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RESEARCH PAPER

Major plant biome changes in the Primorye Region (Far East of Russia) during the Paleogene

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ABSTRACT

Major plant biome changes in Primorye (Far East of Russia) during the Paleogene are studied using the Integrated Plant Record vegetation analysis for the first time, based on palaeobotanical records. Palaeobotanical data employed for the reconstruction comprises 54 palaeofloras covering the early Paleocene to late Oligocene, a time-span of ca. 42 myr. Our data indicate the presence of more forested conditions in Primorye during the Paleogene than at present and demonstrate the major plant biome changes from the subtropical MMF/BLEF ecotone in the late Paleocene to the warm-temperate BLDF/MMF ecotone in the late Oligocene. The obtained major plant biome changes coincide in general with the climate cooling trend.

Keywords: vegetation types, climate, spatial gradients, time series

РЕЗЮМЕ

Бондаренко О.В., Блохина Н.И., Утешер Т. Основные изменения растительных биомов Приморья (Дальний Восток России) в палеогене. Основные изменения растительных биомов в Приморье (Дальний Восток России) в палеогене впервые изучены с использованием анализа растительности методом Integrated Plant Record, основанного на палеоботанических данных. Палеоботанические данные, примененные для реконструкции, включают 54 палеофлоры в интервале от раннего палеоцена до позднего олигоцена включительно, около 42 млн. лет. Наши данные указывают на наличие в Приморье более лесных условий в палеогене, чем в настоящее время, и демонстрируют основные изменения растительных биомов от субтропического экотона MMF/BLEF в позднем палеоцене до теплого умеренного экотона BLDF/MMF в позднем олигоцене. Полученные основные изменения растительных биомов в целом совпадают с тенденцией похолодания климата.

Ключевые слова: типы растительности, климат, пространственные градиенты, временные тренды

The Paleogene (65.5–23.03 Ma) globally was an interval of significant climatic and biotic reorganization (Akhmetiev 2004). It was a period of climate changes from greenhouse to icehouse conditions in the so-called "doubthouse" times marked by climatic cooling, rapid growth of the Antarctic ice sheet, and a supposed drop in atmospheric CO_2 levels leading to the Eocene-Oligocene Transition (EOT) event (Pagani et al. 2005, Dupont-Nivet et al. 2007, Eldrett et al. 2009, Pearson et al. 2009, Xiao et al. 2010, Abels et al. 2011).

Paleogene floras provide the potential for detailed interpretation of plant biomes and their response to global change such as warm climate thermal maxima and tectonic events. Therefore, the knowledge of the vegetation evolution during the Paleogene provides unique perspectives for the modeling of actual global changes and helps to probe into the integrated response of the Earth System to various driving forces (Collinson 1992, Zachos et al. 2008, Utescher et al. 2009).

The Primorye Region (or Primorye) is located in the south of the Russian Far East (RFE), on the coast of the Sea of Japan, bordering the Eurasian continent and Pacific Ocean. Located in the transitional zone "continent-ocean", this territory constantly experiences the influence of circulation patterns related to the interaction of ocean, continental area, and atmosphere (Gerasimov 1969). Vegetation dynamics in the Paleogene can be reconstructed from the palaeobotanical record. Primorye is one of the Russian Far East regions, where large burials of Paleogene plants are concentrated, therefore the Paleogene flora of Primorye was a subject to extensive taxonomic studies. Results are presented in the works of Ablaev (1974, 1977, 1978, 2000), Ablaev & Akhmetiev (1977), Ablaev et al. (2005, 2006), Akhmetiev (1973, 1974, 1988, 1993), Akhmetiev & Shevyreva (1989), Akhmetiev et al. (1973, 1978), Baskakova & Gromova (1979, 1984), Baskakova & Lepekhina (1990), M.D. Bolotnikova (1979), M.D. Bolotnikova & Sedykh (1987), T.N. Bolotnikova

(1988, 1989, 1993, 1994), Borsuk (1952), Gromova (1980), Klimova (1981, 1988), Klimova et al. (1977), Klimova & Tsar'ko (1989), Koshman (1964), Krassilov (1989a, b), Kundyshev & Petrenko (1987), Kundyshev & Verkhovskaya (1989), Mikhailov et al. (1989), Pavlyutkin (2007a, b, 2011), Pavlyutkin & Petrenko (1993, 1994, 1997, 2010), Pavlyutkin et al. (2006, 2012, 2014), Rybalko et al. (1980), Tashchi et al. (1996), Varnavskii et al. (1988), Verkhovskaya & Kundyshev (1989). However, these works are mainly devoted to the description of plant fossil remains, new fossil taxa, taxonomic diversity of Paleogene plants, or palaeofloristic aspects. Our knowledge of the evolution of the vegetation of Primorye in the Paleogene is still very poor and fragmentary, since most of the conclusions were made by different researchers on different materials (mainly based on few floras and/or limited territory) using different methods. These studies only provide some insights into local vegetation and its evolution, as well as indirectly about climate.

In the present detailed study we use the exceptionally rich palaeobotanical heritage of Primorye to reconstruct the Paleogene vegetation evolution of this region in space and time. Based on a total of 54 reasonably well-dated pollen and leaf floras we apply for the first time a consistent, timely method, the Integrated Plant Record vegetation analysis (IPR). The vegetation is reconstructed for seven stratigraphic levels and its dynamics is traced in a time-span of ca. 42 Myr, in total. Thus, our study not only unravels the regional vegetation evolution during the Paleogene but also promotes the understanding of the formation of modern vegetation in this region. Recently, Bondarenko et al (in print) provided a coherent palaeoclimate reconstruction for the Paleogene of Primorye based on the same palaeobotanical record. Thus, the present IPR-based biome reconstruction can be discussed in a palaeoclimatic context.

MATERIAL AND METHODS

Study area

The palaeobotanical record of Primorye studied herein originates from 19 basins (Fig. 1). The Paleogene strata of Primorye comprise volcanic and sedimentary deposits, unconformably overlying Mesozoic basement. The sedimentary facies includes fine- to coarse-grained continental clastics and intercalated lignites excavated in several active opencast mines. For some basins, mainly generated by extensional tectonics (Pavlovskii, Pushkinskii and Maksimovskii Basins), intercalated volcanoclastic layers and tholeitic lava flows (Maksimovskii Basin: Takhobinskaya and Kuznetsovskaya formations) allow for radiometric dating of the strata (Table 1, Fig. 2). The sedimentary successions in the individual basins are characterized by numerous unconformities related to regional tectonics and phases of rifting and subsidence (Pavlyutkin & Petrenko 2010). When combining the strata of the individual basins a time-span of ca. 42 myr is represented, spanning the early Paleocene (Danian) to late Oligocene (Chattian).

The regional stratigraphic correlation chart for the basins (Fig. 2; adapted from Pavlyutkin & Petrenko 2010) is based on a variety of stratigraphic data obtained from radiometric dating, regional and inter-regional pollen zonation, as well as lithological, palaeobotanical and vertebrate fauna correlations (Akhmetiev 1973, Varnavskii et al. 1988, Popov et al. 2005, Pavlyutkin & Petrenko 2010, Chatshin et al. 2013). The stratigraphic scheme has been tied to the International Stratigraphic Chart (Pavlyutkin & Petrenko 2010, Cohen et al. 2013) and allows for dating the flora-bearing horizons at the stage level (Fig. 2). For some of the floras stratigraphic ages are better constrained (cf. Table 1: radiometric datings for the Zanadvorovka, Gladkaya17, Kluch Stolbikova and Sobolevka floras).

