova (1980)
				IRC, SC	18	Shamanikhovskaya (lower part)	LP	P	Fradkina (1995), Grinenko et al. (1989), Zharikova (1980)
15	Medvezhye ozera, Republic of Sakha, Russia	65,50	153,00	IRC	19	Kopachskaya	EE	P	Fradkina (1995), Grinenko et al. (1989, 1997), Zharikova (1980)
16	Tigil', Kamtchatka Peninsular, Russia	57,98	158,34	IRC	20	Khulgunskaya	LP	P	Bolotnikova (1977)
17	Urkan, Amur Region, Russia	54,10	124,39	IRC	21	Kivdinskaya	LP	P	Sorokin and Belousov (1984)
18	Snezhnegorskoe, Amur Region, Russia	54,10	127,60	IRC	22	Raichikhinskaya	EE	P	Kezina and Ol'kin (2000)
19	Pikanskii, Amur Region, Russia	53,50	127,10	IRC	23	Verkhnetsagayanskaya	EP	P	Kezina (1997, 2005)
20	Tygda245, Amur Region, Russia	53,06	126,20	IRC	24	Verkhnetsagayanskaya	EP	P	Kezina (2005)
21	Ushumunskii5, Amur Region, Russia	52,50	126,30	IRC, SC	25	Raichikhinskaya	EE	P	Varnavskii et al. (1988)
				IRC, SC	26	Kivdinskaya	LP	P	Varnavskii et al. (1988)
22	Malomikhailovka, Khabarovsk Region, Russia	52,00	140,00	IRC	27	Malomikhailivskaya	EP	P, L	Akhmetiev (1973, 1993), Akhmetiev and Golovneva (1998), Akhmetiev et al. (2009), Pavlyutkin and Petrenko (2010)
23	Bukhta Siziman, Khabarovsk Region, Russia	50,40	140,30	IRC	28	Kizinskaya	EE	L	Ablaev et al. (2005), Akhmetiev (1973, 1988), Pavlyutkin and Petrenko (2010)
24	Erkovtsy, Amur Region, Russia	50,36	128,30	IRC, SC	29	Raichikhinskaya	EE	P, L	Baikovskaya (1950), Brattseva (1969), Kezina (2005)
				IRC, SC	30	Kivdinskaya	LP	P, L	Kamaeva (1990), Kezina (2005), Mamontova (1977), Naryshkina (1973), Ziva (1973)
					31	Verkhnetsagayanskaya	EP	P, L	Kezina (2005), Kezina and Litvinenko (2007), Ziva (1973)
25	Darmakan, Amur Region, Russia	49,60	129,60	IRC	32	Verkhnetsagayanskaya	EP	L	Krassilov (1976), Zaklinskaya et al. (1977)
26	Raichikhinsk, Amur Region, Russia	49,50	129,20	IRC, SC	33	Raichikhinskaya	EE	P, L	Fedotov (1983), Kezina (2005)
				IRC, SC	34	Kivdinskaya	LP	P	Kezina (2005), Ziva (1973)
27	Avgustovka, Sakhalin Island, Russia	49,40	142,10	IRC	35	Kamenskaya (Podkonglomeratnye sloi)	EP	P, L	Ablaev (1976), Gladenkov et al. (2002), Kodrul (1999), Zaklinskaya (1976)
28	Svobodnoe53, Amur Region, Russia	49,30	129,30	IRC, SC	36	Raichikhinskaya	EE	P	Kezina (2005)
				IRC, SC	37	Kivdinskaya	LP	P	Kezina (2005)
				IRC, SC	38	Verkhnetsagayanskaya	EP	P	Kezina (2005)
29	Snezhinka, Sakhalin Island, Russia	49,20	142,15	IRC, SC	39	Snezhinskaya (upper subformation)	EE	P, L	Gladenkov et al. (2002), Kodrul (1999)
				IRC, SC	40	Snezhinskaya (middle subformation)	LP	L	Gladenkov et al. (2002), Kodrul (1999)
				IRC, SC	41		EP	P, L	

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Table 1 (continued)

Site	Location	Coordinate		Age control	PA	Formation/group (member)	Age	Fossil type	References
		Lat	Lon						
30	Snezhinka, Sakhalin Island, Russia	49,20	142,10	IRC	42	Snezhinskaya (lower subformation)	EP	P	Gladenkov et al. (2002), Kalishevich et al. (1981), Kodrul (1999)
31	Kama, Sakhalin Island, Russia	49,20	142,06	IRC	43	Boshnyakovskaya (Kamskie sloi)	EP	L	Gladenkov et al. (2002), Kalishevich et al. (1981)
32	Arkharo-Boguchan, Amur Region, Russia	49,18	130,12	IRC	44	Verkhnetsagayanskaya	LP	L	Akhmetiev et al. (1978), Gladenkov et al. (2002), Kodrul (1999), Sycheva (1975)
33	Baishantou, Heilongjiang Province, China	49,14	129,28	IRC	45	Wuyun	EP	P, L	Moiseeva et al. (2018)
34	Shakhtnyi, Sakhalin Island, Russia	48,30	142,40	IRC	46	Krasnoyarkovskaya (Sinegorskie sloi)	EP	P	Chen et al. (2004), Hao et al. (2010), Kezina (2005), Manchester et al. (1999), Muling (1983), Tao and Xiong (1986)
35	Birofel'd, Jewish Autonomous Region, Russia	48,20	132,50	IRC	47	Cernorechenskaya (lower subformation)	EE	P	Gladenkov et al. (2002), Zaklinskaya (1976)
36	Naiba, Sakhalin Island, Russia	47,50	142,30	IRC	48	Boshnyakovskaya (Kamskie sloi)	EP	P	Pavlyutkin and Petrenko (2010), Ziva and Lukashova (1977)
37	Ozero Toni, Primorye Region, Russia	47,40	138,30	IRC	49	Kizinskaya	EE	P, L	Gladenkov et al. (2002), Zaklinskaya (1976)
38	Krasnoyarka, Sakhalin Island, Russia	47,40	142,50	IRC, SC	50	Naibutinskaya (upper levels)	EE	P, L	Oleinikov and Klimova (1977), Varnavskii et al. (1988)
				IRC, SC	51	Naibutinskaya (lower levels)	LP	L	Gladenkov et al. (2002), Kodrul (1999)
39	Alchan, Primorye Region, Russia	46,87	134,94	IRC	52	Uglovskaya	EE	P	Pavlyutkin and Petrenko (2010), Krasnyi (1994)
40	Bikin, Primorye Region, Russia	46,57	135,09	IRC	53	Unnamed unite	EE	P	Pavlyutkin and Petrenko (2010), Krasnyi (1994)
41	Luchegorsk540/541, Primorye Region, Russia	46,30	134,20	IRC	54	Unnamed unite	EE	P, L	Pavlyutkin and Petrenko (2010)
42	Kril'on, Sakhalin Island, Russia	46,30	142,10	IRC, SC	55	Snezhinskaya (upper subformation)	EE	P	Fotjanova et al. (2001), Gladenkov et al. (2002)
				IRC, SC	56	Krasnoyarkovskaya (Sinegorskie sloi)	EP	P	Fotjanova et al. (2001), Gladenkov et al. (2002)
43	Kluch Kedrovyyi, Primorye Region, Russia	46,17	137,78	IRC	57	Kedrovskaya	LP	P	Varnavskii et al. (1988)
44	Yilan, Heilongjiang Province, China	46,10	129,30	GD	58	Xin'ancun	EE	P	Quan et al. (2012a, b)
45	Kluch Stolbikova, Primorye Region, Russia	46,05	137,50	GD	59	Kuznetsovskaya	LP	L	Pavlyutkin and Petrenko (2010), Varnavskii et al. (1988)
46	Sobolevka, Primorye Region, Russia	46,05	137,50	GD	60	Takhobinskaya	EP	L	Akhmetiev (1973, 1988), Borsuk (1952)
47	Krylovskii524, Primorye Region, Russia	45,10	133,40	IRC	61	Uglovskaya	EE	P	Pavlyutkin and Petrenko (2010)
48	Hualin, Heilongjiang Province, China	44,80	129,80	PD, SC	62	Bahuli	EE	P	Quan et al. (2012a, b)
49	Shulan, Jilin Province, China	44,50	126,90	M, PD	63	Bangchuiou	EE	P	Fan (1985), Quan et al. (2012a)
50	Rettikhovka, Primorye Region, Russia	44,10	132,40	IRC	64	analog of Uglovskaya	EE	P	Pavlyutkin and Petrenko (2010)
51	Arsen'evka, Primorye Region, Russia	44,10	133,10	IRC	65	analog of Uglovskaya	EE	P	Bolotnikova (1988)
52	Kluch Tuyanov, Primorye Region, Russia	44,10	135,10	IRC	66	Tujanovskaya	EE	L	Baskakova and Lepekhina (1990), Varnavskii et al. (1988)
53	Ustinovka, Primorye Region, Russia	44,10	135,10	IRC, SC	67	Tadushinskaya	LP	L	Pavlyutkin and Petrenko (2010)
				IRC, SC	68	Bogopol'skaya	EP	L	Ablaev et al. (2005), Krassilov (1989)
54	Kluch Ugolnyi, Primorye Region, Russia	43,30	134,10	IRC	69	analog of Uglovskaya	EE	P, L	Chekryzhov et al. (2010), Pavlyutkin and Petrenko (2010)
55	Tavrichanka9142, Primorye Region, Russia	43,20	131,50	M	70	Uglovskaya	EE	P	Pavlyutkin and Petrenko (2010)
56	Smolyaninovo, Primorye Region, Russia	43,20	132,30	IRC	71	Uglovskaya	EE	P, L	Baskakova and Gromova (1979, 1984), Pavlyutkin and Petrenko (2010), Tashchi et al. (1996), Varnavskii et al. (1988), Verkhovskaya and Kundyshev (1989)
57	Fushun, Liaoning Province, China	41,80	123,90	GD, PD	72	Guchengzi	EE	P	Hong et al. (1980), Quan et al. (2012a)
58	Fushun, Liaoning Province, China	41,50	123,54	IRC	73	Guchengzi	EE	P	Wang et al. (2010)
				IRC	74	Lizigou	LP	P	Hong et al. (1980), Wang et al. (2010)
				GD, PD	75	Laohutai	EP	P	Hong et al. (1980), Wang and Wang (1982, 1985), Wang et al. (1982, 2010)
59	Etuoke, Inner Mongolia, China	39,10	107,90	M	76	Unnamed unite 1 (lower)	EE	P	Song and Zhang (1990), Quan et al. (2012a)
60	Shache, Xinjiang Province, China	38,30	77,30	CN, Fo	77	Kalataer	EE	P	Wang et al. (1986), Quan et al. (2012a)
61	Huanghua, Hebei Province, China	38,30	117,30	GD, PD	78	Shahejie (part IV)	EE	P	Zhang and Yin (2005), Quan et al. (2012a)

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Table 1 (continued)

Site	Location	Coordinate		Age control	PA	Formation/group (member)	Age	Fossil type	References
		Lat	Lon						
62	Changle, Shandong Province, China	36,70	118,80	G, V	79	Wutu	EE	P	Wang (2005), Quan et al. (2012a)
63	Xining, Qinghai Province, China	36,50	101,70	O, PD	80	Qijiachuan (parts III, IV)	EE	P	Sun et al. (1980), Quan et al. (2012a)
64	Wutu, Shandong Province, China	36,39	118,55	M	81	Wutu	EE	P	Zhang et al. (2016), Quan et al. (2012a)
65	Lanzhou, Gansu Province, China	36,10	103,80	PD	82	Unnamed unite 2 (lower)	EE	P	Ma et al. (1995), Quan et al. (2012a)
66	AS_Japan, Japan	36,00	138,00	IRC	83	Unnamed unite	EE	L	Tanai (1972)
67	Luanchuan, Henan Province, China	33,80	116,60	M, R	84	Tantou (lower)	EE	P	Wang et al. (1984), Quan et al. (2012a)
68	Gaoyou, Jiangsu Province, China	32,80	119,40	O	85	Dianan	EE	P	Zhang and Qian (1992), Quan et al. (2012a)
69	Hefei, Anhui Province, China	31,86	117,28	C, D	86	Dingyuan (part III)	EE	P	Wang et al. (1987), Quan et al. (2012a)
70	Jianghau, Hubei Province, China	30,40	112,80	O	87	Xingouzui	EE	P	Wang and Zhao (1980), Quan et al. (2012a)
71	Qingjiang, Jiangxi Province, China	27,90	116,10	C, M, O	88	Qingjiang (part I)	EE	P	He and Sun (1977), Quan et al. (2012a)
72	Donghai, Zhejiang Province, China	26,40	121,70	Fo, CN	89	Oujiang	EE	P	Zhang et al. (1990), Quan et al. (2012a)
73	Zhujiang, Guangdong Province, China	22,60	113,30	GD, MA	90	Lufeng	EE	P	Li (1998), Quan et al. (2012a)

References and complete flora lists including Nearest Living Relatives used for vegetation analysis are given in Appendix 2. Sites are shown in Fig. 3. Age control in addition to plant assemblages (PA): IRC – inter-regional correlation; C – charophyte; CN – calcareous nannofossils; D – dinoflagellate; Fo – foraminifera; G – gastropods; GD – geochemical dating; M – mammals; MA – marine animals; Mo – mollusks; O – ostracods; PD – paleomagnetic dating; SC – stratigraphical correlation; R – reptiles; V – vertebrates. Age: EE – early Eocene; LP – late Paleocene; EP – early Paleocene. Fossil type: L – leaf; P – pollen and spores; C – seeds and fruits.

Basin (northern Koryakiya), and coastal sections of northwestern and central Kamchatka.

The regional stratigraphic correlation chart for single basins (Appendix 2) is adapted from Quan et al. (2012a) for China, Kezina (2005) and Pavlyutkin and Petrenko (2010) for the continental part of the south RFE, Gladenkov et al. (2002) for Sakhalin Island, Gladenkov et al. (2005) for the Kamchatka Peninsula and Grinenko et al. (1997) for the continental part of the north RFE and Eastern Siberia. Age control of the selected early Paleogene fossil floras of eastern Eurasia is based on a variety of stratigraphic data obtained from radiometric dating, well log correlations, and regional sequence-stratigraphical concepts, considering the position of volcanogenic units and main phases of peat forming, vertebrate fauna, mollusks, foraminifera, and regional and inter-regional pollen zonation (Table 1). The stratigraphic schemes of the Russian Far East and Eastern Siberia has been tied to the International Stratigraphic Chart (Cohen et al., 2013; Gladenkov et al., 2002, 2005; Grinenko et al., 1997; Kezina, 2005; Pavlyutkin and Petrenko, 2010) and allows for dating the flora-bearing horizons at the stage level. For some of the floras, stratigraphic ages are better constrained (cf. Appendix 2).

3. Materials and methods

3.1. The floral record

The palaeobotanical record of the Pacific coastal areas of Eurasia (including China, Japan, the Far East of Russia and Eastern Siberia) is diverse and has been subject to extensive taxonomic studies (cf. Appendix 2 for references). In this study, all palaeofloras considered here were carefully re-evaluated regarding the validity of taxonomic identifications and Nearest Living Relatives (NLRs) of the fossil taxa. We analyse a total of 110 floras including 79 palynofloras (PF), 30 leaf floras (LF) and one carpoflora (CF) with respect to palaeoclimate considering three time slices, namely the early Paleocene, late Paleocene, and early Eocene. The floras cover a total time-span of ca. 25 myr, ranging from the early Paleocene (Danian) to early Eocene (Ypresian).

The assignment of the palaeofloras to the three time slices considered here is done on the basis of stratigraphic information available in literature and compiled in Table 1. In many cases, flora-bearing horizons

originate from longer successions that are tied to regional stratigraphy and partly cover the entire early Paleogene (e.g., Kolyma1, Slezovka15, Erkovtsy, etc.) thus facilitating a consistent sample selection. The single floras are listed in Appendix 2, 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 Appendix 2.

3.2. Application of the Coexistence Approach (CA)

To reconstruct quantitative temperature data from the plant fossil record we use the Coexistence Approach (CA) (Mosbrugger and Utescher, 1997; Utescher et al., 2014). This approach is organ-independent, so that both macro- and microfossil floras are eligible as long as their modern botanical affinities are determinable (Bruch et al., 2011; Mosbrugger and Utescher, 1997; Utescher et al., 2007). 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 data sets from the Palaeoflora Database (Utescher and Mosbrugger, 2018) as source for climatic requirements of extant plant taxa. New climate records were compiled using chorological information from Fang et al. (2009, 2011) and Sokolov et al. (1977, 1980, 1986), and climatological data from Müller and Hennings (2000) and 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 Appendix 2.