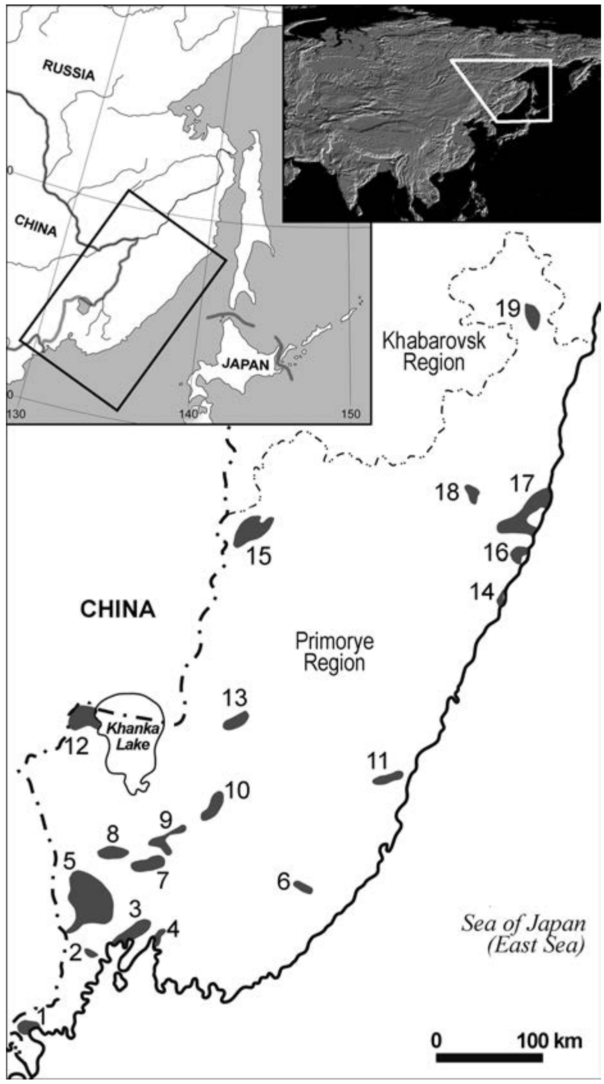

Figure 1 Map showing the location of the Primorye Region within the Russian Far East and the location of the studied basins. Filled areas: the basins after Pavlyutkin & Petrenko (2010). 1 – Khasanskii, 2 – Ambinskii, 3 – Artemo-Tavrichanskii, 4 – Shkotovskii, 5 – Pushkinskii, 6 – Vanchinskii, 7 – Ivanovskii, 8 – Pavlovskii, 9 – Snegurovskii, 10 – Chernyshevskii, 11 – Zerkal'nenskii, 12 – Tur'erogskii, 13 – Krylovskii, 14 – Kemskii, 15 – Nizhnebikinskii, 16 – Amginskii, 17 – Maksimovskii, 18 – Svetlovodnenskii, 19 – Ozero Toni. The single floras are listed in Table 1, together with information on basin provenience, type of flora, stratigraphic age, method of dating, and references. The complete flora lists, assigned NLRs and their allocation to the components are given in Supplementary electronic information.

Floral record

The palaeobotanical record of Primorye is diverse and has been subject to extensive taxonomic studies (cf. Table 1

Table 1. Palaeofloras studied. P: palynofloras; L: leaf floras; IRC: inter-regional correlation based on paleobotany

Strat. level	Locality name (Lon/Lat)	Type of flora	No. of fossil taxa	Basin, formation	Age, method of dating	References
1. Late Oligocene	1. Zanadvorovka (131.4/43.2)	P	30	Ambinskii, analog of Pavlovskaya	Chattian, K/Ar, (24.0±3.0 Ma), IRC	Pavlyutkin & Petrenko 2010, Popov et al. 2007
	2. Pushkinskii 9180 (131.5/43.3)	P L	30 28	Pushkinskii, Pavlovskaya	Chattian, IRC	Pavlyutkin et al. 2012
	3. Pavlovka 9035-D (132.1/44.1)	P	35	Pavlovskii, Pavlovskaya	Chattian, IRC	Pavlyutkin & Petrenko 2010
	4. Turii Rog 8 (131.6/45.1)	P	32	Tur'erogskii, analog of Pavlovskaya	Chattian, IRC	Pavlyutkin & Petrenko 2010
	5. Luchegorsk 6212 (134.2/46.3)	P	32	Nizhnebikinskii, Upper Coal	Chattian, IRC	Pavlyutkin & Petrenko 2010
2. Early Oligocene	6. Kraskino 9182/9196 (130.4/42.1)	P L	71 161	Khasanskii Nizhnefatashinskaya	Rupelian, IRC	Pavlyutkin et al. 2014
	7. Pavlovka 9035-D (132.1/44.1)	P	37	Pavlovskii, Pavlovskaya	Rupelian, IRC	Pavlyutkin & Petrenko 2010
	8. Rettikhovka (132.4/44.1)	P L	36 48	Snegurovskii, analog of Pavlovskaya	Rupelian, IRC	Ablaev 1977, Akhmetiev et al. 1973, Klimova et al. 1977, Pavlyutkin & Petrenko 1994, 2010
	9. Voznovo 9206 (135.3/44.2)	P L	79 80	Zerkal'nenskii, Voznovskaya	Rupelian, IRC	Pavlyutkin et al. 2014
	10. Tikhii Kluch (137.1/45.4)	L	49	Kemskii, Kizinskaya	Rupelian, IRC	Akhmetiev 1988, Rybalko et al. 1980, Varnavskii et al. 1988
	11. Amgu 9302 (137.4/45.6)	L	62	Amginskii, Granatnenskaya	Rupelian, IRC	Akhmetiev 1988, Akhmetiev & Shvyareva 1989, Klimova 1981, 1988, Pavlyutkin et al. 2014
	12. Maksimovka (137.5/46.1)	L	81	Maksimovskii, Maksimovskaya	Rupelian, IRC	Akhmetiev 1988, Rybalko et al. 1980, Varnavskii et al. 1988
3. Late Eocene	13. Gladkaya17 (130.5/42.4)	P L	41 33	Khasanskii, Khasanskaya	Priabonian, K/Ar (35.6–36.0 Ma), IRC	Chatshin et al. 2013, Gromova 1980, Pavlyutkin & Petrenko 1997, 2010, Pavlyutkin et al. 2006, 2014
	14. Tavrichanka 9142 (131.5/43.2)	P L	46 75	Artemo-Tavrichanskii, Ust'-davydovskaya	Priabonian, vertebrate fauna, IRC	Flerov et al. 1974, Pavlyutkin 2007a, Pavlyutkin & Petrenko 1993, 2010, Pavlyutkin et al. 2006, Yanovskaya 1954
	15. Shkotovo (132.2/43.2)	P	26	Shkotovskii, Upper Coal Fm.	Priabonian, IRC	Pavlyutkin & Petrenko 2010
	16. Ivanovka 610 (132.3/43.6)	P	50	Ivanovskii, analog of Pavlovskaya	Priabonian, IRC	Pavlyutkin & Petrenko 2010
	17. Pavlovka 9035-D (132.1/44.1)	P L	50 25	Pavlovskii, Pavlovskaya	Priabonian, IRC	Bolotnikova 1993, 1994, Pavlyutkin & Petrenko 2010, Varnavskii et al. 1988
	18. Svetlyi (135.1/44.1)	P L	14 22	Zerkal'nenskii, Svetlinskaya	Priabonian, IRC	Mikhailov et al. 1989, Pavlyutkin & Petrenko 2010
	19. Luchegorsk (134.2/46.3)	P L	61 56	Nizhnebikinskii, Bikinskaya	Priabonian, IRC	Ablaev et al. 2006, Bolotnikova & Sedykh 1987, Koshman 1964, Kundyshev & Verkhovskaya 1989
	20. Salibeza (137.5/46.1)	L	48	Svetlovodnenskii, Salibezskaya	Priabonian, IRC	Klimova & Tsar'ko 1989, Varnavskii et al. 1988
4. Middle Eocene	21. Vol'no-Nadezhdinskoe (131.5/43.2)	P L	59 25	Artemo-Tavrichanskii, Nadezhdinskaya	Bartonian, IRC	Akhmetiev et al. 1978, Pavlyutkin 2007a, Pavlyutkin & Petrenko 1993, 2010
	22. Bolotnaya (131.1/43.2)	P L	45 75	Artemo-Tavrichanskii, Nadezhdinskaya	Lutetian, IRC	Ablaev 2000, Ablaev & Akhmetiev 1977, Akhmetiev 1973, Kundyshev & Petrenko 1987, Pavlyutkin 2007, Pavlyutkin & Petrenko 2010
	23. Shkotovo (132.2/43.2)	P	31	Shkotovskii, Nadezhdinskaya	Middle Eocene, IRC	Baskakova & Gromova 1982
	24. Terekhovka (131.3/43.4)	P	44	Pushkinskii, Nadezhdinskaya	Middle Eocene, IRC	Pavlyutkin & Petrenko 2010
	25. Luchegorsk 540/541 (134.2/46.3)	P	33	Nizhnebikinskii, Luchegorskaya	Middle Eocene, IRC	Pavlyutkin & Petrenko 2010
5. Early Eocene	26. Tavrichanka 9142 (131.5/43.2)	P	58	Artemo-Tavrichanskii, Uglovskaya	Ypresian, IRC	Pavlyutkin and Petrenko 2010
	27. Smolyaninovo (132.3/43.2)	P L	56 42	Shkotovskii, Uglovskaya	Ypresian, IRC	Baskakova & Gromova 1979, 1984, Pavlyutkin & Petrenko 2010, Tashchi et al. 1996, Varnavskii et al. 1988, Verkhovskaya & Kundyshev 1989
	28. Kluch Ugolnyi (134.1/43.3)	P L	19 20	Vanchinskii, analog of Uglovskaya	Ypresian, IRC	Chekryzhov et al. 2010, Pavlyutkin & Petrenko 2010
	29. Rettikhovka (132.4/44.1)	P	56	Snegurovskii, analog of Uglovskaya	Ypresian, IRC	Pavlyutkin & Petrenko 2010
	30. Arsen'evka (133.1/44.1)	P	57	Chernyshevskii, analog of Uglovskaya	Ypresian, IRC	Bolotnikova 1988
	31. Kluch Tuyanov (135.1/44.1)	L	62	Zerkal'nenskii, Tujanovskaya	Ypresian, IRC	Baskakova & Lepekhina 1990, Varnavskii et al. 1988
	32. Krylovskii524 (133.4/45.1)	P	59	Krylovskii, Uglovskaya	Ypresian, IRC	Pavlyutkin & Petrenko 2010
	33. Luchegorsk 540/541 (134.2/46.3)	P L	58 12	Nizhnebikinskii, Lower Coal Fm.	Ypresian, IRC	Pavlyutkin & Petrenko 2010
	34. Ozero Toni (138.3/47.4)	P L	32 44	Ozero Toni, Kizinskaya	Early Eocene, IRC	Oleinikov & Klimova 1977, Varnavskii et al. 1988
6. Late Paleocene	35. Ustinovka (135.1/44.1)	L	25	Zerkal'nenskii, Tadushinskaya	Selandian, IRC	Pavlyutkin & Petrenko 2010
	36. Kluch Stolbikova (137.5/46.1)	L	14	Maksimovskii, Kuznetsovskaya	Thanetian, K/Ar (55.0 Ma), IRC	Pavlyutkin & Petrenko 2010, Varnavskii et al. 1988
	37. Kluch Kedrovyi (137.8/46.2)	P	37	Maksimovskii, Kedrovskaya	Thanetian, IRC	Varnavskii et al. 1988
7. Early Paleocene	38. Ustinovka (135.1/44.1)	L	31	Zerkal'nenskii, Bogopol'skaya	Danian, IRC	Ablaev et al. 2005, Krassilov 1989
	39. Sobolevka (137.5/46.1)	L	64	Maksimovskii, Takhobinskaya	Danian, K/Ar (64.0 Ma), IRC	Akhmetiev 1973, 1988, Borsuk 1952