In this study, three temperature variables are reconstructed: mean annual temperature (MAT), cold and warm month mean temperature (CMMT, WMMT). 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 80 (mean 33.0) taxa contribute to determining the Coexistence Intervals (Appendix 3). Except for the early Paleocene LF 7, early Eocene PF 38 and LF 23 with only nine taxa, the palaeofloras are diverse enough to obtain reliable results. The climatic resolution of the CA results also depends on the taxonomical level of NLR identification (Mosbrugger and Utescher, 1997). For the Paleogene floras we use genera or family levels for NLRs. For the monotypic genera

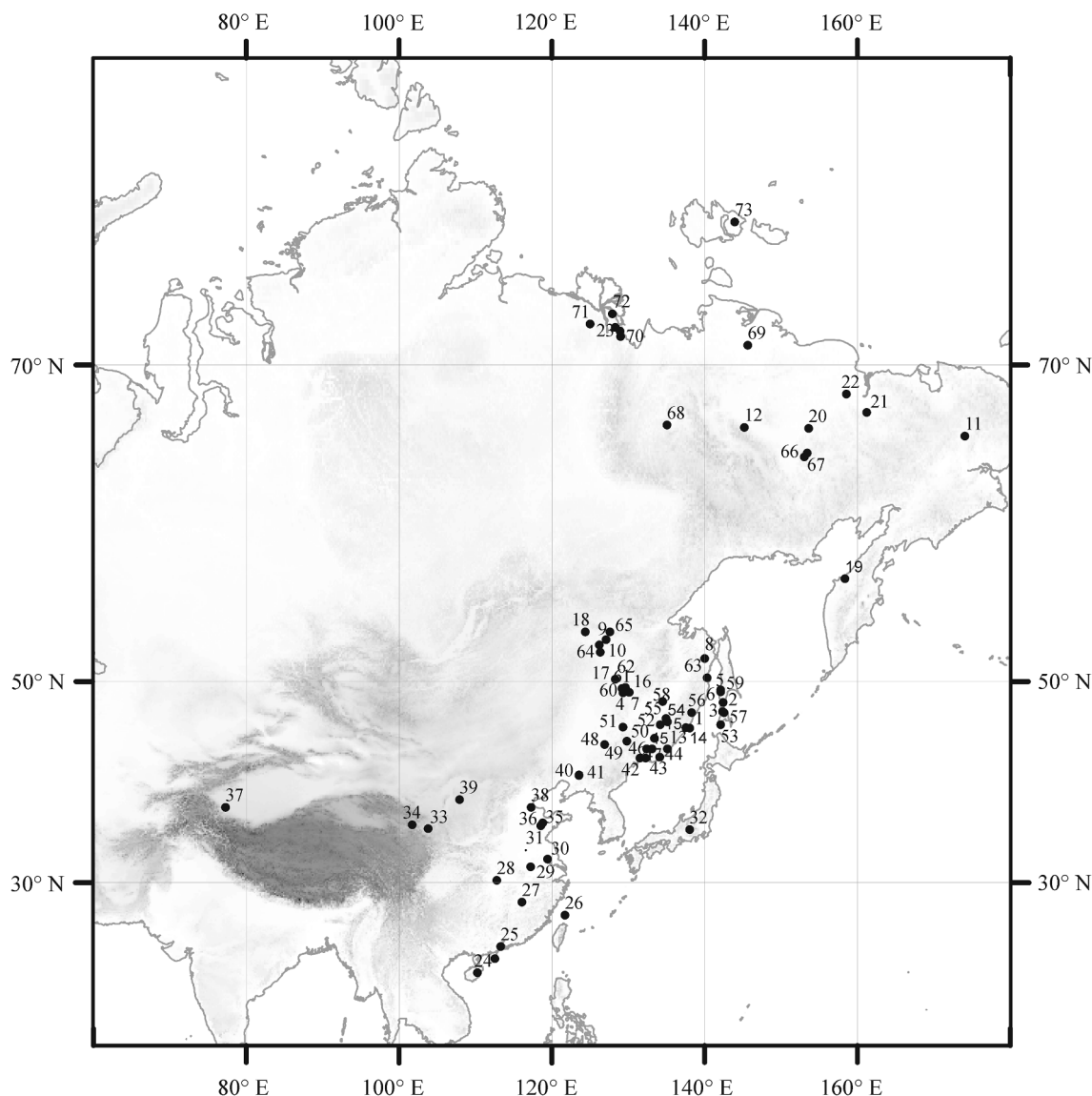


Fig. 1. Location of the selected early Paleogene sites of the Pacific side of Eurasia. Locality code numbers are explained in [Appendix 1](#).

(but not monotypic families) we use climate data for (sub)families. For example, climate data of Trochodendraceae Eichler were used for *Trochodendron aralioides* Siebold et Zucc. and *Tetracentron sinense* Oliver, Hamamelidaceae R. Br. – for *Disanthus cercidifolius* Maxim., Myricaceae Blume – *Comptonia peregrina* (L.) Coult., Juglandaceae A. Richard ex Kunth – for *Cyclocarya paliurus* (Batal.) Iljinsk., Abietoideae Bercht. et J. Presl – for *Pseudolarix amabilis* (J. Nelson) Rehd., Cupressaceae Gray – for *Taiwania cryptomerioides* Hayata, Sequoioideae Quinn – for *Metasequoia glyptostroboides* Hu et W.C. Cheng and *Sequoia sempervirens* (D. Don) Endl., Taxodioideae Endl. ex K.Koch – for *Cryptomeria japonica* (Thunb. ex L.f.) D. Don, *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch and *Taxodium* Richard). For *Alfaroa* Standl. and *Oreomunnea* Oerst., distributed in the subtropical to tropical realm and identified as warm outliers in the analysis, we use climate data for Engelhardioideae Iljinsk. Probably these pollen present extinct forms pre-dating the Paleogene speciation in Juglandaceae. Moreover, ca. 50 (sub)-cosmopolitan taxa were not considered in CA analysis, for a total of ca. 10 taxa climatic tolerances could not reliably be identified ([Table 2](#)). *Eucommia ulmoides* Oliver, *Ginkgo biloba* L. and *Sciadopitys verticillata* (Thunb.) Siebold et Zucc. were excluded from the analysis for being monotypic taxa. *Larix* Mill. may represent a cold outlier, mainly in pollen floras of the mid- and lower latitudes where it is interpreted as an altitudinal element

([Bondarenko et al., 2020a](#)). To avoid interference in temperature reconstruction, the taxon was excluded from the CA calculations. Its occurrence is discussed in [Bondarenko et al. \(2020a\)](#). *Picea* A. Dietr. is likewise considered an altitudinal element and is present in many microfloras. Although its temperature requirements may overlap with the majority of taxa in most of the floras the taxon was also excluded from CA analysis to avoid restrictions in defining the Coexistence Intervals (CIs), caused by a potentially allochthonous component. However, we display climatic limits of both, *Larix* and *Picea* together with CIs whenever present (see Discussion).

The distribution of modern MAT and Koeppen–Geiger climate types over Eurasia is given in [Fig. 2](#). To illustrate temperature gradients along the Pacific side of Eurasia during the early Paleogene, the floras are allocated to three time intervals. Time intervals are defined according to the international standard: early and late Paleocene, and early Eocene. To visualize the results, a series of palaeogeographic maps and latitudinal transects are provided and discussed below. The maps, allowing to tracing the evolution of the three temperature variables throughout the early Paleogene, are based on means of coexistence intervals for each palaeoflora and averaged for the time intervals regarded ([Fig. 3](#)). The distinguishing of climatic zones is based on a significant change in the prevailing mean values of MAT and CMMT. The transects display the

Table 2

Taxa excluded from CA analysis.

Reason for excluding	Excluded taxa
1 unspecific due to wide distribution (cosmopolitan and subcosmopolitan taxa)	<i>Adiantum</i> L., Alismataceae Vent., Apiaceae Lindl., <i>Artemisia</i> L., <i>Arundo</i> L., <i>Asplenium</i> L., Athyriaceae Alston, <i>Athyrium</i> Roth, <i>Botrychium</i> Swartz, Brassicaceae Burnett, <i>Carex</i> L., Ceratophyllaceae Gray, <i>Convolvulus</i> L., Cucurbitaceae Juss., Cyperaceae Juss., Elaeagnaceae Adans., <i>Equisetum</i> L., Lamiaceae Lindl., Liliaceae Juss., Lycopodiaceae P.Beauv. ex Mirb., <i>Lycopodium</i> L., Onagraceae Juss., Ophioglossaceae Agardh, <i>Phragmites</i> L., Poaceae Barnh., Polygalaceae Hoffmanns. et Link, Pteridaceae E.D.M. Kirchn., Ranunculaceae Juss., <i>Ranunculus</i> L., Rubiaceae Juss., <i>Salvinia</i> Seguier, <i>Selaginella</i> Beauv., <i>Spiraea</i> L., <i>Typha</i> L., Urticaceae Juss., etc.
2 insufficient chorological information	<i>Ginkgo</i> L., <i>Riella</i> Mont., etc.
3 endemic and monotypic taxa	<i>Cercidiphyllum</i> Siebold et Zucc., <i>Eucommia ulmoides</i> Oliver, <i>Ginkgo</i> L., <i>Regnellidium</i> Lindm., <i>Sciadopitys</i> <i>verticillata</i> (Thunb.) Siebold et Zucc., Taxaceae Gray, etc.

latitudinal MAT gradients for each time slice and show the CIs obtained for the single floras, together with other climatic key data (Fig. 4). The complete set of coexistence intervals for all floras and climate variables studied is provided in Appendix 3. For the technical preparation of the maps, ArcMAP 10.4 was used. Moreover, we use box-and-whisker diagrams, based on variable means, representing zonal means of MAT and CMMT by time slice (box plots, PAST software; Fig. 5). Based on these data, early Eocene latitudinal gradients are calculated and compared to the Present (Fig. 6). We use rotated coordinates for the palaeo sites and the box plots showing zonal means (Figs. 3–7).

In order to determine temperature seasonality of the early Paleogene climate of the Pacific side of Eurasia, the mean annual range of temperature (MART) was calculated as the difference of WMMT and CMMT for the time intervals studied (Appendix 3).

4. Results

Complete lists of taxa for each of the localities, including their NLRs with climatic requirements, are provided in Appendix 2. Climate data calculated for the 110 floras are given in Appendix 3. We do not show the maps for WMMT because no clear trends result from the analysis.

In the early Paleocene, there are 25 floras in the narrowest latitudinal range from 41.50 to 67.06° N (Fig. 3c and f). In the late Paleocene, there are 21 floras in the range from 41.50 to 71.50° N (Fig. 3b and e). In the early Eocene, there are 64 floras covering the widest latitudinal range, from 19.38 to 75.53° N (Fig. 3a and d). Based on means of coexistence intervals for each palaeoflora, a gradual warming from the early Paleocene to early Eocene for both MAT and CMMT is observed. Moreover, there is a gradual increase in the range of mean values of both MAT and CMMT from the early Paleocene to early Eocene. A gradual increase of the mean annual range of temperature (MARP), calculated as the difference of CMMT and WMMT, from the early Paleocene to early Eocene indicates a trend to more seasonal climates. Our data suggest the existence of two different regional climatic zones in the early and late Paleocene and three zones in the early Eocene (Fig. 3a–f).

The reconstructed latitudinal transects display MAT and CMMT gradients for each time slice and show the coexistence intervals obtained for the single floras, together with other climatic key data (Fig. 3a–f, 4a–f). As is evident from our results, the latitudinal temperature gradients within the latitudinal transects are very weak for the early Paleocene

and two climatic zones can be distinguished with a suggested boundary ca. 60° N (Fig. 3c and f, 4c and f). For the late Paleocene, the latitudinal temperature gradients are still very weak. Also at that time, two climatic zones may have existed, with a suggested boundary between 62 and 68° N (Fig. 3b and e, 4b and e). In the early Eocene, the gradients became more clearly pronounced and three climatic zones can be distinguished with suggested boundaries ca. 43 and 47° N respectively (Fig. 3a and d, 4a and d).

Box-plots showing zonal means of MAT and CMMT by time slice and calculated using CI means, suggest very shallow latitudinal gradients in the order of a few degrees Celsius for the early and late Paleocene from 75 to 55° N (Fig. 5b, c and e, f). Latitudinal means at 45° N even tend to be lower, however, this aberration may be referred to the low number of sites and possible bias introduced by altitude. A much clearer latitudinal gradient between 75 and 25° N, ranging in the order of 6 °C for CMMT, is resolved for the early Eocene (Fig. 5a and d). Clear gradual increasing is observed in the range of mean values of both MAT and CMMT from the early Paleocene to early Eocene (Fig. 5a–f).

MART slightly increases during the early Paleogene (Appendix 3). In the early Paleocene MART varies from 12.6 to 22.2 °C (mean 16.0 °C), in the late Paleocene – from 13.2 to 19.9 °C (mean 16.5 °C), in the early Eocene – from 12.6 to 21.2 °C (mean 16.9 °C).

The latitudinal temperature gradients of the Pacific side of Eurasia in the early Eocene, as presently reconstructed, were distinctly lower compared to modern values (Fig. 6).

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 this early Paleogene CA reconstruction. For the 79 microfloras, the number of taxa contributing with climate data ranges from 9 to 80 (mean 36.8, std. 13.8). The analysis of 30 macrofloras is based on 9 to 56 (mean 23.5, std. 13.3) climate datasets of extant reference taxa. Hence, all results are considered reliable (>10 taxa; cf. Mosbrugger and Utescher, 1997), except for the early Paleocene LF 7, early Eocene PF 38 and LF 23.

Climatic requirements of 99.9 % of identified NLRs of the fossil taxa, in both microfloras and macrofloras, show overlapping. Generally, in 97 out of 110 cases, all NLRs can coexist, in all other cases over 98 % 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, also in the early Paleogene palaeobotanical record. 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). As regards MAT, the mean precision of the results, i.e., the mean width of the CIs for all floras amounts to 7.1 °C (std. 1.2 °C). When reconstructing MAT, CA intervals obtained from macrofloras are relatively narrower (mean width of CIs near 6.1 °C, std. 1.4 °C).

Apart from the fact that the highest values of all reconstructed climatic parameters refer to palynofloras, no regularities in the distribution of the parameters for different organ types have been found. Higher means observed 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 CI means to higher values. However, all the CIs obtained from micro- and macrofloras overlap if the floras originate from the same locality. From 110 palaeofloras studied, 18 microfloras originate from levels where likewise macrofloras were found, and in all cases the reconstructed climate data are largely congruent. However, the overall narrower climate

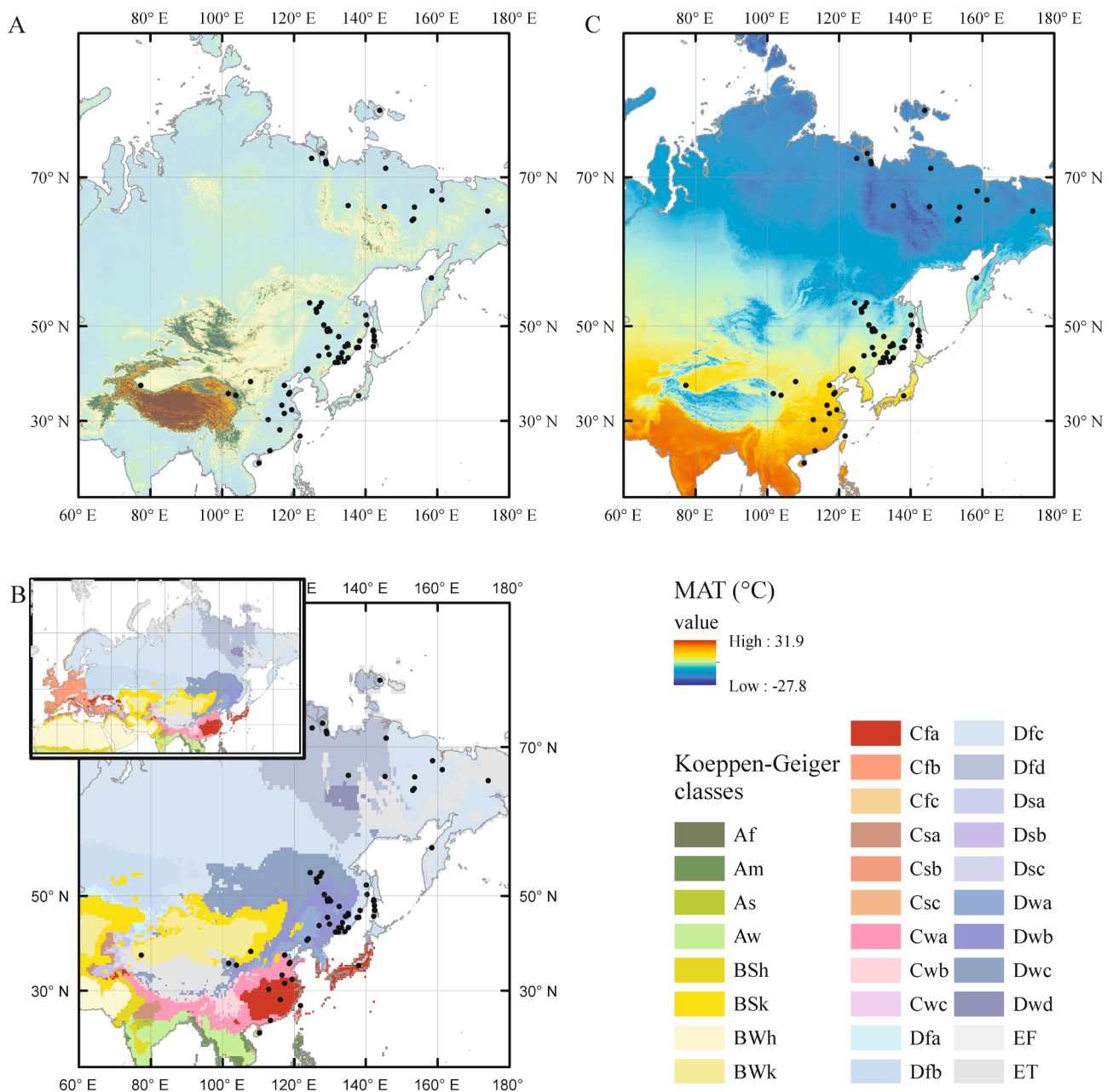


Fig. 2. Maps showing early Paleogene sites in the context of modern orography (A), modern Koeppen–Geiger type climates of Eurasia (B), and modern distribution of MAT (C) (source: WORLDCLIM). Koeppen-Geiger acronyms: A – equatorial, B – arid (BS – steppe; BW – desert), C – warm temperate (megathermal), D – snow climates (microthermal), E – polar (ET – tundra, EF – frost); w – winterdry, s – summerdry, f – fully humid, m – monsoon, h – hot, k – cold. Additional qualifiers (in C and D climates): a – hot summer, b – warm summer, c – cold summer and cold winter, d – extremely continental.

ranges obtained from the mainly local macroflora tend to cover the cooler and/or drier ends of the broader ranges derived in the microflora-based reconstruction having a lower climatic resolution and rather reflecting regional than local climate. The fact that microflora-based data tend to indicate warmer conditions may partly be explained by a mainly northward aeolian transport of pollen grains (cf. Bondarenko et al., 2013).

5.2. Comparison with proxy-based temperature reconstructions and zonal gradients

Eurasia is the largest and most heterogeneously built continent of the planet, spanning a wide range of climate types. In addition, Eurasia is the northernmost continent of the planet, the climate of which was the

most dynamic due to the cold snap spreading from the pole. Today the main feature of the climate of Eurasia is diversity because of the considerable zonal extent of the continent. Moreover, Eurasian climate is characterized by a distinct contrast between the western (Atlantic) and eastern (Pacific) side, with a central region marked by strong seasonality typical of continental interiors (Rhines and Häkkinen, 2003; Takaya and Nakamura, 2005). The presently observed gradients largely result from prevailing global and regional circulation patterns of the atmosphere and oceans and their variability. The northward energy transport by ocean and atmosphere causes a displacement of the January isotherms by up to 20° N as evident from climatological data (New et al., 2002), and the asymmetric distribution of Koeppen–Geiger climate types over Eurasia (Fig. 2b; Kottek et al., 2006). The comparison of the Cenozoic continental climate evolution from the Atlantic and Pacific

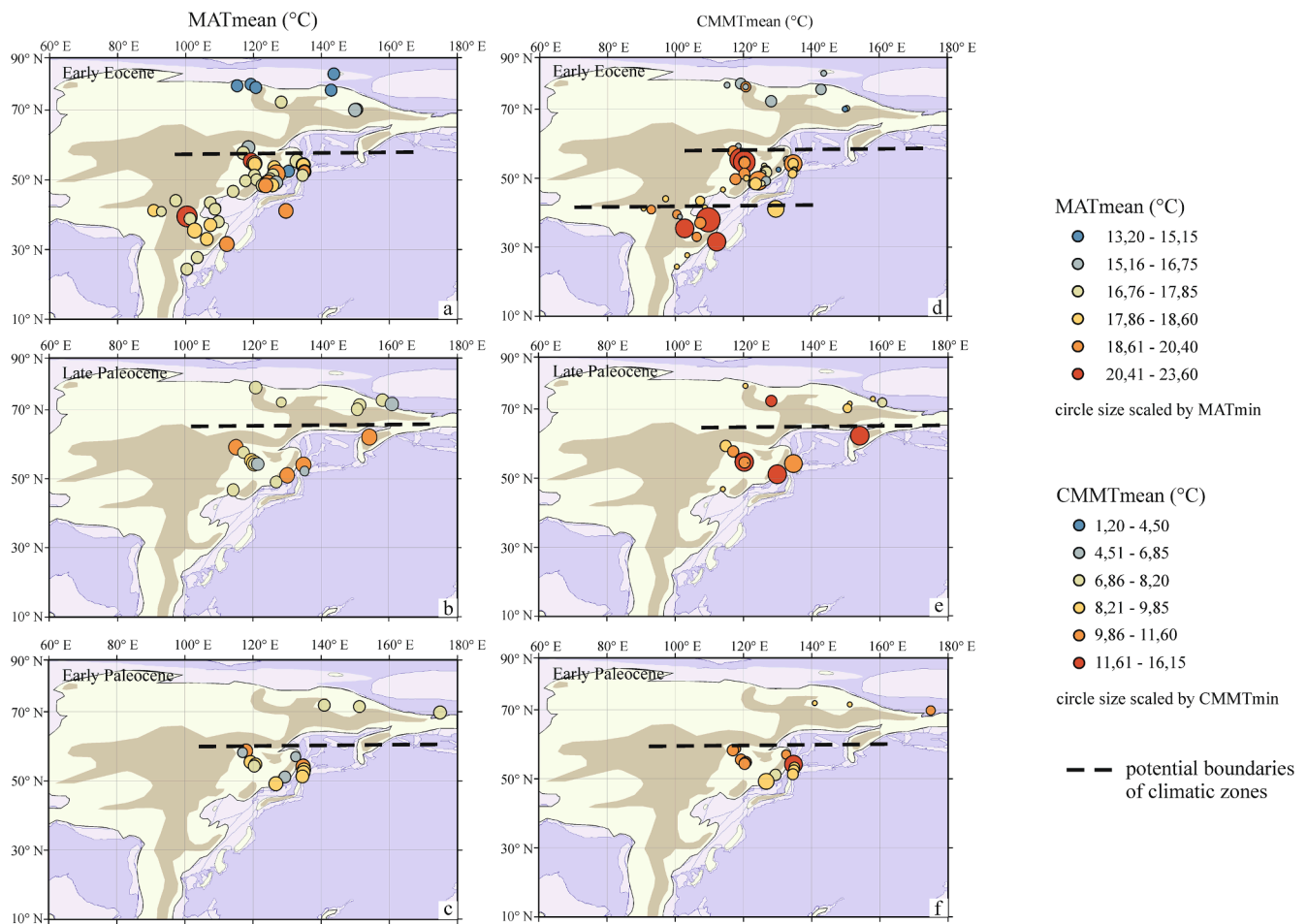


Fig. 3. Spatial temperature distributions along the Pacific side of Eurasia during the early Paleocene.

side of Eurasia reveals the existence of differing regional patterns and spatial gradients from west to east, also in the Past (Utescher et al., 2015). However, the spatial gradient from south to north has not yet been studied in detail.

The Paleocene climate at high latitudes in both the Southern and Northern Hemispheres was characterized by an extremely low latitudinal temperature gradient, small amplitudes of seasonal, monthly, and daily temperatures (Greenwood et al., 2001). On the contrary, Budantsev (1999), based on a comparative analysis of the palaeoclimates of the eastern and western sectors of Asia, found evidence for a predominantly meridional zonation over Asia, which indicates the predominance of meridional over latitudinal differentiation, in contrast to modern zonal climate differentiation.

5.2.1. Paleocene

For the early Paleocene, our palaeotemperature reconstruction reveals the most equable conditions for the studied region, among the other time slices considered. With temperatures in the High Arctic being at the highest level among all time slices considered here, polar amplification obviously had a most prominent effect at that time. However, the available sites only provide data for the latitudinal sector N of ca. 48° N so that conditions at lower latitudes cannot be assessed. A minor gradient is observed between the southern and northern sectors, with MATmin mostly being as high as ca. 13 °C (CMMTmin at ca. 5 °C) at 70° N, and ca. 17 °C (CMMTmin at 6–9 °C) at 50° N (Fig. 2c and f). These results are in general agreement with a CLAMP-based reconstruction by Akhmetiev (2004) revealing two climatic zones in the Northern Hemisphere during the Paleocene, namely a (warm) temperate humid zone, and a humid subtropical and paratropical zone. According to Akhmetiev

(2004), the southern boundary of the first zone of temperate warm climate at the beginning of the Paleocene passed near 59° N (Akhmetiev, 2004). Based on CLAMP Akhmetiev (2004) suggested MAT from 10 to 14 °C and CMMT up to 4 to 7.8 °C for the northerly zone, and MAT from 14 to 16 °C and CMMT up to 6 to 9 °C for southerly zone. All values well overlapping with the actual CA-based reconstruction.

According to Budantsev (1999), in the south of the RFE (Sakhalin, Primorye) MAT reached 13.8 °C, WMMT and CMMT were 20 and 7.8 °C, respectively, while in the north (Koryak Upland) MAT ranged within 10.3–11.9 °C, and WMMT and CMMT were 18.8–19.7 and 3.1–5.0 °C, respectively.

The late Paleocene temperature pattern in our reconstruction does not show any substantial changes compare to the early Paleocene. While the High Arctic persisted to be very warm, data indicate warmer conditions (higher temperature means, especially for CMMT) for the mid-latitudinal range. Aberrantly high temperatures obtained for the high latitudinal Yarovaya91 site (Fig. 3f) and related to the presence of mangrove elements may be referred to extreme polar warmth during the hyperthermal ETM 2 event.

Also, in previous reconstructions larger northward extension of the subtropical zone is shown. Laukhin et al. (1992) suggest the warmest variant of a warm temperate, possibly subtropical climate for the northern margin of northeastern Asia in the Paleocene. Bondarenko et al. (2020a) indicated the negligible Paleogene temperature gradients over Primorye with MAT values 16–20.8 °C for the early Paleocene and 12.8–21.1 °C for the early Paleocene. Using the CA method, Bondarenko et al. (2020b) documented the persistence of warm to cool temperate, overall humid climate conditions with MAT 16.5–18.5 °C, CMMT 7.5–11.7 °C and WMMT 24.9–25.7 °C throughout the Paleocene in the

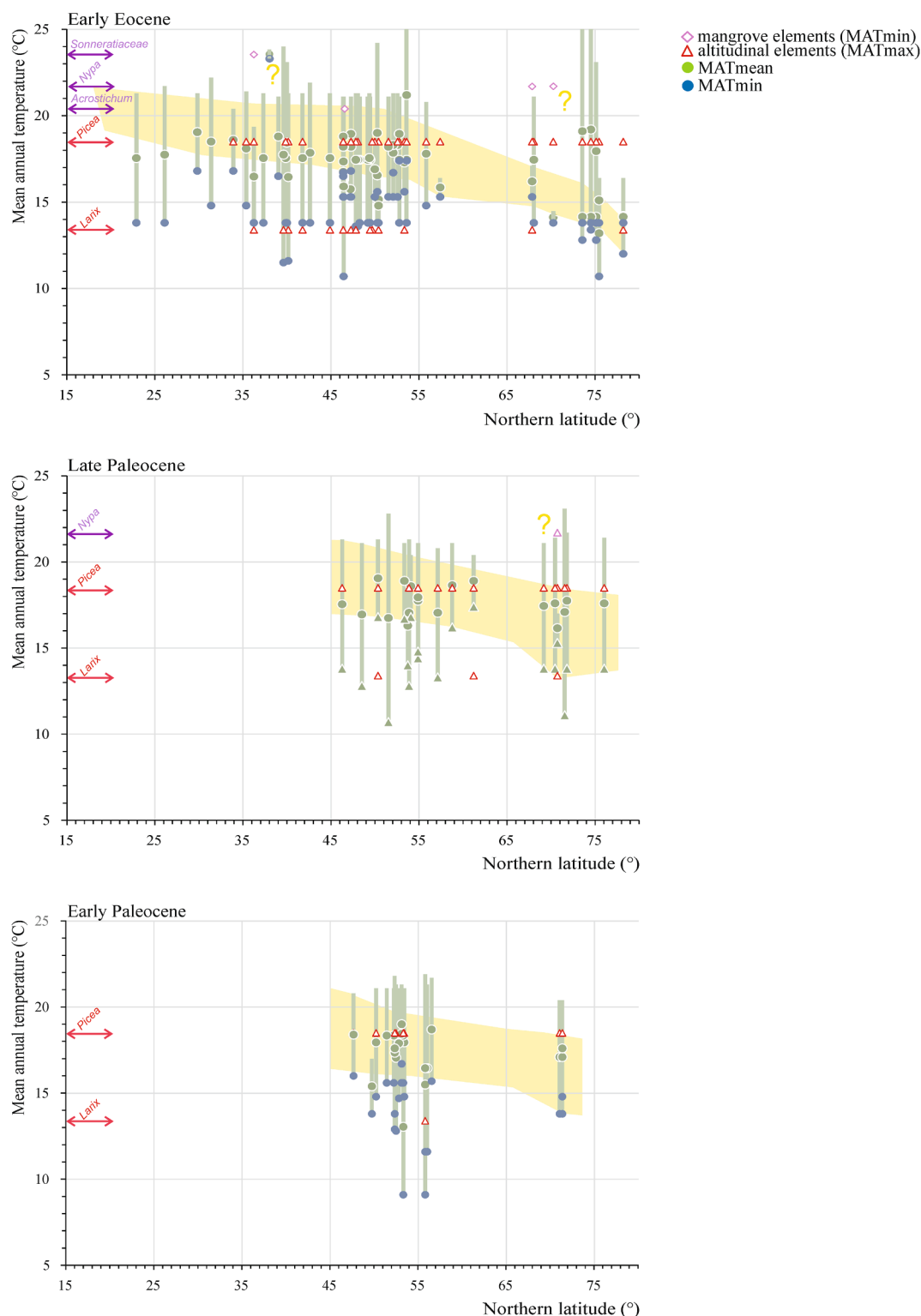


Fig. 4. MAT coexistence intervals obtained from the Pacific early Paleogene floras plotted on palaeo-latitude positions of the single sites and inferred temperature field highlighted in yellow. Red double arrows and triangles refer to MAT_{max} of *Larix* and *Picea* being altitudinal elements in the southern study area and excluded from the analysis. Blue double arrows and diamonds refer to MAT_{min} of mangrove elements that partly form outliers in the CA analyses. Rotation of latitudes: OSDN Plate Reconstruction Service using hotspot frame for 56 Ma.