Note: References and complete flora lists including Nearest Living Relatives used for vegetation analysis are given in Supplementary electronic information.

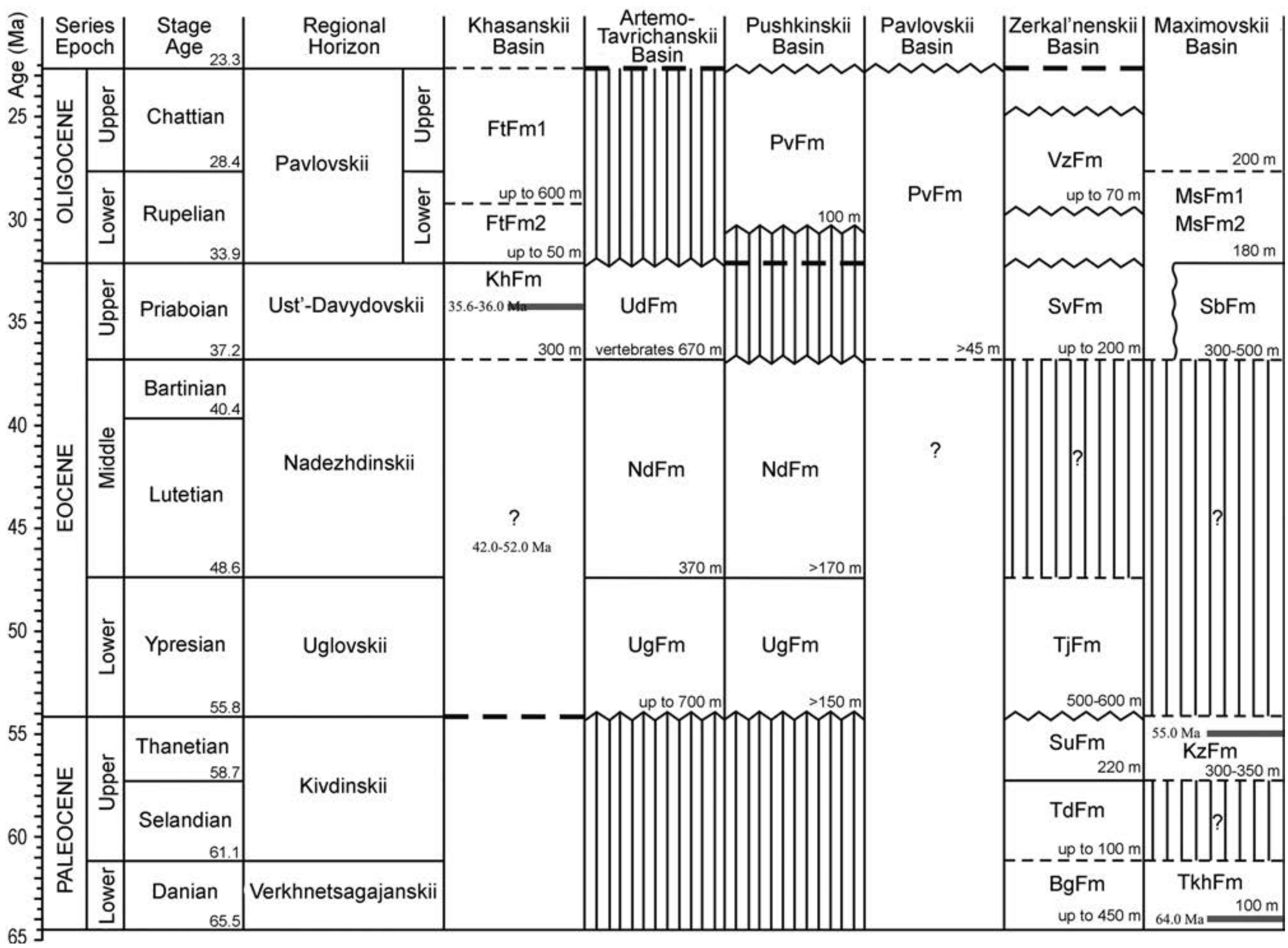

Figure 2 Regional stratigraphic chart for the Paleogene sediments of some Cenozoic basins of Primorye considered in this study (modified from Pavlyutkin & Petrenko 2010), tied to the international standard (Cohen et al. 2013). Jagged boundary: unconformably overlying. Vertical stipple: gap in sedimentation. Details on the palaeofloras are given in Table 1. BgFm – Bogopol'skaya Formation, TkhFm – Takhobinskaya Formation (radiometric age 64.0 Ma by Akhmetiev 1973), TdFm – Tadushinskaya Formation, SuFm – Suvorovskaya Formation, KzFm – Kuznetsovskaya Formation (radiometric age 55.0 Ma by Varnavskii et al. 1988), UgFm – Uglovskaya Formation, TjFm – Tujanovskaya Formation, NdFm – Nadezhdinskaya Formation, KhFm – Khasanskaya Formation, UdFm – Ust'-davydovskaya Formation (radiometric age 35.6-36.0 Ma by Chatshin et al. 2013), SvFm – Svetlinskaya Formation, SbFm – Salibezskaya Formation, FtFm – Fatashinskaya Formation, PvFm – Pavlovskaya Formation, VzFm – Voznovskaya Formation, MsFm – Maksimovskaya Formation

for references). In this study, all palaeofloras considered here were carefully re-evaluated regarding the validity of taxonomic identifications and the Nearest Living Relatives (NLRs) of the fossil taxa, i.e. the taxonomical concept of the fossil materials and modern botanical affinity were carefully revised. In the present study, a total of 54 floras including 30 palynofloras (PF) and 24 leaf floras (LF) were studied with respect to palaeovegetation at seven stratigraphic levels. The floras cover a total time-span of ca. 42 myr, ranging from the early Paleocene (Danian) to late Oligocene (Chattian). The single floras are listed in Table 1, together with information on basin provenience, type of flora, stratigraphic age, method of dating, and references. Climate data for all floras are provided in Bondarenko et al. (in print).