Amur Region (RFE). The zone of humid subtropical and paratropical climate, according to Akhmetiev (2004), in the Paleocene occupied the middle latitudes of the Northern Hemisphere. The southern part of the Boreal region, included in the zone of temperate warm climate, is characterized by MAT up to 14–16 °C, relatively high WMMT (up to

20–22 °C) and CMMT (about 6 to 9 °C) for the late Paleocene (Akhmetiev, 2004). In North America, “paratropical”, subtropical and similar to tropical floras spread partly in southern Canada, but mainly in the western and central regions of the US, as well as in the framing of the sea gulf extending north of the modern Mexican and reaching the

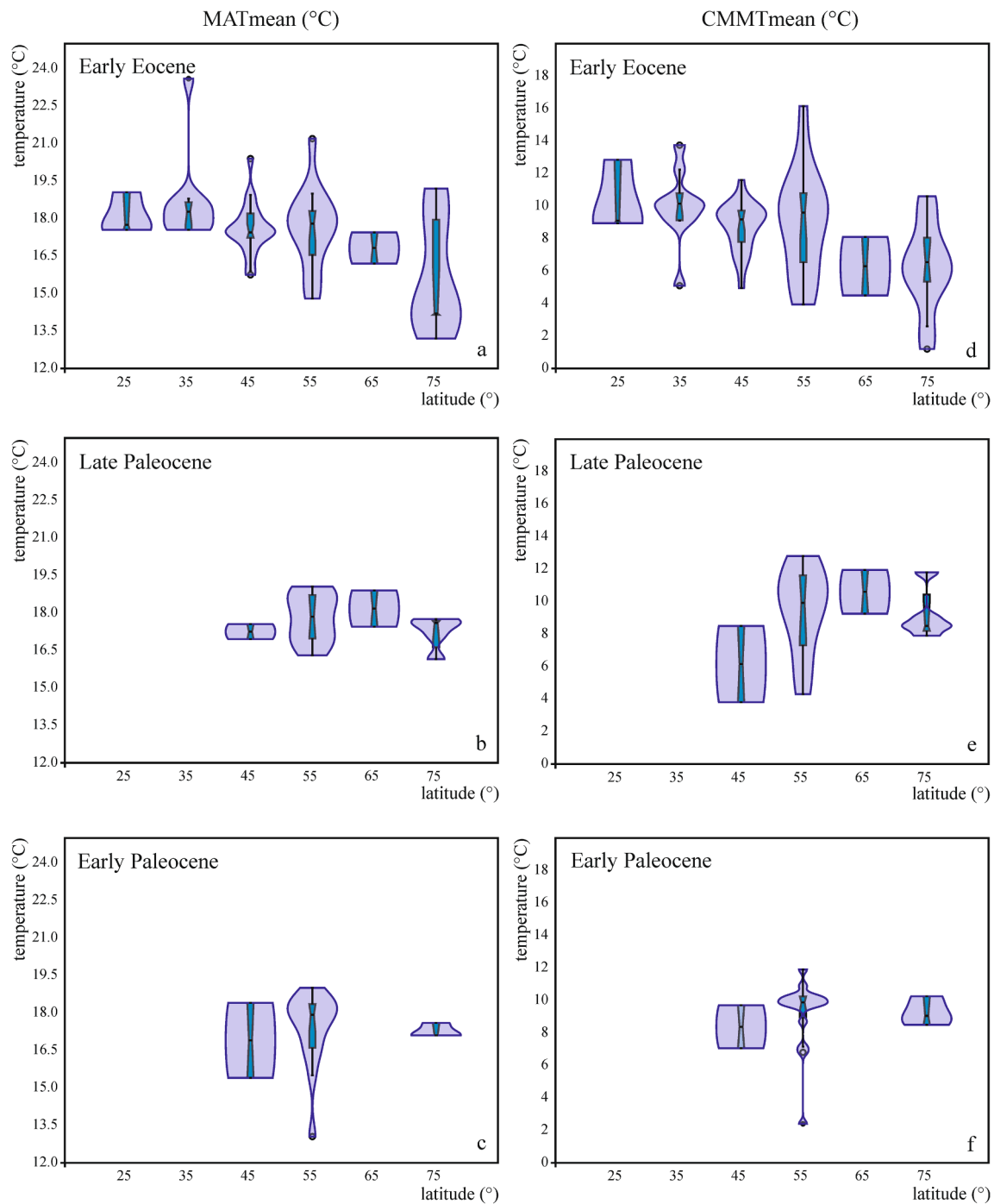


Fig. 5. Box-plots of zonal means (10° steps) of MAT and CMMT during the early Paleogene calculated using coexistence interval means and based on rotated latitude values (cf. Fig. 4).

confluence area the Mississippi and Missouri rivers (Akhmetiev, 2004). Our data indicate similar conditions for the Pacific areas of Eurasia in range of the climatic zone both the early and late Paleocene.

5.2.2. Early Eocene

Spanning a latitudinal range of ca. 20°N to the High Arctic, early Eocene data most comprehensively reflect the latitudinal temperature pattern in the Paleogene of Pacific Eurasia. For the High Arctic, CA interval means indicate cooling in the order of 3°C for MAT and CMMT compared to the Paleocene level (Fig. 4) and may have been as low as ca. 10°C for MAT and close to 0°C for CMMT, or even slightly below (Fig. 5). These data are close to CLAMP-based temperature estimates for

early Eocene floras of northern Yakutia and the Far East (MAT 9.7°C , WMMT 18.6°C , CMMT 1.6°C , cf. Budantsev, 1999). While the mid-latitude temperatures did not differ significantly from the earlier time slices studied, the moderate temperature level obtained from the lower latitude sites located south of 45°N is noteworthy. With MAT not exceeding ca. 22.5°C and CMMT $< 15^\circ\text{C}$, temperatures in the studied latitudinal range of $20\text{--}45^\circ\text{N}$ did not reach the tropical level. These temperature levels are cool given the low palaeolatitude at a time of global warmth (Zachos et al., 2008). Similar cool conditions of the southern Chinese realm were previously reported in a study on temperature anomalies with respect to modern considering a middle Eocene time slice (Utescher et al., 2011). Also, recent studies on middle and late

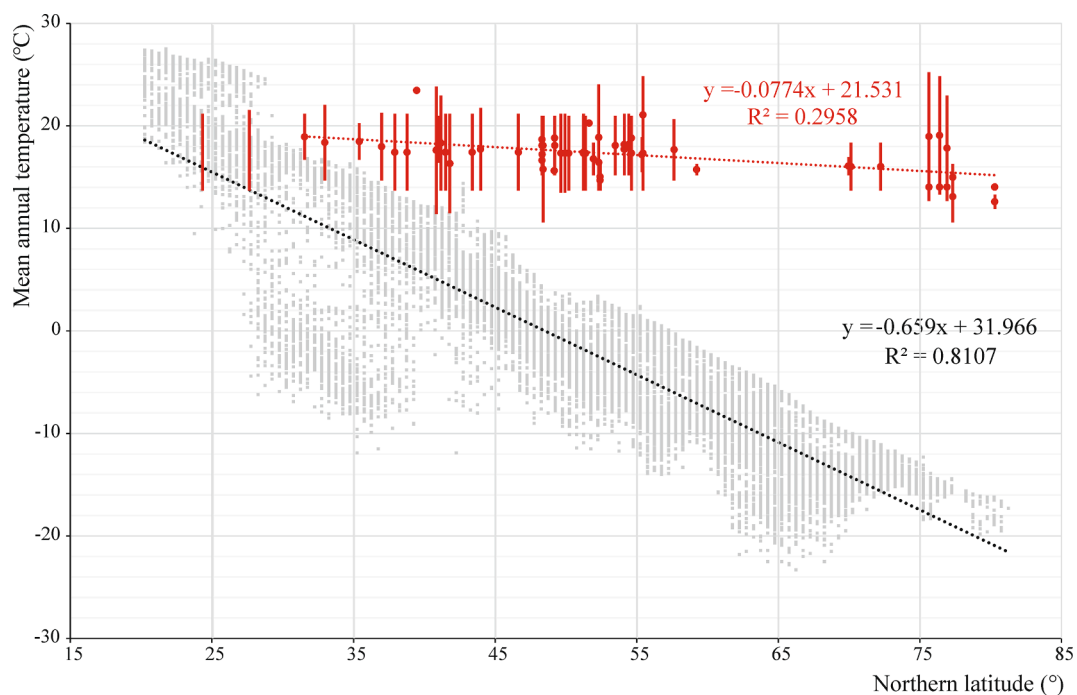


Fig. 6. Modern and past latitudinal MAT gradients together with linear regressions, based on Coexistence Interval means for the palaeo-data, excluding both most southerly floras having unspecific results. The modern MAT space refers to a sector from 80 to 180 °E and is obtained from the (oversampled) WORLDCLIM dataset.

Eocene floras of South China revealed a comparatively moderate temperature level, with CLAMP-based estimates being in the order of the presently reconstructed early Eocene data (MAT 20–24 °C; CMMT 9–15 °C; cf. Jin et al., 2017).

As for the late Paleocene, mangrove elements, sporadically present, even at high latitudes, may indicate hyperthermal phases, also within the early Eocene. It can be assumed that during such phases extreme shallow hemispherical gradients existed, under a strong warming of the polar region. The role of altitudinal elements that may have contributed to the low temperature estimates from floras at lower latitude is discussed in section 5.5.

Based on CLAMP data, Wolfe (1994, 1995) for Pacific North America indicates that Eocene MAT was generally high (the early Eocene MAT ca. 19 °C at paleolatitude 70 °N and > 27 °C at paleolatitude 45 °N) and thus reveal conditions that are comparable to our East Asian Pacific data. For the early Eocene floras from London Clays, the following climatic parameters were determined: MAT 16–19 °C, WMMT 23 °C and CMMT 8–16 °C (Van Beuskom, 1971).

As regards the lower latitudes of the Atlantic realm during the early Eocene published records provided overall warmer conditions, compared to our Pacific record. In the southeast of North America, the floras are already predominantly tropical type (Akhmetiev, 2004). Climatic characteristics, calculated by Greenwood and Wing (1995) using the CLAMP method for the early Eocene or early – middle Eocene floras of the Canadian Arctic Archipelago (79°55' N), is MAT of 9.3 °C, and CMMT –0.8 °C. In southern Europe, the considered climatic zone was gradually replaced by a tropical one. It is characteristic that most of the floras of the described climatic zone contain the remains of the *Nypa* mangrove palm, as well as other pinnate and fan palms, representatives of the herpetofauna (Akhmetiev, 2004).

In various earlier publications, East Asian Paleogene climates were subdivided into three categorically latitudinal zones controlled by the planetary wind system (e.g., Akhmetiev, 2004; Guo et al., 2008; Liu, 1997; Wang et al., 1999; Z. Zhang et al., 2012) that partly are reflected in the actual temperature reconstructions. However, these zones are at least partly defined by hydrological constraints, not subject to the present reconstruction. Lithologically, two humid zones located separately

in the south and north are characterized by the occurrence of coals and/or oil shales, while the third broad arid zone resided in the middle and flanked by the two humid zones is largely designated by the widespread red beds and/or evaporites along ca. 30° N paleolatitude (ranging between ~ 25° N and ~ 35° N), allegedly driven by the then subtropical highs (Guo et al., 2008; Liu, 1997; Wang et al., 1999; Z. Zhang et al., 2012).

5.3. Plant-based early Paleogene continental temperature in view of other proxies and modelling studies

Very warm conditions in the early Eocene at high latitudes as evident from our plant-based data are supported by results obtained from other continental and marine proxies. High MAT (~16–21 °C; Suan et al. 2017 and ~ 18–25 °C; Weijers et al., 2007) and SST (~18–25 °C; Sluijs et al., 2009) values based on tetraether membrane lipids are reported from Arctic lower Eocene strata of IODP Site 302, Lomonosov Ridge. Also, from lower to middle Eocene strata of Arctic Canada and Greenland high temperatures with MAT (8 and 17 °C) and CMMT (3–9 °C) result from faunal and other proxy data (Eldrett et al., 2009; Huber and Caballero, 2011; Markwick, 1994).

The very warm SST, MAT and CMMT values reported in the aforementioned works for the Arctic and the high continental temperatures we presently reconstruct for E Asia north of 65° latitude demonstrate that the early Eocene extreme warmth was a pan-Arctic phenomenon and confirm the view that models unrealistically simulate greenhouse climates (e.g., Sagoo et al., 2013). State-of-the-art climate models can indeed only simulate such elevated temperatures at high latitudes using extremely high atmospheric CO₂ contents (>4000 ppm), which are not only well above proxy estimates, but also difficult to explain in terms of CO₂ degassing (Hoareau et al., 2015; Huber and Caballero, 2011; Jag-niecki et al., 2015). Suggested mechanisms to further warm polar areas include enhanced high-latitude wetland methane emissions, higher polar humidity, or highly modified configurations of cloud properties, water vapor, or atmospheric heat transport (Beerling et al., 2011; Greenwood et al., 2010; Kiehl and Shields, 2013; Sagoo et al., 2013). Clay mineral and pollen data of Suan et al. (2017) for the New Siberian

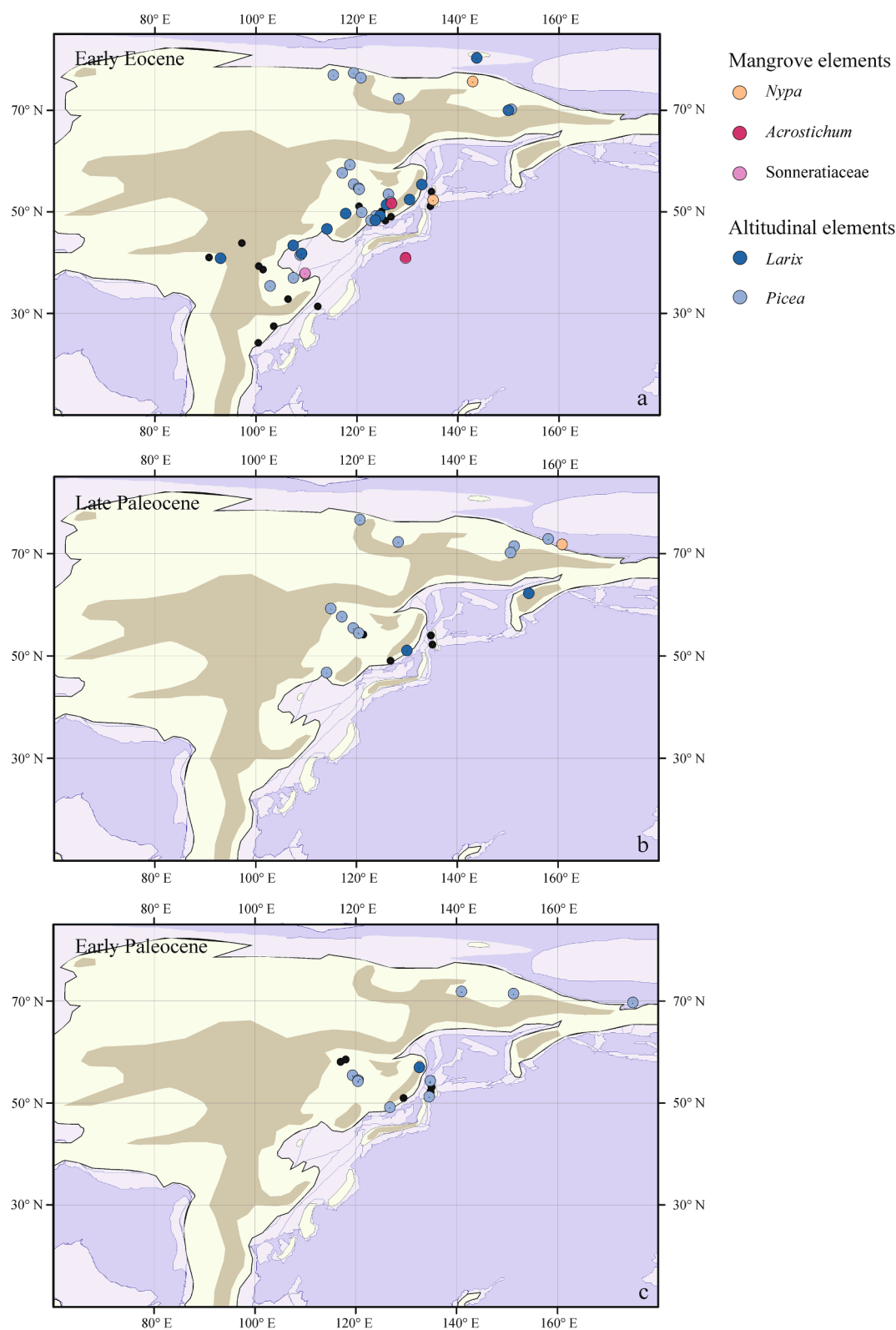


Fig. 7. Distribution of mangrove and altitudinal elements along the Pacific side of Eurasia during the early Paleogene.

Islands show for the first time that the unusually high MAP (>1000 mm) previously evidenced for North American and Greenland margins (Eldrett et al., 2009; Greenwood et al., 2010; West et al., 2015; Wolfe et al., 2012) also characterized Arctic Siberia, and point to elevated rainfall in all pan-Arctic drainage basins.

During times of peak global warmth in the early Eocene, proxies

indicate that high-latitude southwest Pacific SSTs warmed to over 30 °C (Bijl et al., 2009; Creech et al., 2010; Hollis et al., 2009). This either implies a virtual collapse of the zonally averaged equator-to-pole thermal gradient, which cannot be reconciled with the climate dynamics that underpin climate and circulation models (e.g., Huber and Sloan, 2001; Lunt et al., 2012; Winguth et al., 2010), or indicates a peculiarity

of the regional climate and circulation. Even in the warmest Eocene climate simulations, the equator-to-pole gradient is > 20 °C and mean annual SST for 55–65° S is ~ 17 °C. In addition to this proxy-model discrepancy, these SSTs are 10 °C warmer than local mean annual air temperatures (MAAT) derived from leaf fossil studies (18–22 °C; Greenwood et al., 2003, 2004) and are excessively warm in relation to proxy SSTs from other regions. The single exception is the Arctic Ocean where TEX86-based SST is also significantly (~ 7 °C) warmer than modelled SST (Sluijs et al., 2006, 2009).

For the lower latitudes, the majority of modelling scenarios prescribing high atmospheric CO₂ show strongly raised temperatures (Lunt et al., 2021). Our plant-based temperature estimates for the early Eocene in the East Asian Pacific realm at 20–30 °N tend to be close to or even below the modern level. CLAMP-based reconstructions from the middle to late Eocene floral record of South China likewise revealed comparably cool conditions, thus suggesting that low latitude Eocene climates may not have been uniformly warm (Jin et al., 2017; Spicer et al., 2014). For a possible reason, a larger extension of the Pacific tropical pool and enhanced northward oceanic heat transport can be cited.

5.4. Distribution of mangrove elements – Implications for continental temperature and SSTs

It is generally accepted that mangroves and palms are the most reliable climatic indicators among flowering trees (Akhmetiev, 2004). The ranges of most of their species lie in the tropics, i.e., do not go beyond the average annual isotherm of 18 °C. Today, mangrove forests occur world-wide on tropical, sheltered shores (Chapman, 1976; Tomlinson, 1986). Mangroves include halophytes and share a suite of convergent adaptations to saline, anoxic habitats (e.g., Ball, 1988; Duke et al., 1998; Stewart and Popp, 1987; Tomlinson, 1986). However, during the early Paleogene mangroves were found even in the High Arctic.

Fossil evidence of mangroves suggests the continuous presence of this highly specialized coastal vegetation since the end of Paleozoic which has predated the origin of angiosperms (Tomlinson, 1986). *Nypa/Sonneratia/Acrostichum* records known for the early Paleogene in the global context can be extended (cf. Ellison et al., 1999; Popescu et al., 2021; Srivastava and Prasad, 2019). In our records, mangroves are noted in the late Paleocene and early Eocene (Table 3, Fig. 7). *Avicennia* pollen appears confidently in Europe in the early Eocene (Chandler, 1964; Sein, 1961), and New Siberian Islands (Suan et al., 2017; Suc et al., 2020). In the Eocene, the range of mangroves reached about 50° N, especially in Western Eurasia, but also in the western part of Northern America (Utescher and Mosbrugger, 2007). Popescu et al. (2021) indicate two palaeolatitudinal thresholds for the *Avicennia* mangrove at 65–70° N and 35° N during the warmest Palaeogene phases (PETM and EECO).

In our East Asian Pacific record, mangrove taxa occur in a single late Paleocene flora at ca. 70 °N. In the early Eocene, various mangrove taxa are recorded, attaining even 75 °N, and present in a total of four floras, located between ca. 50 and 35 °N. In the CA analysis, the presence of mangrove taxa may lead to non-overlapping of temperature ranges of the single taxa while taphocoenoses represented by pollen floras may

include both, elements from warm coastal stands and from cooler up-land phytocoenoses. Nevertheless, the occurrence of mangroves may point to the existence of very warm phases in the early Paleogene during which temperature levels may have been higher by up to 10 °C, compared to the average situation shown in Fig. 5.

Generally, paleoclimate proxies indicate exceptional warmth with reduced pole-to-equator temperature gradients during the early Eocene (Eldrett et al., 2009; Huber and Caballero, 2011; Pross et al., 2012; Weijers et al., 2007; West et al., 2015). The extension of thermophilic vegetation into high latitudes, the wide distribution of mangroves and the presence of a forest cover in the polar regions coincide with a latitudinal thermal gradient being about only one third of the Present (e.g., Greenwood and Wing, 1995; Wolfe, 1978) or even lesser, as suggested by our Pacific data. The presence of mangroves in the early Eocene records at high latitudes is largely in line with the climate reconstructions and is associated with the hyperthermal events such as the PETM, ETM2 and/or EECO (Bondarenko et al., 2022; Bondarenko and Utescher, in press; Salpin et al., 2019; Suan et al., 2017; Suc et al., 2020).

5.5. The role of altitudinal elements

As mentioned above, *Larix* and *Picea* were excluded from climatic calculations for the early Paleogene of the Pacific coast of Eurasia, because they potentially may bias the reconstruction for being too restrictive. However, fossil evidence for these genera may provide valuable clues about the regional early Paleogene climate and topography in the study area. At present, larch grows in boreal, cold temperate regions of the Northern Hemisphere, (FNA Editorial Committee, 1993; Kharkevich, 1989; Wu and Raven, 1999). In addition to Russia, the natural range of *Larix* covers the mountainous areas of Europe and Asia. In nature, it is also quite widespread in Canada, less often in the northern states of the USA, including Alaska. Larch grows at the (0)300–4,300 (4,600) m a.s.l., mainly in mountains, hills, slopes, rare in swamps, valleys and lowland subarctic plains (FNA Editorial Committee, 1993; Kharkevich, 1989; Wu and Raven, 1999). Spruce grows in temperate and cold (subarctic and subalpine) regions of the Northern Hemisphere, including Europe, Asia, and North America (Kharkevich, 1989; FNA Editorial Committee, 1993; Wu and Raven, 1999), at (0)300–3,800 (4,100) m a.s.l., mainly on N-facing slopes, rare in river basins and valleys (FNA Editorial Committee, 1993; Kharkevich, 1989; Wu and Raven, 1999). Thus, the presence of these elements in the warm temperate and subtropical phytocoenoses existing in the early Paleogene of the Pacific coast of Eurasia needs further considerations.

Early Paleogene floras of the Pacific coast of Eurasia containing *Larix* and *Picea* remains are shown in Fig. 7. While *Larix* was very rare in the early and late Paleocene floras, the earliest records of *Picea* pollen are known from both the early and late Paleocene floras. In the early Eocene, *Larix* pollen and even macro-remains are reported from various sites located at high and mid-latitudes of the study area as well as *Picea*.

Summarizing these facts, we assume that *Larix* and *Picea* may have occurred near sea-level at latitudes north of ca. 65°. In this region, overlapping of their climatic requirements with the majority of taxa is observed and hence, these taxa probably confined the upper ends of

Table 3
Location of the early Paleogene floras containing mangroves in Pacific side of Eurasia.

Mangrove species	Age	Locality name	Lat (°N)	Lon (°E)	Type of flora	References
<i>Acrostichum</i> L.	EE	Bikin	46.57	135.09	PF	Pavlyutkin and Petrenko (2010)
	EE	AS_Japan	36.00	138.00	LF	Tanai (1972)
<i>Avicennia</i> L.	EE	Novosibirskie Islands	75.53	143.91	PF	Suan et al. (2017)
<i>Nypa</i> Steck	LP	Yarovaya91	67.80	161.20	PF	Belaya and Litvinenko (1989)
	EE	Bykovskaya Protoka	72.20	127.90	PF	Grinenko and Kiseleva (1971)
	EE	Tastakh Lake	70.90	145.60	PF	Kulkova (1973)
<i>Phoenix</i> L.	EE	Tastakh Lake	70.90	145.60	PF	Kulkova (1973)
Sonneratiaceae Engl. et Gilg.	EE	Gaoyou	32.80	119.40	PF	Zhang and Qian (1992), Quan et al. (2012a)

Age: EE – early Eocene; LP – late Paleocene. Fossil type: L – leaf; P – pollen and spores.

MAT CIs to ca. 18 °C and 13 °C, respectively when occurring. The concentration of *Larix* records in the middle latitudes (<65° N) was probably related to regional uplift processes. In the Primorye area these may have been related to the present-day Sikhote-Alin Range (Bondarenko et al., 2020a), connected with coeval volcanic activities. The elevation may have exceeded 500 m a.s.l. (Akhmetiev et al., 2009), and it was already assumed in other studies that this uplift was sufficient for the manifestation of altitudinal vegetation zones (Blokhina, 1987). Thus, it may be assumed, that in the Paleogene, larch was, most likely, an element of extrazonal altitudinal vegetation, at least in its southerly distribution area. Since the early Oligocene and in the Neogene (cf. Blokhina, 1999, 2012; Bobrov, 1972), *Larix* became more abundant and widespread in the pollen record, probably linked to the observed general cooling trend and/or uplift processes. Palynological studies on the Tibetan Plateau (QTP) and neighboring areas suggest that conifers were present in the region some 50 Ma but that *Picea* species only started to be an important fraction of the pollen record on the QTP around 38 Ma (Wang et al., 1990; Dupont-Nivet et al., 2008).

6. Conclusions

For the first time, a comprehensive quantitative palaeotemperature data set has been compiled for the Pacific side of Eurasia for the early Paleogene. The results obtained fill a regional gap in currently available datasets for Eurasia, with a focus on Russian Far East and Eastern Siberia, where data paucity seriously hinders their understanding in a global context. Based on the generalization and analysis of 110 floras, for the first time detailed spatial gradients and temporal trends in temperature changes along the Pacific coast of Eurasia in the early Paleogene are quantified.

Generally, there is a gradual warming from the early Paleocene to early Eocene based on mean values of two temperature variables. There is a gradual increasing in the range of mean values of two temperature variables from the early Paleocene to early Eocene. Moreover, a weak gradual increase of temperature seasonality from the early Paleocene to early Eocene was obtained.

The latitudinal temperature gradient along the Pacific coast of Eurasia estimates as an extremely low, especially during the early Paleocene. Nevertheless, based on mean values of MAT and CMMT, two different regional climatic zones can be distinguished in the Paleocene representing in each case the cooler and warmer (subtropical) part of warm temperate climate of the Koeppen-Geiger system. In the early Eocene, the gradient became more clearly pronounced and in addition, a cool temperate zone can be distinguished.

The altitudinal elements may have occurred near sea-level at latitudes north of about 56 °N. The concentration of *Larix* and *Picea* records in the middle latitudes was probably related to regional uplift processes. The presence of mangroves in our early Eocene records is largely in line with our climate reconstruction and possible can be related to hyperthermal events.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jseae.2022.105401>.

References

- Abels, H.A., Dupont-Nivet, G., Xiao, G., Bosboom, R., Krijgsman, W., 2011. Step-wise change of Asian interior climate preceding the Eocene – Oligocene Transition (EOT). *Paleogeogr., Paleoclimatol., Paleocool.* 299 (3–4), 399–412.
- Ablaev, A.G., 1976. An excursion into the early Cenozoic history of the geological development of the West Sakhalin sedimentary basin. In: Ablaev, A.G. (Ed.), *Essays on the Geology and Paleontology of the Far East*. Far Eastern Scientific Center of the Academy of Sciences of the USSR, pp. 15–19 [in Russian].
- Ablaev, A.G., Vasiliev, I.V., 1998. Miocene Kraskian flora of Primorya. *Dal'nauka, Vladivostok* 107 [in Russian].
- Ablaev, A.G., 2000. Paleogene biostratigraphy of the coastal region in south Primor'e. *Dal'nauka, Vladivostok*, 117 p. [in Russian].
- Akhmetiev, M.A., 1976. On climatic fluctuations in the Paleogene and Neogene in the middle and high latitudes of the globe (according to paleobotanical data). In: Sidorenko, A.V. (Ed.), *International Geological Congress, 25 Session (Sydney, 1976), Reports of Soviet Geologists: Paleontology, Marine Geology*. Academy of Sciences of the USSR, Ministry of Geology of the USSR, Nauka, pp. 138–146 [in Russian].
- Akhmetiev, M.A., 2015. High-latitude regions of Siberia and northeast Russia in the Paleogene: stratigraphy, flora, climate, coal accumulation. *Stratigr. Geol. Correl.* 23 (4), 421–435.
- Akhmetiev, M.A., Golovneva, L.B., 1998. New data on the composition and age of the Malomikhailovskaya flora (Upper Cretaceous, Lower Amur Region). *Stratigr. Geol. Correl.* 6 (3), 43–55 [in Russian].
- Akhmetiev, M., Walther, H., Kvaček, Z., 2009. Mid-latitude Palaeogene floras of Eurasia bound to volcanic settings and palaeoclimatic events – experience obtained from the Far East of Russia (Sikhote-Alin) and Central Europe (Bohemian Massif). *Acta Musei Naturalis Pragae, Series B, Historia Naturalis* 65, 61–129.
- Akhmetiev, M.A., Zaklinskaya, E.D., Medyulyanov, V.I., 1978. Paleobotanical characteristics of the Danish, Paleocene and Lower Eocene deposits of Western Sakhalin. *Soviet Geol.* 5, 77–89 [in Russian].
- Akhmetiev, M.A., Zaporozhets, N.I., Benyamovskiy, V.N., Aleksandrova, G.A., Iakonleva, A.I., Oreshkina, T.V., 2012. The Paleogene history of the Western Siberian seaway – a connection of the Peri-Tethys to the Arctic Ocean. *Austrian J. Earth Sci.* 105 (1), 50–67.
- Akhmetiev, M.A., 1973. Paleocene and Eocene flora of the southern Far East of the USSR and adjacent countries and their stratigraphic position. *Sovetskaya geologiya* 7, 14–29. [in Russian].
- Akhmetiev, M.A., 1988. Cenozoic flora of eastern Sikhote-Alin. *Geologicheskii institut Akademii nauk SSSR, Moscow*, 48 p. [in Russian].
- Akhmetiev, M.A., 1993. *Phytostratigraphy of Paleogene and Miocene Continental Deposits of Boreal Asia (Transactions of the Geological Institute of the Russian Academy of Sciences 475)*. Nauka, Moscow, 143 p. [in Russian].
- Akhmetiev, M.A., 2004. The Paleocene and Eocene Global Climate. Paleobotanical evidences. In: Semikhatov, M.A., Chumakov, N.M. (Eds.), *Climate in the Epochs of Major Biospheric Transformations (Trudy Geologicheskogo Instituta RAN, Vol. 550)*. Geologicheskii institut Rossiiskoi akademii nauk, pp. 10–43. [in Russian].
- Baikovskaya, T.N., 1950. Paleocene flora of the Zee-Bureya Plain. *Voprosy Paleontologii* 1, 348–381 [in Russian].
- Ball, M.C., 1988. *Ecophysiology of mangroves*. *Trees* 2, 129–142.
- Baskakova, L.A., Gromova, N.S., 1979. Biostratigraphic dismemberment of the Uglovskii horizon according to palynological data. In: Poyarkov, B.V. (Ed.), *Paleontology and stratigraphy of the Far East*. Dal'nevostochnyi nauchnyi tsentr Akademii nauk SSSR, pp. 109–114. [in Russian].
- Baskakova, L.A., Gromova, N.S., 1984. Stratigraphy of Smolyaninovskii coal mine in the Southern Primorye. In: Ablaev, A.G. (Ed.), *Materials on stratigraphy and paleogeography of East Asia*, Dal'nevostochnyi nauchnyi tsentr Akademii nauk SSSR, pp. 59–69. [in Russian].