Integrated Plant Record vegetation analysis

The Integrated Plant Record vegetation analysis (IPR-vegetation analysis) is a semi-quantitative method first introduced by Kovar-Eder & Kvaček (2003) to assess zonal vegetation based on the fossil plant record (leaf, fruit, and pollen assemblages). In order to employ the IPR, thirteen basic taxonomic-physiognomic groups, termed components, defined to reflect key ecological characteristics of an assemblage (Kovar-Eder & Kvaček 2003, 2007, Kovar-Eder et al. 2008, Teodoridis et al. 2011) are used: conifer component (CONIF), broad-leaved deciduous component (BLD), broad-leaved evergreen component (BLE), sclerophyllous component (SCL), legume-like component (LEG), zonal palm component (ZONPALM), arborescent fern component (ARBFERN), dry herbaceous component (D-HERB), mesophytic herbaceous component (M-HERB). Azonal components, i.e. azonal woody component (AZW), azonal non-woody component (AZNW) and aquatic component (AQUA). The component PROBLEMATIC TAXA includes elements with uncertain taxonomic-physiognomic affinity. For further analysis, all taxa (but not their abundances) of every single assemblage have to be assigned to those components and their relative proportions have to be calculated. The complete flora lists, assigned NLRs and their allocation to the components are given in Supplementary electronic information. The number of taxa assigned to the components for each flora is given in Table 2.

To characterize zonal vegetation, the following proportions of components are regarded as relevant: (a) the proportion of the BLD, BLE, and SCL+LEG components of zonal woody angiosperms, where "zonal woody angiosperms" means sum of BLD+BLE+SCL+LEG+ZONPALM +ARBFERN components; (b) the proportion of the ZONAL HERB (D-HERB+M-HERB) component of all zonal taxa, where "zonal taxa" means sum of the CONIF+BLD+BLE+SCL+LEG+ZONPALM+ARBFERN+D-HERB+M-HERB components. The reliability of the results increases with increasing number of zonal taxa preserved. Ten zonal taxa are regarded as a minimum to perform this method (Kovar-Eder et al. 2008). Recently, Kovar-Eder & Teodoridis (2018) raised the former threshold to 15 zonal taxa for the application of the IPR-vegetation analysis. The proportions of the components were calculated for each flora and are given in Table 3.

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

Table 2. Number of taxa allocated to the components (abbreviations are explained in text).

Stratigraphic level	Locality name	Type of flora	ZONAL									AZONAL			Problematic taxa
			CONIF	BLD	BLE	SCL	LEG	ZON PALM	ARB FERN	D-HERB	M-HERB	AZW	AZNW	AQU	
1. Late Oligocene	1. Zanadvorovka	P	5.5	15.14	2.81	1.28	0	0	0	0.2	0.4	4.44	0.2	0	0
	2. Pushkinskii9180	P	5.5	15.14	2.81	1.28	0	0	0	0.2	0.4	4.44	0.2	0	0
		L	0	17.16	0	0.66	2	0	0	0	0	6.16	0	2	0
	3. Pavlovka9035-D	P	9.5	12.72	3.89	1.53	1	0	0	0.2	0.4	5.52	0.2	0	0
	4. Turii Rog8	P	6.5	15.14	2.81	1.28	0	0	0	0.2	0.4	5.44	0.2	0	0
	5. Luchegorsk6212	P	8	14.69	2.86	1.53	0	0	0	0.2	0.2	4.49	0	0	0
2. Early Oligocene	6. Kraskino9182/9196	P	12	25.62	6.29	1.78	1	0	0	0.78	4.48	12.67	1.28	2	0
		L	20.5	74.63	28.63	1.5	10	0	0	0.5	2	20.63	1.5	1	0
	7. Pavlovka9035-D	P	9.5	14.05	4.22	1.53	1	0	0	0.2	0.4	5.85	0.2	0	0
	8. Rettikhovka	P	1.5	11.32	7.32	1.5	0	0.5	1	0.33	0.33	8.32	1.83	0	0
		L	7	24.99	4.99	0.5	0	0	0	0	1.5	8.49	0.5	0	0
	9. Voznovo9206	P	13.5	28.03	7.7	1.78	1	0	1	1.11	4.81	13.58	2.36	1	0
		L	24.5	31.06	5.56	0.25	0	0	0	1	1	14.56	2	0	0
	10. Tikhii Kluch	L	11	27.91	2.58	0.58	0	0	0	0.5	0.5	3.91	2	0	0
	11. Amgu9302	L	16	25.14	5.81	0.33	1	0	0	0	1	11.64	0	1	0
	12. Maksimovka	L	17	34.72	3.98	1.49	1	0	0	0.5	4.25	13.22	2.75	2	0
3. Late Eocene	13. Gladkaya17	P	6.5	12.73	6.07	1.41	0	0	0	0.33	0.33	9.23	1.33	0	0
		L	5	16.41	1.91	0.25	0	0	0	0	1	7.41	1	0	0
	14. Tavrichanka9142	P	9.5	16.9	3.57	1.08	0	0	0	0.33	0.33	8.9	1.33	0	0
		L	4	36.89	8.48	0.91	3	0	0	0.5	0.5	17.39	0.25	0	2
	15. Shkotovo	P	4	9.24	2.41	1.08	0	0	0	0.33	0.33	5.24	0.33	0	0
	16. Ivanovka610	P	12	14.07	7.24	1.58	0	0	0	0.33	0.83	9.07	0.83	0	0
	17. Pavlovka9035-D	P	11	16.51	4.01	0.5	1	0	1	0.99	2.69	8.51	2.19	1.5	0
		L	0	16.66	2.83	0.83	0	0	0	0	0	3.66	0	1	0
	18. Svetlyi	P	0.5	4.83	4.33	1	0	0	0	0	0	3.33	0	0	0
		L	5.5	3.33	0.33	0	0	0	0	0	5.5	4.83	2.5	0	0
	19. Luchegorsk	P	3.5	22.23	9.07	1.41	0	0	0	0.58	6.83	9.98	2.83	1.5	0
		L	1	29.98	5.49	1.49	0	0	0	0	1	14.98	0	0	1
	20. Salibeza	L	9	13.32	2.32	0	0	0	0	0	7	10.32	2	4	0
4. Middle Eocene	21. Vol'no-Nadezhdinskoe	P	8.5	20.81	6.98	1.83	0	0	0	0.33	2.33	9.81	2.33	0	0
		L	1	11.66	2.08	0.58	0	0	0	0	2.25	6.16	0.75	0.5	0
	22. Bolotnaya	P	10.5	16.65	3.82	1.83	0	0	0	0.33	1.33	9.15	0.33	0	0
		L	0	46.05	9.47	0.83	1	0	0	0.25	1.75	14.3	0.25	0	1
	23. Shkotovo	P	4.5	12.15	2.82	0.83	0	0	0	0	0	6.65	0	0	0
	24. Terekhovka	P	8	17.47	7.64	1.28	0	0	0	0.2	0.4	7.77	0.2	0	0
	25. Luchegorsk540/541	P	7.5	11.85	4.52	1.33	0	0	0	0	0.2	5.35	0.2	0	0
5. Early Eocene	26. Tavrichanka9142	P	9	19.73	7.4	1.58	0	0.5	1	0.33	1.83	10.23	1.33	0	0
	27. Smolyaninovo	P	11.5	16.73	8.9	1.58	0	0	0	0.33	1.33	10.23	0.33	0	0
		L	0	26.41	5.66	0	1	0	0	0	0.25	7.41	0.25	0	1
	28. Kluch Ugolnyi	P	0.5	5.83	5.33	1	0	0	0	0	0	3.33	0	0	0
		L	2	10	0.5	0	0	0	0	0	2	5.5	0	0	0
	29. Rettikhovka	P	9.5	13.57	8.74	1.58	0	0	1	0.33	3.83	10.57	0.83	0	0
	30. Arsen'evka	P	9	13.98	7.4	1.08	0	0	0	0.58	8.58	8.73	2.08	0.5	0
	31. Kluch Tuyanov	L	11	24.57	3.82	0.5	0	0	0	0	4.25	15.57	2.25	0	0
	32. Krylovskii524	P	10	18.63	8.3	1.78	0	0	1	1.03	3.73	11.43	1.03	0	0
	33. Luchegorsk540/541	P	8.5	19.26	6.43	1.58	0	0	0	0.33	3.03	11.76	2.53	0.5	0
		L	1	5.5	0	0	0	0	0	0	0	4.5	1	0	0
	34. Ozero Toni	P	6	13.81	0.98	0.53	1	0	0	0.78	2.23	4.86	0.78	1	0
		L	7	17.57	1.24	0.58	0	0	0	1	3	11.57	1	1	0
6. Late Paleocene	35. Ustinovka	L	1	14.33	0	0.33	0	0	0	0.33	2.83	5.33	0.83	0	0
	36. Kluch Stolbikova	L	2	8.16	1.16	0	0	0	0	0	0	2.66	0	0	0
	37. Kluch Kedrovyi	P	7.5	12.73	4.57	1.41	0	0	0	0.33	1.33	6.73	0.83	0.5	0
7. Early Paleocene	38. Ustinovka	L	4.5	14.66	0.83	0.33	1	0	0	0	2	6.66	0	0	0
	39. Sobolevka	L	10.5	26.65	5.07	0.58	0	0	0	0.5	5.75	13.15	0.75	0	0