- Baskakova, L.A., Lepekhina, V.G., 1990. New data on the phytostratigraphy of the Paleogene of the Zerkal'nenskii Basin. In: Ablav, A.G. (Ed.), New data on stratigraphy of the Far East and the Pacific Ocean. Dal'n vostochnoe otdelenei Rossiiskoi akademii nauk, pp. 52–60. [in Russian].
- Beerling, D.J., Fox, A., Stevenson, D., Valdes, P.J., 2011. Enhanced chemistry-climate feedbacks in past greenhouse worlds. *Proc. Natl. Acad. Sci.* 108 (24), 9770–9775.
- Belaya, B.V., Litvinenko, I.S., 1989. Structure and age of Cenozoic sediments in the Khatachan - Yarovaya interfluvium (Anyui depression). In: Volobueva, V.I. (Ed.), Continental Paleogene and Neogene of the North-East of the USSR. Izdatel'stvo SVKNII DVO AN SSSR, pp. 18–32. [in Russian].
- Beltenev, E.B., Varnavsky, V.G., 1977. Paleogeographic conditions for the development of the territory of the Khabarovsk Territory and the Amur Region in the Paleogene and Neogene time. In: Khomentovskiy, A.S. (Ed.), Issues of lithogenesis in the south of the Far East. Nauka, pp. 17–35 [in Russian].
- Bijl, P.K., Schouten, S., Sluijs, A., Reichert, G.-J., Zachos, J.C., Brinkhuis, H., 2009. Early Paleogene temperature evolution of the southwest Pacific Ocean. *Nature* 461, 776–779.
- Blokhina, N.I., 1987. An attempt of reconstruction of relief and plant communities of the past using xylotomic data. *Botanicheskii Zhurnal* 72 (2), 197–201 [in Russian].
- Blokhina, N.I., 1999. Fossil larches of the Sikhote-Alin. In: Man'ko, Yu.I. (Ed.), Forest and forest formation process in the Far East: Proceedings of International Conference, devoted to the 90-th anniversary of B.P. Kolesnikov. IBSS DVO RAN, pp. 170–171. [in Russian].
- Blokhina, N.I., 2012. The origin and possible ways of distribution of the Far Eastern larches by palaeobotanical data. In: Akhmetiev, M.A., et al. (Eds.), Biogeography: methodology, regional and historical aspects: Proceedings of the conference dedicated to the 80-th anniversary of V.N. Tikhomirov (1932–1997). KMK Scientific Press, pp. 41–44. [in Russian].
- Bobrov, E.G., 1972. History and systematics of larches. *Komarovskie chteniya* 25, 1–96 [in Russian].
- Bolotnikova, M.D., 1979. Spore-pollen complexes of Tertiary sediments of the western coast of the Sea of Japan. *Nauka* 196, p [in Russian].
- Bolotnikova, T.N., 1988. Palynological characteristics and age of coal-bearing deposits of the Chernyshevskii Brown Coal Field (Southern Primorye). *Tikhookeanskaya Geologiya* 4, 101–105 [in Russian].
- Bolotnikova, M.D., 1977. Palynocomplex of the Khulgunskaya Formation of the Tigil'sky Reference Section (Western Kamchatka). In: Krassilov, V.A. (Ed.), Paleobotany in the Far East. Far Eastern Scientific Center of the AN USSR, pp. 38–44. [in Russian].
- Bondarenko, O.V., Utescher, T., in press. Late early to early middle Eocene climate and vegetation change at Tastakh Lake (northern Yakutia, Eastern Siberia). *Palaeobiodiversity and Palaeoenvironments*. <https://doi.org/10.1007/s12549-022-00530-6>.
- Bondarenko, O.V., Blokhina, N.I., Utescher, T., 2019. Major plant biome changes in the Primorye Region (Far East of Russia) during the Paleogene. *Botanica Pacifica* 8 (1), 3–18.
- Bondarenko, O.V., Blokhina, N.I., Mosbrugger, V., Utescher, T., 2020a. Paleogene climate dynamics in the Primorye Region, Far East of Russia, based on a Coexistence Approach analysis of palaeobotanical data. *Palaeobiodivers. Palaeoenviron.* 100 (1), 5–31.
- Bondarenko, O.V., Blokhina, N.I., Utescher, T., 2013. Quantification of Calabrian climate in southern Primorye, Far East of Russia – An integrative case study using multiple proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 386, 445–458.
- Bondarenko, O.V., Utescher, T., Blokhina, N.I., Evstigneeva, T.A., Kezina, T.V., 2020b. Temporal climate and vegetation gradient of the Paleocene in the Amur Region (Far East of Russia). *Botanica Pacifica* 9 (2), 13–35.
- Bondarenko, O.V., Blokhina, N.I., Henrot, A.-J., Utescher, T., 2021. Paleogene vegetation changes in Primorye, Far East of Russia — a study based on diversity of plant functional types. *Geol. J.* 56, 650–672.
- Bondarenko, O.V., Blokhina, N.I., Evstigneeva, T.A., Utescher, T., 2022. Short-term climate and vegetation dynamics in Delta Lena River (northern Yakutia, Eastern Siberia) during the early Eocene. *Palaeoworld*. <https://doi.org/10.1016/j.palwor.2021.09.006>.
- Borsuk, M.O., 1952. Fossil flora of the Upper Cretaceous sediments of Primorye. *Gosgeoltekhizdat*, 52 p. [in Russian].
- Bosboom, R.E., Abels, H.A., Hoorn, C., van den Berg, B.C.J., Guo, Z., Dupont-Nivet, G., 2014. Aridification in continental Asia after the Middle Eocene Climatic Optimum (MECO). *Earth Planet. Sci. Lett.* 389, 34–42.
- Bosboom, R., Mandic, O., Dupont-Nivet, G., Proust, J.N., Ormukov, C., Aminov, J., 2015. Late Eocene palaeogeography of the proto-Paratethys Sea in Central Asia (NW China, southern Kyrgyzstan and SW Tajikistan). In: Brunet, M.F., McCann, T., Sobel, E.R. (Eds.), Geological Evolution of Central Asian Basins and the Western Tien Shan Range (Special Publications). Geological Society, 427 p.
- Brattseva, G.M., 1969. Palynological studies of upper Cretaceous and Paleogene of the Far East. *Geological Institute Transactions. Academy Sciences USSR* 207, 1–57 [in Russian].
- Bruch, A.A., Utescher, T., Mosbrugger, V., and NECLIME members, 2011. Precipitation patterns in the Miocene of Central Europe and the development of continentality. *Palaeogeography, Palaeoclimatology, Palaeoecology* 304, 202–211.
- Budantsev, L.Y., 1983. History of the Arctic flora of the early Kainophytic era. *Nauka*, 156 p. [in Russian].
- Budantsev, L.Y., 1999. The reconstruction of the Cenozoic climates in eastern-north Asia based on palaeobotanical data. *Botanicheskii Zhurnal* 84 (10), 36–45 [in Russian].
- Budantsev, L.Yu., 1997. Late Eocene flora of Western Kamchatka. (Proceedings of the Komarov Botanical Institute of the Russian Academy of Sciences 19). Izdatel'stvo "Petro-RIF", 115 p. [in Russian].
- Chandler, M.E.J., 1964. The Lower Tertiary Floras of Southern England IV. *British Museum (Natural History)* 151 p.
- Chapman, V.J., 1976. Mangrove vegetation. J. Cramer, Vaduz.
- Chekrzyzhov, I.Y., Popov, V.K., Panichev, A.M., Seregin, V.V., Smirnova, E.V., 2010. New data on stratigraphy, volcanism, and zeolite mineralization of the Cenozoic Vanchinskii Basin. *Primorsky Krai. Tikhookeanskaya geologia* 29 (4), 45–63 [in Russian].
- Chen, P.J., Wan, X.Q., Jiang, J.H., Li, X.H., Cao, L., Li, G., Liu, J.C., Yin, D.S., Yan, W., Li, W.X., 2004. Searching for the stratotype of the Furao stage in Heilongjiang Province, Northeast China. *J. Stratigraphy* 28 (2), 97–104.
- Cohen, K.M., Finney, S.M., Gibbard, P.L., Fan, J.X., 2013. The ICS International Chronostratigraphic Chart. *Episodes* 36, 199–204.
- Creech, J.B., Baker, J.A., Hollis, C.J., Morgans, H.E.G., Smith, E.G.C., 2010. Eocene sea temperatures for the mid-latitude southwest Pacific from Mg/Ca ratios in planktonic and benthic foraminifera. *Earth Planet. Sci. Lett.* 299 (3/4), 483–495.
- Duke, N.C., Ball, M.C., Ellison, J.C., 1998. Factors influencing biodiversity and distributional gradients in mangroves. *Glob. Ecol. Biogeogr.* 7, 27–47.
- Dupont-Nivet, G., Krijgsman, W., Langereis, C., Abels, H.A., Dai, S., Fang, X., 2007. Tibetan plateau aridification linked to global cooling at the Eocene-Oligocene transition. *Nature* 445, 635–638.
- Dupont-Nivet, G., Hoorn, C., Konert, M., 2008. Tibetan uplift prior to the Eocene-Oligocene climate transition: evidence from pollen analysis of the Xining basin transition. *Geology* 6, 987–990.
- FNA Editorial Committee (Eds.), 1993. Flora of North America North of Mexico. vol. 2 (Pteridophytes and Gymnosperms). Oxford University Press, 496 p.
- Eldrett, J.S., Greenwood, D.R., Harding, I.C., Huber, M., 2009. Increased seasonality through the Eocene to Oligocene transition in northern high latitudes. *Nature* 459, 969–973.
- Ellison, A.M., Farnsworth, E.J., Merkt, R.E., 1999. Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Glob. Ecol. Biogeogr.* 8, 95–115.
- Fan, M., 1985. Spore-pollen assemblages of Paleocene Xincun formation in Shulan Coalfield. *Coal Technology of Northeast China* 13–26.
- Fang, J., Wang, Z., Tang, Z., 2009. Atlas of Woody Plants in China. Vol. 1 and Index. Higher Education Press, Beijing.
- Fang, J., Wang, Z., Tang, Z., 2011. Atlas of Woody Plants in China. Vol. 2 and Index. Higher Education Press, Beijing.
- Fedotov, V.V., 1983. Eocene flora of Raychikha of the Amur region. Vol. 1 and 2. (Dep. VINITI No. 2774-83). 287 p. [in Russian].
- Fotjanova, L.I., Serova, M.Y., Gall'versen, V.G., Zharov, A.E., Grokhotova, N.M., Tuzov, V.P., 2001. The Paleogene Reference section of the Kril'on Peninsula (the Kitosiya River, Southern Sakhalin). *Stratigr. Geol. Correl.* 9 (2), 58–76 [in Russian].
- Fradkina, A.F., Laukhin, S.A., 1984. A brief palynological characteristic of the Paleogene in the Lower Kolyma and the problem of the Eocene-Oligocene boundary in Northeast Asia. In: Shatskii, S.B., Volkova, V.S., Kulkova, I.A. (Eds.), Environment and life at the boundaries of the Cenozoic eras in Siberia and the Far East (Transactions of Institututa geologii i geofiziki, Vol. 593). Nauka, Siberian Branch, pp. 34–41. [in Russian].
- Fradkina, A.F., Trufanov, G.V., Vakulenko, A.S., 1979. Eocene Deposits of New Siberian islands. In: Schilo, N.A., Baranova, Y.P. (Eds.), Continental Tertiary deposits of North-East Asia (Stratigraphy, Correlation, Paleoclimates). Nauka, Siberian Branch, pp. 22–30 [in Russian].
- Fradkina, A.F., 1985. Paleogene and Neogene of the lower reaches of the Kolyma River according to palynological data. In: Volkova, V.S., Fradkina, A.F. (Eds.), Palynostratigraphy of the Mesozoic and Cenozoic of Siberia (Transactions of Institututa geologii i geofiziki RAN, Vol. 620). Nauka, pp. 52–65. [in Russian].
- Fradkina, A.F., 1995. Palynostratigraphy of Paleogene and Neogene Sediments of North-Eastern Russia (Transactions of the UIGGM SB RAS, Vol. 806). Nauchno-izdatel'skii tsentr OIGGiM SO RAN, 82 p. [in Russian].
- Gladenkov, Yu.B., Bazhenova, O.K., Grechin, V.I., Margulis, L.S., Salnikov, B.A., 2002. The Cenozoic Geology and the Oil and Gas Presence in Sakhalin. *GEOS*, 225 p. [in Russian].
- Gladenkov, Yu.B., Sinel'nikova, V.N., Chelebaeva, A.I., Shantser, A.E., 2005. Biosphere – Ecosystem – Biota in the Earth Past. The North Pacific Cenozoic ecosystems: Eocene – Oligocene of West Kamchatka and adjacent regions (To the centenary of Academician V.V. Menner). *Trans. Geol. Inst.* 540 (GEOS), 480 [in Russian].
- Golozubov, V.V., 2006. Tectonics of the Jurassic and lower Cretaceous complexes of the north-western framing of the Pacific Ocean. *Dal'nauka*, 231 p. [in Russian].
- Greenwood, D., Moss, P., Rowett, A., Vadala, A., Keefe, R., 2003. Plant communities and climate, change in southeastern Australia during the early Paleogene. In: Wing, S.L., Gingerich, P.D., Schmitz, B., Thomas, E. (Ed.), Causes and consequences of globally warm climates in the early Paleogene. Geological Society of America, special paper 369, 365–380.
- Greenwood, D.R., Wing, S.L., 1995. Eocene continental climates and latitudinal temperature gradients. *Geology* 23, 1044–1048.
- Greenwood, D.R., Vadala, A.J., Moss, P., Keefe, R., 2001. Early Paleocene climates and vegetation in SE Australia. Climate and biota of the Early Paleogene: International meeting, Abstract volume, Smithsonian Institution, p. 38.
- Greenwood, D.R., Wilf, P., Wing, S.L., Christophel, D.C., 2004. Paleotemperature estimation using Leaf-Margin Analysis: is Australia different? *Palaios* 19, 129–142.
- Greenwood, D.R., Basinger, J.F., Smith, R.Y., 2010. How wet was the Arctic Eocene rain forest? Estimates of precipitation from Paleogene Arctic macrofloras. *Geology* 38, 15–18.
- Gripenko, O.V., Kiseleva, A.V., 1971. On the age of coal-bearing deposits of the Bykovskaya channel in the delta of the Lena River. In: Tomskaya, A.I., Vozin, V.F. (Eds.), Palynological characteristics of Paleozoic, Mesozoic and Cenozoic deposits of Yakutia, Yakutskoe knizhnoe izdatel'stvo, pp. 75–87 [in Russian].

- Grinenko, O.V., Fradkina, A.F., 1988. Palynological characteristics of the Paleogene deposits of the Northern Kharaulakh, In: Volkova, V.S., Shatskii, S.B. (Eds.), *Microphytofossils and stratigraphy of the Mesozoic and Cenozoic of Siberia*. Transactions of Institut Geologii i Geofiziki, Sibirskoe Otdelenie, Akademiia Nauk SSSR, Vol. 697, pp. 136–142. [in Russian].
- Grinenko, O.V., Zharikova, L.P., Fradkina, A.F., et al., 1989. The Paleogene and Neogene of the North-Eastern USSR. *Yakut Scientific Center SB AS USSR*, 184 p. [in Russian].
- Grinenko, O.V., Sergeenko, A.I., Belolubskiy, I.N., 1997. Stratigraphy of the Paleogene and Neogene deposits of the North-East of Russia. *Otechestvennaya geologiya* 8, 14–20 [in Russian].
- Guo, Z.-T., Sun, B., Zhang, Z.-S., Peng, S.-Z., Xiao, G.-Q., Ge, J.-Y., Hao, Q.-Z., Qiao, Y.-S., Liang, M.-Y., Liu, J.-F., Yin, Q.-Z., Wei, J.-J., 2008. A major reorganization of Asian climate by the early Miocene. *Clim. Past* 4, 153–174.
- Hao, H., Ferguson, D.K., Feng, G.P., Ablav, A., Wang, Y.F., Li, C.S., 2010. Early Paleocene vegetation and climate in Jiayin, NE China. *Clim. Change* 99, 547–566.
- He, Y.M., Sun, X.J., 1977. Palynological investigation of Palaeogene in the Qingjiang Basin in Kiangsi Province I. *Acta Botanica Sinica* 19, 72–82.
- He, C.X., Tao, J.R., 1997. A study on the Eocene flora in Yilan County, Heilongjiang. *Acta Phytotaxonomica Sinica* 35, 249–256.
- Hirooka, K., 1990. Paleomagnetic studies of Pre-Cretaceous rocks in Japan. *Publ. of IGSP Project 224*, 401–406.
- Hoareau, G., Bomou, B., van Hinsbergen, D.J.J., Carry, N., Marquer, D., Donnadieu, Y., Le Hir, G., Vrielynck, B., Walter-Simonnet, A.-V., 2015. Did high Neo-Tethys subduction rates contribute to early Cenozoic warming? *Clim. Past* 11, 1751–1767.
- Hollis, C.J., Handley, L., Crouch, E.M., Morgans, H.E.G., Baker, J.A., Creech, J., Collins, K.S., Gibbs, S.J., Huber, M., Schouten, S., Zachos, J.C., Pancost, R.D., 2009. Tropical sea temperatures in the high-latitude South Pacific. *Geology* 37, 99–102.
- Hong, Y.C., Yang, Z.Q., Wang, S.T., Sun, X.J., Du, N.Q., Sun, M.R., Li, Y.G., 1980. A Research on the Strata and Palaeontology of the Fushun Coal Field in Liaoning Province. Science Press, Beijing.
- Hoorn, C., Poggio, A., Antonelli, A., (Eds.), 2018. *Mountains, Climate and Biodiversity*, John Wiley & Sons. 544 p.
- Hoorn, C., Straathof, J., Abels, H.A., Hu, Y.D., Utescher, T., Dupont-Nivet, G., 2012. A late Eocene palynological record of climate change and Tibetan Plateau uplift (Xining Basin, China). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 344–345, 16–38.
- Huang, Q.H., Huang, F.T., Zhang, Y., Chen, C.R., Kong, H., Jin, X.X., 1998. New advance in the Tertiary strata study of the Tangyuan Rift. *Journal of Stratigraphy* 22, 73–80 [in Chinese with English abstract].
- Huber, M., Caballero, R., 2011. The early Eocene equable climate problem revisited. *Clim. Past* 7, 603–633.
- Huber, M., Sloan, L.C., 2001. Heat transport, deep waters, and thermal gradients: coupled simulation of an Eocene greenhouse climate. *Geophys. Res. Lett.* 28 (18), 3481–3484.
- Jagniecki, E.A., Lowenstein, T.K., Jenkins, D.M., Demicco, R.V., 2015. Eocene atmospheric CO₂ from the nahcolite proxy. *Geology* 43 (12), 1075–1078.
- Jin, J.H., Herman, A.B., Spicer, R.A., Kodrul, T.M., 2017. Palaeoclimate background of the diverse Eocene floras of South China. *Science Bulletin* 62, 1501–1503.
- Jolley, D.W., Widdowson, M., 2005. Did Paleogene North Atlantic rift-related eruptions drive early Eocene climate cooling? *Lithos* 79, 355–366.
- Kalishevich, T.G., Zaklinskaya, E.D., Serova, M.Y., 1981. Development of the organic world of the Pacific belt at the turn of the Mesozoic and Cenozoic. *Nauka* 164 p [in Russian].
- Kamaeva, A.M., 1990. Stratigraphy and flora of the boundary deposits of Cretaceous and Paleogene of the Zeya-Bureya Depression. *Amur Integrated Research Institute DVO AN SSSR* 67, p [in Russian].
- Kezina, T.V., 1997. Palynostratigraphy of the Maastrihtian-Danian deposits of the Pikanskii Basin (Amur region). *Tikhookeanskaya geologia* 16, 140–142 [in Russian].
- Kezina, T.V., 2005. Palynostratigraphy of coal deposits of the Late Cretaceous and Cenozoic of the Upper Amur River Region. *Dal'nauka*, 206 p. [in Russian].
- Kezina, T.V., Litvinenko, N.D., 2007. Palynostratigraphy of the Erkovitsy brown coal field (the Zeya-Bureya sedimentary basin). *Stratigr. Geol. Correl.* 15 (4), 385–400.
- Kezina, T.V., Ol'kin, G.F., 2000. Palynological characteristics of Cenozoic coal-bearing deposits, the Snezhnogorskii locality in the Verkhnyaya Zeya Basin. *Stratigr. Geol. Correl.* 8 (5), 482–490.
- Kharkevich, S.S. (Ed.), 1989. *Sosudistye rasteniya sovetskogo Dal'nego Vostoka*. Tom 4. *Nauka*, 380 p. [in Russian].
- Kiehl, J.T., Shields, C.A., 2013. Sensitivity of the Palaeocene-Eocene Thermal Maximum climate to cloud properties. *Philosophical Transactions of the Royal Society A* 371, 20130093.
- Kisterova, I.B., Narhinova, V.E., Terekhova, V.E., 1979. On the issue of identifying Palaeocene sediments in the north of the Chukotka Peninsula. In: Baranova, Y.P., Shilo, N.A. (Eds.), *Continental Tertiary strata of Northeast Asia*. *Nauka*, pp. 52–55 [in Russian].
- Kodrul, T.M., 1999. Paleogene stratigraphy of South Sakhalin. *Transaction of the Geological Institute Vol. 519*. *Nauka*, 150 p [in Russian].
- Kolesov, E.V., 2003. Paleotektonicheskaya evolyutsiya Severo-Vostochnogo regiona Rossii po paleomagnetnym dannym. In: Byalobzhetskii, S.G., et al. (Eds.), *Materialy vserezhisskogo sovetshaniya "Geodinamika, magmatizm i mineralogiya kontinental'nykh okrain Severnoi Patsifikii"*. *Izdatel'stvo SVKNII*, pp. 101–102. [in Russian].
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. *Weltkarte der Köppen-Geiger Klimaklassifikation aktualisiert*. *Meteorol. Z.* 15 (3), 259–263.
- Krasnyi, L.I. (Ed.), 1994. Decisions of the IV Interdepartmental Regional Stratigraphic Meeting on Precambrian and Phanerozoic in the South of the Far East and Eastern Transbaikalia. *Izdatel'stvo KhGGGP*, 124 p. [in Russian].
- Krassilov, V.A., 1976. *Tsayanskaya flora of the Amur Region*. *Nauka*, 92 p. [in Russian].
- Krassilov, V.A., 1989. Change of flora on the border of Cretaceous and Paleogene in the Kavalerovskii District, Primorye, In: Krassilov, V.A., Klimova, R.S. (Eds.), *Cenozoic of the Far East*. *Dal'nevostochnoe otdelenie Akademii nauk SSSR*, pp. 34–37. [in Russian].
- Kryshstofovich, A.N., 1958. Fossil floras of Penzhinskaya Bay, Tastakh Lake and Rarytkin Ridge. In: Takhtadjan, A.L. (Ed.), *Trudy BIN AN SSSR, Seria 8, Vol. 3*. *Nauka*, pp. 73–124 [in Russian].
- Kulkova, I.A., 1971. Eocene flora of the Yana-Indigirskaya lowland and its comparison with coeval floras of the Northern Hemisphere, In: Saks, V.N., Volkova, V.S. (Eds.), *Cenozoic floras of Siberia according to palynological data*. *Transactions of Academy of Sciences of USSR, Siberian Branch, Vol. 135*, pp. 34–37. [in Russian].
- Kulkova, I.A., 1973. Palynological studies of the Eocene deposits of the Yano-Indigirskaya lowland. *Nauka*, 116 p. [in Russian].
- Laukhin, S.A., Akhmetiev, M.A., Fradkina, A.F., Zyryanov, E.V., 1988. Palynological characteristics of the Kungin Paleogene of North Yakutia. *Doklady Akademii nauk SSSR* 299 (3), 686–689 [in Russian].
- Laukhin, S.A., Fradkina, A.F., 1984. Comparative characteristics of the pssimums of the Eocene-Oligocene and Oligocene-Miocene boundaries in Northeast Asia. *Doklady Akademii Nauk SSSR* 278 (6), 1439–1442 [in Russian].
- Laukhin, S.A., Grinenko, O.V., Fradkina, A.F., 1992. Climate evolution of the Cenozoic on the Arctic coast of Northeast Asia. *Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya* 1, 131–139 [in Russian].
- Lee, G., Besse, J., Courtillot, V., Montigny, R., 1987. Eastern Asia in Cretaceous: new paleomagnetic data from South Korea and a new look at Chinese and Japanese data. *J. Geophys. Res.* 92, 3580–3596.
- Li, Y.T., 1984. *The Tertiary system of China*. Geological Publishing House, Beijing.
- Li, Z.X., 1998. Eocene palynology of Well LF13-2-1 in Pearl River Mouth Basin. *China Offshore Oil and Gas (Geology)* 12, 168–173.
- Liu, T., 1997. Geological environments in China and global change, In: Wang, H., Jahn, B., Mei, S. (Eds.), *Origin and History of the Earth*. *Proceedings of the 30th International Geological Congress*, 1. VSP, pp. 15–26.
- Lopatina, D.A., 2004. Vegetation and climate of the Eocene – Miocene, Eastern Sikhotealin (from paleobotanical analysis data). *Russian J. Pacific Geol.* 23 (3), 98–112.
- Lunt, D.J., Dunkley Jones, T., Heinemann, M., Huber, M., LeGrande, A., Winguth, A., Loptson, C., Marotzke, J., Roberts, C.D., Tindall, J., Valdes, P., Winguth, C., 2012. A model-data comparison for a multi-model ensemble of early Eocene atmosphere-ocean simulations: EoMIP. *Clim. Past* 8, 1717–1736.
- Lunt, D.J., Bragg, F., Chan, W.L., Hutchinson, D.K., Ladant, J.B., Morozova, P., Niezgodzki, I., Steinig, S., Zhang, Z.S., Zhu, J., Abe-Ouchi, A., Anagnostou, E., de Boer, A.M., Coxall, H.K., Donnadieu, Y., Foster, G., Inglis, G.N., Knorr, G., Langebroek, P.M., Lear, C.H., Lohmann, G., Poulsen, C.L., Sepulchre, P., Tierney, J. E., Valdes, P.J., Volodin, E.M., Jones, T.D., Hollis, C.J., Huber, M., Otto-Bliesner, B. L., 2021. DeepMIP: model intercomparison of early Eocene climatic optimum (EECO) large-scale climate features and comparison with proxy data. *Clim. Past* 17, 203–227.
- Ma, Y., Tao, M., Chen, F., 1995. The red bed spore-pollen assemblages and geological age from Zheerzhuang of Yaojie, Gansu. *Acta Sedimentologica Sinica* 13, 64–72.
- Mamontova, I.B., 1977. Palynology of the transitional Cretaceous-Paleogene beds in the Amur-Zeya depression, In: Krassilov, V.A. (Ed.), *Paleobotany in the Far East*. *Far Eastern Scientific Center of the AN USSR*, pp. 32–37. [in Russian].
- Manchester, S.R., Crane, P.R., Golovneva, L.B., 1999. An extinct genus with affinities to extant *Davidia* and *Campotheca* (Cornales) from the Paleocene of North America and Eastern Asia. *Int. J. Plant Sci.* 160 (1), 188–207.
- Markwick, P.J., 1994. "Equability", continentality and Tertiary "climate": the crocoidian perspective. *Geology* 22, 613–616.
- Maruyama, S., Isozaki, Y., Kimura, G., Terabayashi, M., 1997. Paleogeographic maps of the Japanese Islands: Plate tectonic synthesis from 750 Ma to the present. *The Island Arc* 6, 121–142.
- Miao, Y., Fang, X., Song, Z., Wu, F., Han, W., Dai, S., Song, C.H., 2008. Late Eocene Pollen Records and Palaeoenvironmental Changes in Northern Tibetan Plateau. *Sci. China, Ser. D Earth Sci.* 51, 1089–1098.
- Moiseeva, M.G., Kodrul, T.M., Herman, A.B., 2018. Early Paleocene Boguchan flora of the Amur Region (Russian Far East): Composition, age and palaeoclimatic implications. *Rev. Palaeobot. Palynol.* 253, 15–36.
- Mosbrugger, V., Utescher, T., 1997. The coexistence approach - a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 134, 61–86.
- Mosbrugger, V., Utescher, T., Dilcher, D., 2005. Cenozoic continental climatic evolution of Central Europe. *Proc. Natl. Acad. Sci.* 102 (42), 14964–14969.
- Muling, L., 1983. The late Upper Cretaceous to Paleocene spore-pollen assemblages from the Furao area, Heilongjiang Province. *Bulletin of the Sheny and Institute of geology and mineral resources*. *Chinese Acad. Geol. Sci.* 7, 99–137.
- Müller, M.J., Hennings, D., 2000. *The Global Climate 592 Data Atlas* on CD Rom. University Flensburg, Institute für Geografie, Flensburg.
- Naryshkina, A.V., 1973. On the boundary between the Cretaceous and Paleogene deposits in the Amur-Zeya depression. *Soviet Geol.* 6, 148–151 [in Russian].
- New, M., Lister, D., Hulme, M., Makin, I., 2002. A high-resolution data set of surface climate over global land areas. *Climate Research* 21, 1–25.
- Oleinikov, A.V., Klimova, R.S., 1977. New data on stratigraphy of Neogene volcanogenic sediments of the Samarga River basin, In: Varnavskii, V.G. (Ed.), *Stratigraphy of the Cenozoic sediments of the Far East*. *Dal'nevostochniy nauchnyi tsentr Akademii nauk SSSR*, pp. 76–80. [in Russian].

- Pagani, M., Zachos, J.C., Freeman, K.H., Tipler, B., Bohany, S., 2005. Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. *Science* 309, 600–603.
- Pavlyutkin, B.I., 2007. The Eocene *ust'davydovka* flora of the south Primorye. *Dal'nauka*, 148 p. [in Russian].
- Pavlyutkin, B.I., Petrenko, T.I., 2010. Stratigrafiya paleogen-neogenovykh otlozhenii Primor'ya. *Dal'nauka*, 164 p. [in Russian].
- Pearson, P.N., van Dongen, B.E., Nicholas, C.J., Pancost, R.D., Schouten, S., Singano, J. M., Wade, B.S., 2007. Stable warm tropical climate through the Eocene Epoch. *Geology* 35, 211–214.
- Pearson, P.N., Foster, G.L., Wade, B.S., 2009. Atmospheric carbon dioxide through the Eocene-Oligocene climate transition. *Nature* 461, 1110–1113.
- Pei, J., Sun, Z., Wang, X., Zhao, Y., Ge, X., Guo, X., Li, H., Si, J., 2009. Evidence for Tibetan Plateau uplift in Qaidam Basin before Eocene-Oligocene boundary and its climatic implications. *J. Earth Sci.* 20, 430–437.
- Popescu, S.-M., Suc, J.-P., Fauquatte, S., Bessedik, M., Jimenez-Moreno, G., Robin, C., Labrousse, L., 2021. Mangrove distribution and diversity during three Cenozoic thermal maxima in the Northern Hemisphere (pollen records from the Arctic – North Atlantic – Mediterranean regions). *J. Biogeogr.* 48, 2771–2784.
- Pross, J., Contreras, L., Bijl, P.K., Greenwood, D.R., Bohaty, S.M., Schouten, S., Bendle, J. A., Röhl, U., Tauxe, L., Raine, J.I., Huck, C.E., van de Flierdt, T., Jamieson, S.S.R., Stickley, C.E., van de Schootbrugge, B., Escutia, C., Brinkhuis, H., 2012. Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch. *Nature* 488, 73–77.
- Quan, C., Liu, (Y.S.) C., Utescher, T., 2012a. Eocene monsoon prevalence over China: A palaeobotanical perspective. *Palaeogeography, Palaeoclimatology, Palaeoecology* 365–366, 302–311.
- Quan, C., Liu, (Y.S.) C., Utescher, T., 2012b. Paleogene temperature gradient, seasonal variation and climate evolution of northeast China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 313–314, 150–161.
- Quan, C., Zhang, L., 2005. An analysis of the Early Paleogene climate of the Jiayin Area, Heilongjiang province. *Geol. Rev.* 51, 10–15 [in Chinese with English abstract].
- Quan, C., Liu, Y.C., Utescher, T., 2011. Paleogene evolution of precipitation in Northeastern China supporting the Middle Eocene intensification of the East Asian Monsoon. *Palaios* 26, 743–753.
- Rhines, P.B., Häkkinen, S., 2003. Is the oceanic heat transport in the North Atlantic irrelevant to the climate in Europe? *ASOF Newsletter* 1, 13–17.
- Sagoo, N., Valdes, P., Flecker, R., Gregoire, L.J., 2013. The early Eocene equable climate problem: can perturbations of climate model parameters identify possible solutions? *Philos. Trans. Roy. Soc. Math. Phys. Eng. Sci.* 371, 20130123. <https://doi.org/10.1098/rsta.2013.0123>.
- Salpin, M., Schnyder, J., Baudin, F., Suan, G., Suc, J.-P., Popescu, S.-P., Fauquette, S., Reinhardt, L., Schmitz, M.D., Labrousse, L., 2019. Evidence for subtropical warmth in the Canadian Arctic (Beaufort-Mackenzie, Northwest Territories, Canada) during the early Eocene. In: Piepjohn, K., Strauss, J.V., Reinhardt, L., and McClelland, W.C. (Eds.), *Circum-Arctic Strata: Tectonic Origin of the Arctic Margins and Trans-Arctic Links with Adjacent Orogens*. Geological Society of America Special Paper 541, [https://doi.org/10.1130/2018.2541\(27\)](https://doi.org/10.1130/2018.2541(27)).
- Scotese, C.R., 2013. Map Folio 13, Early Eocene, Ypresian, 52.2 Ma), PALEOMAP PaleAtlas for ArcGIS, volume 1, Cenozoic, PALEOMAP Project, Evanston, IL.
- Sein, M.K., 1961. Fossil spores of the London Clay. University of London, London. PhD thesis.
- Semakin, V.P., Kochergin, A.V., Pitina, T.I., 2016. Neotectonics of the Sea of Okhotsk. *Geodynamics Tectonophysics* 7 (2), 251–271.
- Shelton, C.J., Sloan, L.C., 2006. Reconstructing a lost Eocene paradise: Part I. Simulating the change in global floral distribution at the initial Eocene thermal maximum. *Global Planet. Change* 50, 1–17.
- Shi, F., Xin-rong, Z., Zhao-jun, L., He-yong, W., Jian-guo, Y., 2008. Thrust event of the provenances revealed by zircon fission track ages in Tangyuan Fault-Basin, NE China. *Radiat. Meas.* 43, S324–S328.
- Sloan, L.C., Barron, E.J., 1992. A comparison of Eocene climate model results to quantified paleoclimatic interpretations. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 93, 183–202.
- Sluijs, A., Schouten, S., Pagani, M., Woltering, M., Brinkhuis, H., Damsté, J.S.S., Moran, K., 2006. Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum. *Nature* 441, 610–613.
- Sluijs, A., Schouten, S., Donders, T.H., Schoon, P.L., Röhl, U., Reichert, G.-J., Sangiorgi, F., Kim, J.-H., Sinninghe Damsté, J.S., Brinkhuis, H., 2009. Warm and wet conditions in the Arctic region during Eocene Thermal Maximum 2. *Nat. Geosci.* 2, 777–780.
- Sokolov, S., Svjseva, O., Kubli, V., 1977. Ranges of trees and shrubs of the USSR, Volume 1. Nauka, Leningrad.
- Sokolov, S., Svjseva, O., Kubli, V., 1980. Ranges of trees and shrubs of the USSR, Volume 2. Nauka, Leningrad.
- Sokolov, S., Svjseva, O., Kubli, V., 1986. Ranges of trees and shrubs of the USSR, Volume 3. Nauka, Leningrad.
- Song, Z.C., Zhang, D.H., 1990. Geological age of the Caomuhao gypsum mine in Oto Banner, Nei Mongol with review of research on fossil proteaceous pollen in China. *Acta Palaeobotanica Sinica* 29, 257–269.
- Sorokin, A.P., Belousov, V.I., 1984. Cenozoic of the western part of the Urkanskii Basin. In: Ablae, A.G. (Ed.), *Materials on stratigraphy and paleogeography of East Asia (new data)*. Far Eastern Scientific Center of the AN USSR, pp. 48–52. [in Russian].
- Spicer, R.A., Herman, A.B., Liao, W.B., Spicer, T.E.V., Kodrul, T.M., Yang, J., Jin, J.H., 2014. Cool tropics in the middle Eocene: Evidence from the Changchang flora, Hainan Island, China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 412, 1–16.
- Spicer, R.A., Su, T., Valdes, P.J., Farnsworth, A., Wu, F.X., Shi, G., Spicer, T.E.V., Zhou, Z. K., 2021. Why 'the uplift of the Tibetan Plateau' is a myth. *Natl. Sci. Rev.* 8 (1), nwa091.
- Srivastava, J., Prasad, V., 2019. Evolution and paleobiogeography of mangroves. *Mar. Ecol.* 2019 (00), e12571.
- Stap, L., Lourens, L.J., Thomas, E., Sluijs, A., Bohaty, S., Zachos, J.C., 2010. High-resolution deep-sea carbon and oxygen isotope records of Eocene Thermal Maximum 2 and H2. *Geology* 38, 607–610.
- Stewart, G., Popp, M.C., 1987. The ecophysiology of mangroves. In: Crawford, R. (Ed.), *Plant life in aquatic and amphibious habitats*. Blackwell Scientific Publications, pp. 333–345.
- Su, T., Xing, Y.W., Yang, Q.S., Zhou, Z.K., 2009. Reconstructions of mean annual temperature in Chinese Eocene Paleofloras based on leaf margin analysis. *Acta Palaeontologica Sinica* 48, 65–72.
- Suan, G., Popescu, S.-M., Suc, J.-P., Schnyder, J., Fauquette, S., Baudin, F., Yoon, D., Piepjohn, K., Sobolev, N.N., Labrousse, L., 2017. Subtropical climate conditions and mangrove growth in Arctic Siberia during the early Eocene. *Geology* 45, 539–542.
- Suc, J.-P., Fauquette, S., Popescu, S.-M., Robin, C., 2020. Subtropical mangrove and evergreen forest reveal Paleogene terrestrial climate and physiography at the North Pole. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 551, 109755.
- Sun, X.Y., Zhao, Y.N., He, Z.S., 1980. Late Cretaceous-Early Tertiary pollen assemblages in Xinjing-Minhe Basin and its geological age, paleovegetational, and paleoclimatic significance. *Exp. Petrol. Geol.* 2, 44–50.
- Sycheva, O.A., 1975. On the flora and age of the Kama layers of the Boshnyakovskaya Formation of the Ulegorsky District of Sakhalin Island. In: Zhidkova, L.S. (Ed.), *Stratigraphy, lithology and paleogeography of the Meso-Cenozoic deposits of the Far East*. Proceedings of the SakhKNII, vol. 36. Far Eastern Scientific Center of the AN USSR, pp. 13–18. [in Russian].
- Takaya, K., Nakamura, H., 2005. Mechanisms of intraseasonal amplification of the cold Siberian High. *Journal of Atmospheric Sciences* 62, 4423–4440.
- Tanai, T., 1972. Tertiary history of vegetation in Japan. In: Graham, A. (Ed.), *Floristics and Paleofloristics of Asia and Eastern North America*. Proceedings of Symposia for the Systematics Section, XI International Botanical Congress, Seattle, Wash. 1969, and The Japan-United States Cooperative Science Program, Corvallis, Oregon 1969. Elsevier Publishing Company, pp. 234–255.
- Tao, X.J., Xiong, X.Z., 1986. The latest Cretaceous flora of Heilongjiang Province and the floristic relationship between East Asia and North America. *Acta Phytotaxonomica Sinica* 24 (1), 1–15.
- Tashchi, S.M., Ablae, A.G., Mel'nikov, N.G., 1996. Cenozoic basin of the Western Primorye and adjacent territories of China and Korea. *Dal'nauka*, 168 p. [in Russian].
- Tomlinson, P.B., 1986. *The Botany of Mangroves*. Cambridge University Press, p. 413 pp.
- Ushimura, H., Kono, M., Tsunakawa, H., Kimura, G., Wei, Q., Hao, T., Liu, H., 1996. Paleomagnetism of Late Mesozoic rocks from northeastern China: the role of the Tan-Lu fault in the North China Block. *Tectonophysics* 262, 301–319.
- Utescher, T., Mosbrugger, V., 2018. The Palaeoflora Database. Available at www.palaeoflora.de (last accessed 08 August 2020).
- Utescher, T., Bruch, A.A., Micheels, A., Mosbrugger, V., Popova, S., 2011. Cenozoic climate gradients in Eurasia a palaeo-perspective on future climate change? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 304, 351–358.
- Utescher, T., Bondarenko, O.V., Mosbrugger, V., 2015. The Cenozoic Cooling – continental signals from the Atlantic and Pacific side of Eurasia. *Earth Planet. Sci. Lett.* 415, 121–133.
- Utescher, T., Bruch, A.A., Erdei, B., François, L., Ivanov, D., Jacques, F.M.B., Kern, A.K., Liu, (Y.-S.) C., Mosbrugger, V., Spicer, R.A., 2014. The Coexistence Approach – Theoretical background and practical considerations of using plant fossils for climate 666 quantification. *Palaeogeography, Palaeoclimatology, Palaeoecology* 410, 58–73.
- Utescher, T., Mosbrugger, V., 2007. Eocene vegetation patterns reconstructed from plant diversity – A global perspective. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 247, 243–271.
- Utescher, T., Mosbrugger, V., Bruch, A.A., Milutinovic, D., 2007. Climate and vegetation changes in Serbia during the last 30 Ma. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253, 141–152.
- Utescher, T., Mosbrugger, V., Ivanov, D., Dilcher, D.L., 2009. Present-day climatic equivalents of European Cenozoic climates. *Earth Planet. Sci. Lett.* 284, 544–552.
- Van Beuskom, C.F., 1971. Revision of *Meliosma* (Sabiaceae) section *Lorenzanea* excepted, living and fossil, geography and phylogeny. *Blumea* 19, 355–529.
- Varnavskii, V.G., Sedykh, A.K., Rybalko, V.I., 1988. Paleogene and Neogene of the Amur Region and Primorye. *Izdatel'stvo DVO AN SSSR*, 184 p. [in Russian].
- Verkhovskaya, N.B., Kundyshev, A.S., 1989. Physiognomic features of spore-pollen spectra and their use in stratigraphy. In: Krassilov, V.A., Klimova, R.S. (Eds.), *Cenozoic of the Far East*. *Dal'nevostochnoe otdelenie Akademii nauk SSSR*, pp. 128–134. [in Russian].
- Volkova, V.S., Kuz'mina, O.B., 2005. Flora, vegetation, and climate of the middle Cenophytic (Paleocene – Eocene) of Siberia. *Geologia i geofizika* 46 (8), 844–855 [in Russian].
- Volobueva, V.I., Gladenkov, Yu.B., Belaya, B.V., 1988. Paleogene of the North-East of the USSR. In: Pokhialainen, V.P., Gagiev, M.Kh. (Eds.), *Stratigraphy and Paleontology of the Phanerozoic of the North-East of the USSR*. *Izdatel'stvo SVKNII DVO AN SSSR*, pp. 118–156. [in Russian].
- Wang, X.M., 2005. Eocene palynostratigraphy of Wutu, Shandong and its stratigraphical significance. *J. Stratigraphy* 29, 22–27.
- Wang, Q., Ferguson, D.K., Feng, G.P., Ablae, A.G., Wang, Y.F., Yang, J., Li, Y.L., Li, C.S., 2010. Climatic change during the Palaeocene to Eocene based on fossil plants from Fushun, China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 295, 323–331.