References and complete flora lists including Nearest Living Relatives used for vegetation analysis are given in Supplementary electronic information.

temperate to warm-temperate broad-leaved deciduous forests (broad-leaved deciduous forests, BLDF), zonal warm-temperate to subtropical mixed mesophytic forests (mixed mesophytic forests, MMF), zonal subtropical broad-leaved evergreen forests (broad-leaved evergreen forests, BLEF), zonal subtropical, subhumid sclerophyllous or microphyllous forests (subhumid sclerophyllous forests, ShSF), zonal xeric open woodlands (open woodland), and zonal xeric grasslands or steppe (xeric grassland). Teodoridis et al. (2011) additionally defined ecotones between the BLDF and MMF and the BLEF and MMF and recently, Kovar-Eder & Teodoridis (2018) defined ecotone between the MMF/ShSF.

RESULTS

To apply IPR-vegetation analysis, 30 microfloras and 24 macrofloras were analyzed (Supplementary electronic information and Table 2). Based on the relative proportions of the components, three zonal vegetation types and two ecotones between them were revealed for the Paleogene of Primorye (Table 3).

The first (warmest) zonal vegetation type of subtropical broad-leaved evergreen forests (=broad-leaved evergreen forests, BLEF) was revealed from the late Eocene PF 18 and the early Eocene PF 28. These floras are characterized by low proportions of the BLD component (up to 48 %), high proportions of the BLE component (42–44 %), very low proportion of the SCL+LEG component (up to 10 %), and absence of herbs.

The second zonal vegetation type of warm-temperate to subtropical mixed mesophytic forest (= mixed mesophytic forest, MMF) was revealed mainly based on PFs (from the late Paleocene to late Oligocene) and two LFs (the late Eocene and early Oligocene). The floras assigned to this zonal vegetation type are characterized by proportions of the BLD component from 62 to 75 %, BLE component – 17–29 %, SCL+LEG component – 5–13 %, and 1–17 % of herbs.

The third zonal vegetation type of temperate to warm-temperate broad-leaved deciduous forest (= broad-leaved deciduous forest, BLDF) was mainly reconstructed from LFs (from the early Paleocene to late Oligocene), and from the early Eocene PF 34. All these floras are characterized by high proportions of the BLD component (from 82 to 100 %), low proportions of the BLE (0–16 %), SCL+LEG (1–13 %), and ZONAL HERB components (0–22 %, except the late Eocene LF 18 constituting 37.5 % of herbs).

The ecotones (MMF/BLEF and BLDF/MMF) are characterized by the transitional (intermediate) proportions of components in comparison with the corresponding zonal vegetation types (Table 3). The ecotone MMF/BLEF was revealed only for PFs from the early Eocene to early Oligocene and is characterized by 53–62 % of BLD, 30–35 % of BLE, 5–7 % of SCL+LEG and 2–22 % of herbs. The ecotone BLDF/MMF dominates in the late Oligocene and is characterized by 77–80 % of BLD, 14–18 % of BLE, 3–8 % of SCL+LEG and 0–2 % of herb components.

DISCUSSION

Comparison of micro- and macrofloras

The IPR claims to reconstruct vegetation independent from the type of flora, nevertheless, there is a distinct difference in our results based on micro- and macrofloras. First of all, in the microfloras the number of zonal taxa is more stable in comparison with the macrofloras. The total number of all fossil taxa per site varies between 12 and 161 (Table 1). When ten zonal taxa are regarded as a minimum (Kovar-Eder et al. 2008), a mean number of zonal taxa of 34.8 for all the floras was sufficient to yield reliable results, except the LF 33 (6.5 zonal taxa only). When 15 zonal taxa are regarded as a minimum (Kovar-Eder & Teodoridis 2018) two microfloras and three macrofloras are insufficient to yield reliable results. The number of zonal taxa (Table 3) in each microflora ranged 10.66–58.93 (mean 32.3). The analysis of macrofloras was based on 6.5–137.76 (mean 37.8) zonal taxa.

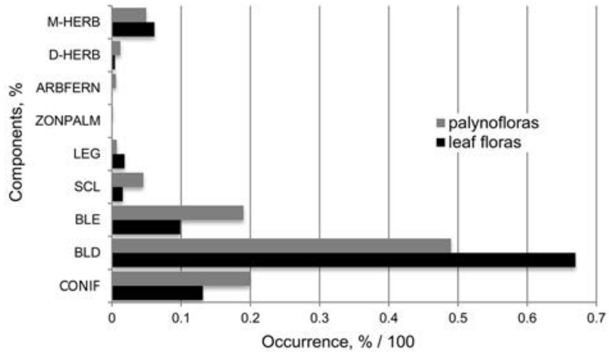

Figure 3 Representation of IPR components in macro- and microfloras. Mean proportions calculated based on a total of 16 late Paleocene to late Oligocene localities yielding both, macro- and microrecords

The components used for calculating of the proportions also vary in the micro- and macrofloras (Table 2, Fig. 3). The CONIF component occurs in all microfloras ranging from 0.5 to 13.5, in the macrofloras – from 0 to 24.5 of zonal taxa. The BLD component is present in all micro- (4.8–28.6 zonal taxa) and macrofloras (3.3–74.6 zonal taxa). The BLE component in the microfloras varies from 1 to 9, whereas in the macrofloras – from 0 to 28.6 but mostly does not exceed 9.5 zonal taxa. The SCL component ranges from 0.5 to 1.8 in the microfloras and from 0 to 1.5 of zonal taxa in the macrofloras. The LEG component occurs rarely: 0–1 in microfloras, 0–2 zonal taxa in the macrofloras (except the early Oligocene LF 6 with 10 zonal taxa of the component). The ZONPALM component occurs only in some microfloras (0.5 zonal taxa) and is absent from the macrofloras. The ARBFERN component also occurs only in some microfloras (1 zonal taxa) and is absent from the macrofloras. The D-HERB component in the microfloras varies from 0.2 to 1.1, in the macrofloras – from 0 to 1 of zonal taxa. The M-HERB component is 0.2–8.6 zonal taxa in the microfloras and 0–7 zonal taxa in the macrofloras.

The ratio of each component in all micro- and macrofloras is given in Figure 3. As seen in the diagram (Fig. 3), IPR data are not independent from organ type regarded in each case. Leaf floras seem to be biased towards higher BLD and lower BLE proportions, microfloras have a lower proportion of LEG but a higher proportion of SCL components. As a result, the BLD forest biome is more frequently reconstructed based on leaves. This may have ta-

Table 3. Proportion of the components.

Stratigraphic level	Locality name	Palynofloras: Number of zonal taxa	Palynofloras: BLD prop, %	Palynofloras: BLE prop, %	Palynofloras: SCL+LEG prop, %	Palynofloras: ZONAL HERB prop, %	Palynofloras: Zonal vegetation type	Leaf floras: Number of zonal taxa	Leaf floras: BLD prop, %	Leaf floras: BLE prop, %	Leaf floras: SCL+LEG prop, %	Leaf floras: ZONAL HERB prop, %	Leaf floras: Zonal vegetation type
1. Late Oligocene	1. Zanadvorovka	25.33	78.73	14.61	6.66	2.37	BLDF/MMF	–	–	–	–	–	–
	2. Pushkinskii9180	25.33	78.73	14.61	6.66	2.37	BLDF/MMF	19.82	86.58	0.0	13.42	0.0	BLDF
	3. Pavlovka9035-D	29.24	66.46	20.32	13.22	2.05	MMF	–	–	–	–	–	–
	4. Turii Rog8	26.33	78.73	14.61	6.66	2.37	BLDF/MMF	–	–	–	–	–	–
	5. Luchegorsk6212	27.48	76.99	14.99	8.02	1.45	BLDF/MMF	–	–	–	–	–	–
2. Early Oligocene	6. Kraskino9182/9196	51.95	73.85	18.13	8.01	10.12	MMF	137.76	65.03	24.95	10.02	1.81	MMF
	7. Pavlovka9035-D	30.9	67.55	20.29	12.16	1.94	MMF	–	–	–	–	–	–
	8. Rettikhovka	23.8	52.31	33.83	6.93	2.77	MMF/BLEF	38.98	81.99	16.37	1.64	3.85	BLDF
	9. Voznovo9206	58.93	70.94	19.49	7.04	10.04	MMF	63.37	84.24	15.08	0.68	3.16	BLDF
	10. Tikhii Kluch	–	–	–	–	–	–	43.07	89.83	8.30	1.87	2.32	BLDF
	11. Amgu9302	–	–	–	–	–	–	49.28	77.88	18.0	4.12	2.03	BLDF/MMF
	12. Maksimovka	–	–	–	–	–	–	62.94	84.29	9.66	6.04	7.55	BLDF
3. Late Eocene	13. Gladkaya17	27.37	62.99	30.03	6.98	2.41	MMF/BLEF	24.57	88.37	10.28	1.35	4.07	BLDF
	14. Tavrichanka9142	31.71	78.42	16.57	5.01	2.08	BLDF/MMF	54.28	74.86	17.21	7.93	1.84	MMF
	15. Shkotovo	17.39	72.58	18.93	8.48	3.79	MMF	–	–	–	–	–	–
	16. Ivanovka610	36.05	61.47	31.63	6.90	3.22	MMF/BLEF	–	–	–	–	–	–
	17. Pavlovka9035-D	37.7	71.72	17.42	6.52	9.76	MMF	20.32	81.99	13.93	4.08	0.0	BLDF
	18. Svetlyi	10.66	47.54	42.62	9.84	0.0	BLEF	14.66	90.98	9.02	0.0	37.52	BLDF
	19. Luchegorsk	43.62	67.96	27.73	4.31	16.99	MMF	38.96	81.11	14.85	4.03	2.57	BLDF
	20. Salibeza	–	–	–	–	–	–	31.64	85.17	14.83	0.0	22.12	BLDF
4. Middle Eocene	21. Vol'no-Nadezhdinskoe	40.78	70.26	23.56	6.18	6.52	MMF	17.57	81.42	14.52	4.05	12.81	BLDF
	22. Bolotnaya	34.46	74.66	17.13	8.21	4.82	MMF	59.35	80.30	16.51	3.19	3.37	BLDF
	23. Shkotovo	20.3	76.90	17.85	5.25	0.0	BLDF/MMF	–	–	–	–	–	–
	24. Terekhovka	34.99	66.20	28.95	4.85	1.71	MMF	–	–	–	–	–	–
	25. Luchegorsk540/541	25.4	66.95	25.54	7.51	0.79	MMF	–	–	–	–	–	–
5. Early Eocene	26. Tavrichanka9142	41.37	65.31	24.49	5.23	5.22	MMF	–	–	–	–	–	–
	27. Smolyaninovo	40.37	61.48	32.71	5.81	4.11	MMF/BLEF	33.32	79.86	17.11	3.02	0.75	BLDF/MMF
	28. Kluch Ugolnyi	12.66	47.94	43.83	8.22	0.0	BLEF	14.5	95.24	4.76	0.0	13.79	BLDF
	29. Rettikhovka	38.55	54.52	35.11	6.35	10.79	MMF/BLEF	–	–	–	–	–	–
	30. Arsen'evka	40.62	62.24	32.95	4.81	22.55	MMF/BLEF	–	–	–	–	–	–
	31. Kluch Tuyanov	–	–	–	–	–	–	44.14	85.05	13.22	1.73	9.63	BLDF
	32. Krylovskii524	44.47	62.71	27.94	5.99	10.70	MMF	–	–	–	–	–	–
	33. Luchegorsk540/541	39.13	70.63	23.58	5.79	8.59	MMF	6.5	100.0	0.0	0.0	0.0	BLDF
	34. Ozero Toni	25.33	84.62	6.0	9.37	11.88	BLDF	30.39	90.61	6.39	2.99	13.16	BLDF
6. Late P aleocene	35. Ustinovka	–	–	–	–	–	–	18.82	97.75	0.0	2.25	16.79	BLDF
	36. Kluch Stolbikova	–	–	–	–	–	–	11.32	87.55	12.45	0.0	0.0	BLDF
	37. Kluch Kedrovyi	27.87	68.04	24.42	7.54	5.96	MMF	–	–	–	–	–	–
7. Early Paleocene	38. Ustinovka	–	–	–	–	–	–	23.32	87.16	4.93	7.91	8.58	BLDF
	39. Sobolevka	–	–	–	–	–	–	49.05	82.51	15.70	1.80	12.74	BLDF

References and complete flora lists including Nearest Living Relatives used for vegetation analysis are given in Supplementary electronic information.

phonomic as well as edaphic reasons. Kovar-Eder & Kvaček (2007) assume that the differences of relative proportions of the components in the micro- versus the macrofloras are probably related to the lower taxonomic resolution of the pollen record and to the fact that pollen assemblages may be much more strongly influenced by long-distance transport than the leaf floras.

Vegetation

As seen in the Table 3, the proportions calculated for determining of the zonal vegetation types differ in the micro- and macrofloras. The BLD proportions in the microfloras range from 52 to 84 %, in the macrofloras the proportions are higher (65–100 %). The BLE proportions in the microfloras are from 6 to 44 %, in the macrofloras – from 5 to 25 %. The SCL+LEG proportions are represented in all microfloras ranging from 5 to 13 %, while in the macrofloras the SCL+LEG proportions are 1–10 % and even in some macrofloras this component is absent. The ZONAL HERB proportions are represented in the microfloras up to 22 %, in the macrofloras – up to 37.5 %.

According to Kovar-Eder et al. (2008) and Teodoridis et al. (2011), with zonal herb proportions ranging from 0 to 22 %, except the late Eocene LF 18 constituting 37.5 % of herbs, no open woodland is reconstructed for the Primorye Region throughout the Paleogene based on the IPR-vegetation analysis. Moreover, according to Bondarenko et al. (2017), in the early Pleistocene the zonal herb proportion was ranging from 18 to 37 %. Thus, a close forest cover likely existed in Primorye throughout most of the Cenozoic. In Western Siberia, however, Popova et al. (2013) point out a steep declining trend of the arboreal component, already at the end of the Eocene.

Based on the microfloras, all three zonal vegetation types and two ecotones between them were revealed for the Paleogene of Primorye. The warmest zonal vegetation type (BLEF) was obtained only based on the microfloras and is represented by the early Eocene PF 28 and the late Eocene PF 18 (Zerkal'nenskii and Vanchinskii Basins correspondently, Fig. 4). The MMF zonal vegetation type dominated in Primorye during the Paleogene, as evident from the microfloras, and occurs from the late Paleocene to late Oligocene on the studied territory. The coldest zonal vegetation type (BLDF) was revealed only for the early Eocene PF 34 in the north of Primorye (Ozero Toni Basin, Fig. 4). The ecotone MMF/BLEF, reconstructed from microfloras, occurred from the early Eocene to early Oligocene, predominantly in the Eocene, in southern and middle part of Primorye, whereas the ecotone BLDF/MMF occurred from the middle Eocene to late Oligocene, but was predominant in the Oligocene.

The results obtained from the macrofloras are fundamentally different from the results based on microflora but may reflect more local conditions and wetland character of vegetation in the depocentres. The BLEF zonal vegetation type and the ecotone MMF/BLEF are not reconstructed from the macrofloras. The MMF zonal vegetation type was revealed only for the late Eocene LF 14 and early Oligocene LF 6 from the south of Primorye (Artemo-Tavrichanskii and Khasanskii Basins correspondently). Unlike the microfloras, the BLDF zonal vegetation type is dominant in the macrofloras and occurred from the early Paleocene to late Oligocene on the studied territory. Moreover, only the ecotone BLDF/MMF was revealed for the early Eocene LF 27 and early Oligocene LF 11.

The modern vegetation of Primorye consists of mesophytic and xerophytic types (forest, wooded steppe, steppe, meadow, and swamp), which are in contact and form complex combinations (Kurentsova 1968). Our palaeobotanical data in general demonstrate a mesophytic forest (mixed broadleaved conifer forest with a diverse undergrowth) of subtropical to warm-temperate character in Primorye during the Paleogene while there is no evidence for xerophytic types and steppe.