- Wang, D.F., Gao, R.F., Wang, J.Y., Fan, Y.Q., 1982. Paleomagnetic determination for lower limits of Early Cretaceous and Palaeocene systems in Liaoning. *Bull. Geol. Soc. Liaoning Province* 1, 116–121 [in Chinese, with English abstract].
- Wang, D.N., Sun, X.Y., Zhao, Y.N., 1984. The Paleocene – Eocene palynoflora from the Tantau Basin in west Henan. *Acta Botanica Sinica* 26, 448–455.
- Wang, D.N., Sun, X.Y., Zhao, Y.N., 1986. Palynoflora from Late Cretaceous to Tertiary in Qinghai and Xinjiang. *Bulletin Institute Geology, Chinese Academy Geological Sciences* 15, 152–169.
- Wang, D.N., Sun, X.Y., Zhao, Y.N., 1990. Late Cretaceous to Tertiary palynofloras in Xinjiang and Qinghai, China. *Rev. Palaeobot. Palynol.* 65, 95–104.
- Wang, J.Y., Wang, D.F., 1982. Age determination by K-Ar method for the bottom of the Palaeocene Laohutai Formation at Fushun district. *Bulletin Geological Society Liaoning Province* 1, 110–115 [in Chinese, with English abstract].
- Wang, J.Y., Wang, D.F., 1985. Age determination of basalt of Palaeocene Laohutai Formation in Fushun district by delation method of K-Ar elements. *Bulletin Geological Society Liaoning Province* 1, 86–90 [in Chinese, with English abstract].
- Wang, J., Wang, Y.J., Liu, Z.C., Li, J.Q., Xi, P., 1999. Cenozoic environmental evolution of the Qaidam Basin and its implications for the uplift of the Tibetan Plateau and the drying of central Asia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 152, 37–47.
- Wang, K.F., Zhang, Y.L., Wang, R., 1987. *Cretaceous-Tertiary Palynological assemblages from Anhui*. Petroleum Industry Press, Beijing.
- Wang, D.N., Zhao, Y.N., 1980. Late Cretaceous-Early Paleogene sporopollen assemblages of the Jiangnan Basin and their stratigraphical significance. *Professional Paper Chinese Academy Geological Sciences (Stratigraphy and Palaeontology)* 9, 1–174.
- Weijers, J.W.H., Schouten, S., Sluijs, A., Brinkhuis, A., Sinninghe Damsté, J.S., 2007. Warm arctic continents during the Palaeocene-Eocene thermal maximum. *Earth Planet. Sci. Lett.* 261, 230–238.
- West, C.K., Greenwood, D.R., Basinger, J.F., 2015. Was the Arctic Eocene ‘rainforest’ monsoonal? Estimates of seasonal precipitation from early Eocene megaflores from Ellesmere Island, Nunavut. *Earth Planet. Sci. Lett.* 427, 18–30.
- Westerhold, T., Marwan, N., Drury, A.J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J.S.K., Bohaty, S.M., De Vleeschouwer, D., Florindo, F., Frederichs, T., Hodell, D.A., Holbourn, A., Kroon, D., Lauretano, V., Littler, K., Lourens, L.J., Lyle, M.W., Pälike, H., Röhl, U., Tian, J., Wilkens, R.H., Wilson, P.A., Zachos, J.C., 2020. An astronomically dated record of Earth’s climate and its predictability over the last 66 million years. *Science* 369, 1383–1387.
- Wilf, P., 2000. Late Paleocene-early Eocene climate changes in southwestern Wyoming: paleobotanical analysis. *Geol. Soc. Am. Bull.* 112, 292–307.
- Wing, S.L., Harrington, G.J., 2001. Floral response to rapid warming in the earliest Eocene and implications for concurrent faunal change. *Paleobiology* 27, 539–563.
- Wing, S.L., Harrington, G.J., Smith, F.A., Bloch, J.I., Boyer, D.M., Freeman, K.H., 2005. Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* 310, 993–996.
- Winguth, A., Shellito, C., Shields, C., Winguth, C., 2010. Climate Response at the Paleocene-Eocene thermal maximum to greenhouse gas forcing: a model study with CCSM3. *J. Clim.* 23, 2562–2584.
- Wolfe, J.A., 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *Am. Sci.* 66, 694–703.
- Wolfe, J.A., 1994. Tertiary climatic changes at middle latitudes of western North America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 108, 195–205.
- Wolfe, J.A., 1995. Paleoclimatic estimates from Tertiary leaf assemblages. *Annu. Rev. Earth Planet. Sci.* 23, 119–142.
- Wolfe, A.P., Csanak, A.Z., Reyes, A.V., McKellar, R.C., Tappert, R., Muehlenbachs, K., 2012. Pristine Early Eocene wood buried deeply in kimberlite from northern Canada. *PLoS ONE* 7 (9), e45537.
- Wu, Z.Y., Raven, P.H. (Eds.), 1999. *Flora of China*. vol. 4 (Cycadaceae through Fagaceae). Science Press, Beijing and Missouri Botanical Garden, 453 pp.
- Wu, J., Zhang, K., Xu, Y., Wang, G., Garzzone, C.N., Eiler, J., Leloup, P.H., Sorrel, P., Maheo, G., 2018. Paleoelevations in the Jianchuan Basin of the southeastern Tibetan Plateau Based on Stable Isotope and Pollen Grain Analyses. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 510, 93–108.
- Xiao, G.Q., Abels, H.A., Yao, Z., Dupont-Nivet, G., Hilgen, F.J., 2010. Asian aridification linked to the first step of the Eocene-Oligocene climate Transition (EOT) in obliquity-dominated terrestrial records (Xining Basin, China). *Clim. Past* 6, 501–513.
- Xiong, Z.G., Ding, L., Spicer, R.A., Farnsworth, A., Wang, X., Valdes, P.J., Su, T., Zhang, Q.H., Zhang, L.Y., Cai, F.L., Wang, H.Q., Lia, Z.Y., Song, P.P., Guo, X.D., Yue, Y.H., 2020. The early Eocene rise of the Gonjo Basin, SE Tibet: From low desert to high forest. *Earth Planet. Sci. Lett.* 543, 116312.
- Yuan, Q., Barbolini, N., Ashworth, L., Rydin, C., Gao, D.L., Shan, F.S., Zhong, X.Y., Vajda, V., 2021. Palaeoenvironmental changes in Eocene Tibetan lake systems traced by geochemistry, sedimentology and palynofacies. *J. Asian Earth Sci.* 214, 104778.
- Zachos, J.C., Dickens, G.R., Zeebe, R.E., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451, 279–283.
- Zaklinskaya, E.D., Brattseva, G.M., Krassilov, V.A., 1977. On the palynoflora of the Tsagaian stratotype. In: Krassilov, V.A. (Ed.), *Paleobotany in the Far East*. Far Eastern Scientific Center of the AN USSR, pp. 28–31. [in Russian].
- Zaklinskaya, E.D., 1976. Key and correlative taxa and palynological correlation of sediments bordering between the Mesozoic and Cenozoic systems in South Sakhalin. In: Ablaev, A.G. (Ed.), *Essays on the geology and paleontology of the Far East*. Far Eastern Scientific Center of the Academy of Sciences of the USSR, pp. 51–65. [in Russian].
- Zhang, Z., Flatoy, F., Wang, H., Bethke, I., Bentsen, M., Guo, Z., 2012. Early Eocene Asian climate dominated by desert and steppe with limited monsoons. *J. Asian Earth Sci.* 44, 24–35.
- Zhang, J.Y., Peng, Y.J., Liu, J., 2007. An important discontinuity of the Paleogene volcanic incidents in northeast China and their prospecting significance. *Jilin Geology* 26, 1–7 [in Chinese with English abstract].
- Zhang, Y.Y., Qian, Z.S., 1992. Eocene palynofloras from the Dainan and Sanduo formations in north Jiangsu with special reference to Eocene climatic changes in southeast China. *Acta Micropalaeontol Sinica* 9, 1–24.
- Zhang, Q.-Q., Smith, T., Yang, J., Li, C.-S., 2016. Evidence of a Cooler Continental Climate in East China during the Warm Early Cenozoic. *PLoS ONE* 11 (5), e0155507.
- Zhang, Y.Y., Wang, K.D., Liu, J.L., Zheng, Y.H., 1990. Eocene palynoflora from the southwestern continental shelf basin of the East China Sea. *Acta Micropalaeontol Sinica* 7, 389–402.
- Zhang, T., Yin, F., 2005. Sporopollen assemblage from the Shahejie Formation in the Tanhai area of Huanghua depression. *J. Northwest Univ. (Natural Science Edition)* 35, 91–94.
- Zharikova, L.P., Kazantsev, A.S., Minyuk, P.S., Savcheshu, A.G., 1982. New data on the stratigraphy of the eastern part of the Primorskaya lowland. In: Spektor, V.B., (Ed.), *Geology of the Cenozoic of Yakutia*. Yakut Branch of the Siberian Department of the USSR Academy of Sciences, pp. 28–34. [in Russian].
- Zharikova, L.P., 1980. Paleogene spore-pollen complexes of the right bank of the Kolyma River. In: Vozin, V.F., (Ed.), *Cenozoic of Eastern Yakutia*. Yakut Branch of the Siberian Department of the USSR Academy of Sciences, pp. 18–35. [in Russian].
- Zhu, Z.W., 1993. Paleomagnetism in Eastern China and the Horizontal Displacement of the Tancheng-Lujiang Fault Zone. In: Xu, J.W. (Ed.), *Tancheng-Lujiang Wrench Fault System*. John Wiley et Sons.
- Ziva, M.V., 1973. In: *Kainofit palynology*, pp. 89–93 [in Russian].
- Ziva, M.V., Lukashova, L.L., 1977. Palynological characteristics of the Paleogene and Neogene deposits of the Middle Amur depression. In: Varnavskii, V.G. (Ed.), *Stratigraphy of the Cenozoic sediments of the Far East*. Dal’nevostochnyi nauchnyi tsentr Akademii nauk SSSR, pp. 42–47. [in Russian].