The results obtained from the IPR-vegetation analysis of the Paleogene floral record of Primorye do not contradict the data obtained by other researchers. Ablaev et al. (2005), studying the late Paleocene LF 35, concluded that, in general, the territory under consideration was covered with coniferous-deciduous forests of warm-temperate type growing in the coastal region under a monsoon-type climate and this contributed to the development of a significant number of thermophilic elements here, compared to more continental areas.

Sedova (1957) and Flerov et al. (1974) infer for the south of Primorye in the early Eocene the presence of lush subtropical coastal vegetation, with the possible spread of mangroves there. However, Tashchi et al. (1996) question such conclusions and suggest warm temperate vegetation. According to present reconstruction, the early Eocene vegetation in Primorye was represented by a warm-temperate to subtropical vegetation according to the microfloras and mainly by a temperate to warm-temperate vegetation as reconstructed based on macrofloras (Table 4).

Pavlyutkin (2007) believes that the late Eocene LF 14 was probably formed in a warm-temperate climate with moderate humidity and represents a mesophytic, deciduous type, warm-temperate with some elements of more southern, subtropical origin. Our data also indicate a temperate to warm-temperate vegetation in the late Eocene according to the macrofloras, while the microfloras suggest a warm-temperate to subtropical vegetation (Table 4).

According to Pavlyutkin (2011) and Pavlyutkin et al. (2014), the early Oligocene LF 6 represents forest vegetation, mesothermal, transitional from warm-temperate to subtropical, mostly deciduous, although with significant participation of warmth-loving conifers and evergreen angiosperms. At the same time, the early Oligocene LF 9 and 11 represent deciduous, mesophilic, warm-temperate vegetation, with a minor participation of elements now found in mountain forests of the subtropics, some of which are evergreen (Pavlyutkin et al. 2014). This in general coincides with our reconstruction showing a warm-temperate to subtropical vegetation based on microfloras, and temperate to warm-temperate vegetation based on macrofloras, respectively, probably existing under specific local settings (Table 4).

There is evidence that in the Russian Far East, thermophilous vegetation persisted in the Neogene, even to the

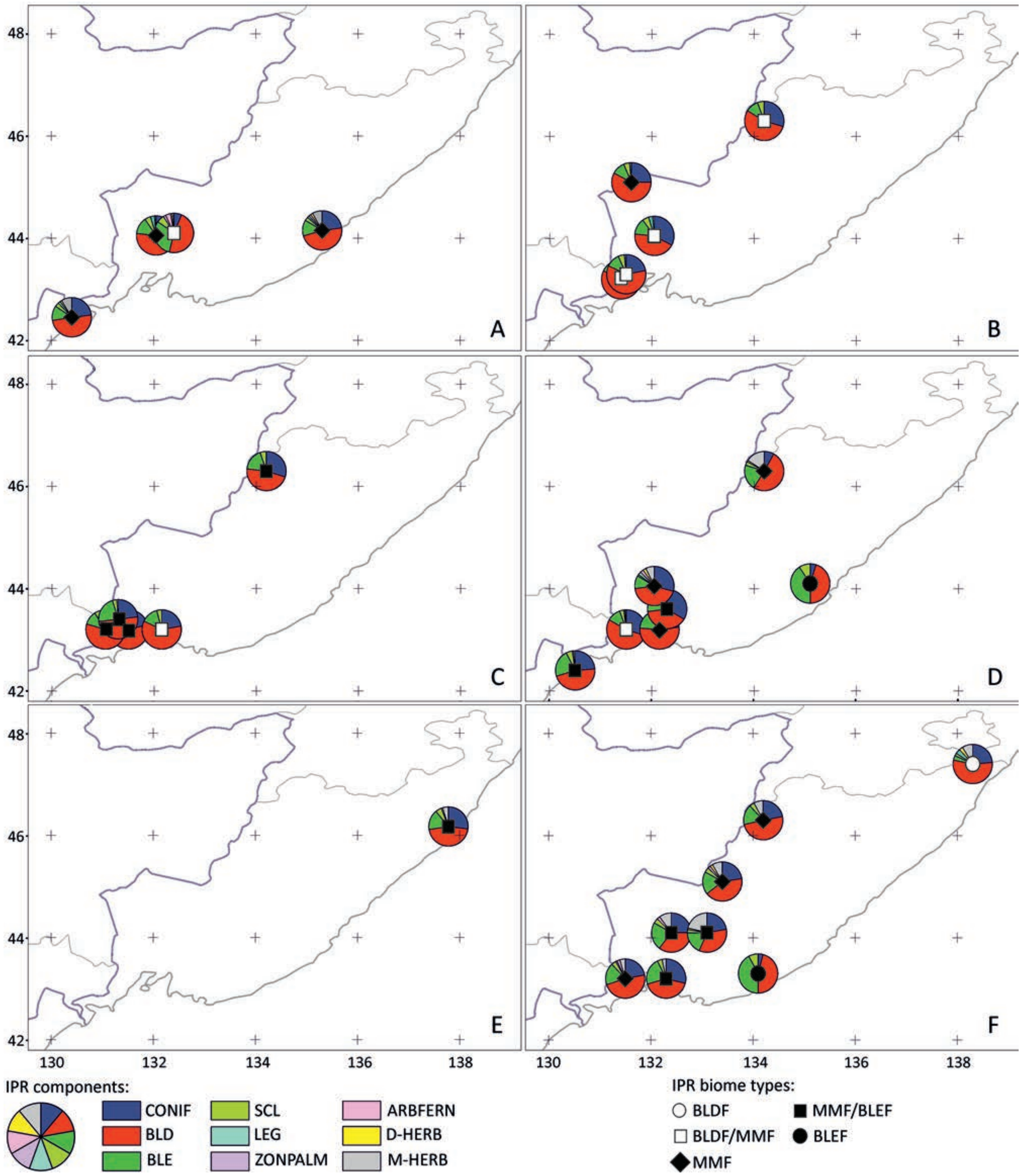

Figure 4 Proportions of the IPR components and corresponding zonal vegetation types in the Paleogene of Primorye based on microfloras: A – Early Oligocene, B – Late Oligocene, C – Middle Eocene, D – Late Eocene, E – Late Paleocene, F – Early Eocene. See explanations for abbreviations of IPR components and IPR biome types in the text

north of our study area. From early Neogene carpofloras of the eastern RFE, Popova et al. (2013) reconstructed a high diversity (40–50 %) of warm-temperate woody plants, including evergreen broad-leaved trees.

Climate

It is known that changes in vegetation are associated with climate changes. Recently, the Paleogene climate dynamics in Primorye are studied using the Coexistence Approach, based on the palaeobotanical records (Utescher et al. 2015, Bondarenko et al. in print). The climatic inferences obtained are consistent with independently-derived global trends, demonstrating general climate cooling throughout the Paleogene (Zachos et al. 2008). The data indicate that the Paleogene climate of Primorye was significantly warmer than present, in general, with the warmest conditions pre-

Table 4. Zonal vegetation types with climate data.

Stratigraphic level	Locality name	Palynofloras						Leaf floras					
		Zonal vegetation type	MAT, C° [1]	MAP, mm [1]	Dominating zonal vegetation type	Mean MAT, C° [2]	Mean MAP, mm [2]	Zonal vegetation type	MAT, C° [1]	MAP, mm [1]	Dominating zonal vegetation type	Mean MAT, C° [2]	Mean MAP, mm [2]
1. Late Oligocene	1. Zanadvorovka	BLDF/MMF	15	1188	BLDF/MMF	15.8	1213	–	–	–	BLDF	14.4	1229
	2. Pushkinskii9180	BLDF/MMF	15	1188				BLDF	14.4	1229			
	3. Pavlovka9035-D	MMF	17.1	1278				–	–	–			
	4. Turii Rog8	BLDF/MMF	15	1132				–	–	–			
	5. Luchegorsk6212	BLDF/MMF	16.9	1278				–	–	–			
2. Early Oligocene	6. Kraskino9182/9196	MMF	16.9	1163	MMF	16.8	1296	MMF	16.3	1118	BLDF	15.6	1150
	7. Pavlovka9035-D	MMF	17.4	1278				–	–	–			
	8. Rettikhovka	MMF/BLEF	16.9	1422				BLDF	14.8	1329			
	9. Voznovo9206	MMF	16	1323				BLDF	15.4	1134			
	10. Tikhii Kluch	–	–	–				BLDF	15.2	1059			
	11. Amgu9302	–	–	–				BLDF/MMF	15.4	1137			
	12. Maksimovka	–	–	–				BLDF	16.5	1126			
3. Late Eocene	13. Gladkaya17	MMF/BLEF	16.9	1554	MMF	16.9	1432	BLDF	17.6	1307	BLDF	17	1171
	14. Tavrichanka9142	BLDF/MMF	16.9	1554				MMF	17.6	1227			
	15. Shkotovo	MMF	17.6	1278				–	–	–			
	16. Ivanovka610	MMF/BLEF	18.2	1404				–	–	–			
	17. Pavlovka9035-D	MMF	16.5	1373				BLDF	17.1	1044			
	18. Svetlyi	BLEF	16.3	1596				BLDF	14.8	1158			
	19. Luchegorsk	MMF	16.1	1265				BLDF	17.2	1198			
	20. Salibeza	–	–	–				BLDF	17.5	1095			
4. Middle Eocene	21. Vol'no-Nadezhdinskoe	MMF	16.9	1554	MMF	17.2	1295	BLDF	17.8	1172	BLDF	17.9	1228
	22. Bolotnaya	MMF	17.4	1170				BLDF	18	1284			
	23. Shkotovo	BLDF/MMF	17.5	1070				–	–	–			
	24. Terekhovka	MMF	17.3	1404				–	–	–			
	25. Luchegorsk540/541	MMF	17.1	1278				–	–	–			
5. Early Eocene	26. Tavrichanka9142	MMF	17.3	1554	MMF/BLEF	17.6	1338	–	–	–	BLDF	16.2	1162
	27. Smolyaninovo	MMF/BLEF	18.2	1295				BLDF/MMF	17.5	1315			
	28. Kluch Ugolnyi	BLEF	18.2	1422				BLDF	17.2	1122			
	29. Rettikhovka	MMF/BLEF	18.2	1351				–	–	–			
	30. Arsen'evka	MMF/BLEF	18.2	1404				–	–	–			
	31. Kluch Tuyanov	–	–	–				BLDF	15.9	1170			
	32. Krylovskii524	MMF	16.6	1278				–	–	–			
	33. Luchegorsk540/541	MMF	16.6	1278				BLDF	15.2	1159			
	34. Ozero Toni	BLDF	17.4	1126				BLDF	15.1	1047			
6. Late Paleocene	35. Ustinovka	–	–	–	MMF	17.6	1158	BLDF	16.9	1045	BLDF	17.1	1127
	36. Kluch Stolbikova	–	–	–				BLDF	17.3	1210			
	37. Kluch Kedrovyi	MMF	17.6	1158				–	–	–			
7. Early Paleocene	38. Ustinovka	–	–	–	–	–	–	BLDF	18.4	1045	BLDF	16.4	1169
	39. Sobolevka	–	–	–				BLDF	14.5	1293			

References and complete flora lists including Nearest Living Relatives used for vegetation analysis are given in Supplementary electronic information. [1] Means of Coexistence Intervals (Bondarenko et al., in print); [2] Means by substage calculated from [1] vailing throughout the Eocene and in the southeast of the study area. Negligible Paleogene temperature gradients over Primorye are related to the global pattern revealing shallow temperature gradients in general (Greenwood & Wing 1995, Utescher et al. 2011), and specific regional aspects (Bondarenko et al. in print). The precipitation reconstruction points to conditions considerably wetter than at present (Utescher et al. 2014). A distinct increase in mean annual precipitation was reconstructed for the study area for the early Eocene and moderately declined throughout the Oligocene (Utescher et al. 2014). The regional rainfall pattern fundamentally differed from modern conditions, and this holds for all studied variables. The inland region and the south of Primorye were significantly more humid than today. The Paleogene pattern was possibly related to a monsoon-type circulation and enhanced landward flow of humid air masses, possibly due to an overall flatter morphology of the East Asian coastal areas (Bondarenko et al. in print) and a weak Siberian High that plays a critical role in the regional atmospheric circulation patterns (Popova et al. 2012).

According to Bondarenko et al. (in print), the mean MAT values based on the microfloras demonstrate the direct cooling trend (Table 4). In general, the obtained major plant biome changes (the dominating zonal vegetation type) in Primorye during the Paleogene, from the subtropical MMF/BLEF ecotone in the late Paleocene to the warm-temperate BLDF/MMF ecotone in the late Oligocene, as reconstructed based on the microfloras (Table 4) coincides with this cooling trend.

At the same time, the mean MAT values reconstructed from the macrofloras, having lower MAT values in general, show warm peaks in the late Paleocene and middle Eocene (Table 4) corresponding to the Paleocene–Eocene Thermal Maximum (PETM) and climatic optimum in the middle Eocene (MECO). However, despite the larger amplitude of temperatures and the presence of warm peaks, the macrofloras do not reflect major changes in vegetation, and show only one dominating type of temperate to warm-temperate forest – the BLDF (Table 4). Most likely, this can be explained by the fact that the leaves of deciduous plants are more likely to be buried than those of evergreen plants, while pollen show their presence more reliably (Krassilov 1972).

According to Akhmetiev (2004), Primorye belonged to a warm-temperate, humid climate zone during the Paleocene. In the early Eocene, this warm-temperate, humid zone was significantly reduced in size and covered mainly the polar region. At the transition from a warm-temperate climate to a subtropical zone in East Asia, especially along the Pacific Coast, a wide ecozone with deciduous and evergreen elements established. Deciduous elements in the conditions of the dissected relief of the oceanic margin penetrated far to the south, and in the zones of coastal evergreen plants, including palm trees, to the north (Akhmetiev 2004). In the middle Eocene, according to Akhmetiev (2004), the zone of temperate and warm-temperate humid climate, which existed from the beginning of the Paleogene, comprised the circumpolar region of the Northern Hemisphere, although its southern boundary shifted somewhat to the south, compared with its position in the Early Eocene. At the beginning of the middle Eocene (Lutetian) in eastern Eurasia, a zone of mesophilic subtropical floras (a zone of humid and variable-humid (seasonal) subtropical climate) encompassed the very south of Primorye.

Paleogene temperature records are available for northeast China and thus from the closer neighborhood of our study area (Quan et al. 2012b). Features in common are the declining trend from the Paleocene to the early Eocene (CMMT), and a very warm late Eocene with subsequent distinct cooling (MAT, CMMT). The very warm late Eocene is not reflected in the global climate evolution and thus may represent a regional signal, possibly related to the initial opening of the Sea of Japan. According to Quan et al. (2012b), among the estimated terrestrial temperature parameters reconstructed from a sequence exposed in the Fushun open cast, MAT slightly changed with an overall declining trend in the Eocene. However, the winter temperature dramatically decreased from the middle Eocene to the late Eocene, while the summer temperature remained almost the same throughout the Eocene. All these data are within the range of the palaeoclimate reconstruction by Bondarenko et al. (in print) or slightly higher (CMMT), respectively, which coincides with the latitude of Fushun, lower by several degrees.

Quan et al. (2012a) demonstrate that in the Eocene, monsoonal climate probably had already been established over China, judging from the presence of apparent seasonality of both temperature and precipitation. In addition, Quan et al. (2012a) point out that, with a slight declining trend of MAT during the Eocene, the winter temperature substantially dropped in tropical southern China during the middle to late Eocene interval. According to Quan et al. (2012a), this might have been related to the development of a weak Eocene Kuroshio Current in the southwestern Pacific, and/or a significantly enhanced palaeo-winter monsoon from Siberia.

CONCLUSIONS

The exceptionally rich palaeobotanical record of Primorye holds the key for reconstructing the detailed Paleogene regional vegetation evolution in space and time. The high diversity of the palaeofloras and up-to-date taxonomy result in useful vegetation interpretations. Our vegetation maps for the first time allow quantifying major plant biome changes in space and time on the Pacific side of Eurasia over the past 42 myr. Our palaeobotanical data indicate more forested conditions within the studied territory during the Paleogene than at present and in general prove the existence of a mesophytic forest (mixed broadleaved conifer forest with a diverse undergrowth) of subtropical to warm-temperate character in Primorye through the Paleogene. Moreover, the obtained major plant biome changes in Primorye from the subtropical MMF/BLEF ecotone in the late Paleocene to the warm-temperate BLDF/MMF ecotone in the late Oligocene, as reconstructed based on the microfloras, coincide with the coeval, globally observed cooling trend.

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