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RESEARCH PAPER

Taxonomic diversity and floristic composition changes of East Asia during the early Paleogene

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ABSTRACT

The early Paleogene floristic background and taxonomical inventory of palaeobotanical data of East Asia are studied for the first time using quantitative techniques. The record comprises 110 micro- and macrofloras from 73 localities of Eastern Siberia, Far East of Russia, China, and Japan. The analysis of the floral record reveals a taxonomical diversity of 1119 species of 578 genera from 132 families. Angiosperms represent the most diverse division accounting for over two-thirds of family diversity. The application of multivariate statistics provides insight into the floristic similarities of the single palaeofloras and the relation between taxonomic entities, and allows to trace the spatio-temporal distribution of six floristic groups characterised by taxonomic associations. The floristic composition in the study area did not undergo any significant changes throughout the early Paleocene, while the early Eocene saw a distinct increase mainly referable to a diversification of angiosperms. This diversification can possibly be related to the coeval warming trend. Our analysis of the Paleocene floras supports their continuity with Late Cretaceous floras, relative floristic homogeneity and the existence of only two floristic provinces. For the early Eocene we suggest at least three floristic provinces. Our results support a diffuse origin of the early Paleogene floras of East Asia and a lower to mid-latitudinal appearance of angiosperm taxa and a pole-ward migration thereafter, which generally supports the Boreotropical hypothesis. The early Paleogene floras of East Asia show minor spatial and temporal variations in taxonomic composition, with new taxa appearing in the fossil record at different times and having different ecologies.

Keywords: taxonomic diversity, floristic composition, floristic provinces, early Paleogene, East Asia

РЕЗЮМЕ

Бондаренко О.В., Утешер Т. Изменения таксономического разнообразия и флористического состава на востоке Азии в раннем палеогене. Флористический фон и таксономический перечень палеоботанических данных востока Азии в раннем палеогене впервые изучены с использованием количественных методов. Летопись включает 110 микро- и макрофлор из 73 местонахождений Восточной Сибири, Дальнего Востока России, Китая и Японии. Наш анализ выявил таксономическое разнообразие 1119 видов 578 родов из 132 семейств. Покрытосеменные представляют собой наиболее многочисленный отдел, на который приходится более 2/3 разнообразия семейств. Применение многомерной статистики дает представление о флористическом сходстве отдельных палеофлор и связи между таксономическими единицами, и позволяет проследить пространственно-временное распределение флористических групп, характеризующихся таксономическими ассоциациями. Флористический состав в исследуемой области не претерпел существенных изменений на протяжении раннего палеоцена, в то время как в раннем эоцене наблюдался отчетливый рост, в основном связанный с диверсификацией покрытосеменных. Диверсификация, возможно, связана с тенденцией к потеплению климата в тот же период. Анализ палеоценовых флор подтверждает их преемственность с позднемеловыми флорами, большую однородность и наличие только двух флористических провинций. В раннем эоцене предполагается наличие по крайней мере трех флористических провинций. Наши результаты подтверждают диффузное происхождение раннепалеогеновых флор востока Азии, появление таксонов покрытосеменных в нижних и средних широтах и последующую миграцию к полюсу, то есть в целом подтверждают бореотропическую гипотезу. Раннепалеогеновые флоры востока Азии демонстрируют незначительные пространственные и временные вариации в таксономическом составе, и то что новые таксоны появлялись в ископаемой летописи в разное время и имели разную экологию.

Ключевые слова: таксономическое разнообразие, флористический состав, флористические провинции, ранний палеоген, восток Азии

In the process of studying any natural phenomena, for their correct description, understanding and identification of patterns, one way or another there is a need to systematize data on their diversity, that is, to classify the objects under study. Vegetation is a difficult object to classify, since its formation is influenced by many factors. At the same time, vegetation is the most important component and an integral part of the structural and functional organization of any ecosystem, and it is its changes that reflect the ecological situation of the region. At present, the vegetation cover of Asia is one of the most interesting world phenomena, both from the point of view of biological diversity and from the point of view of the organization of ecosystems. In this very contrasting territory in terms of relief, climate and soils, the vegetation is also very heterogeneous – from tundra to humid tropical and seasonal forests.

Today, two large floristic regions are distinguished for East Asia (cf. Takhtajan 1986, Krestov 2006, Kamelin 2017, 2022). According to Takhtajan (1986), the vast Circumboreal Region is divided into 15 more or less clearly defined provinces. The East Asian Region is divided into 12 provinces. Krestov (2006) distinguishes the Circumboreal Region with two subregions for the North Pacific: North Boreal (includes four provinces) and South Boreal Asian (one province), as well as the East Asian Region (includes one province). Kamelin (2017, 2022) distinguishes the Boreal and East Asian subkingdoms as two large floristic regions. The Boreal subkingdom includes the Arctoboreal Region with three subregions. The East Asian subkingdom includes two regions: Sino-Japanese and Sino-Himalayan.

Tolmachev (1986) notes that, in the practice of floristic research, the most common approach is to formulate the problem of identifying spatial distribution the patterns of floristic complexes of different appearance, different systematic composition and genesis. This approach is implemented in the form of a hierarchical division of the Earth's surface into spatial units with varying degrees of similarity of the floras located on their territory. Thus, when classifying floras, floristic zoning occurs. Of extreme importance is the position emphasized by Tolmachev (1986) on the need to take into account the genesis of floras, and florogenetic features should be taken into account to no lesser extent than similarities and differences in the systematic composition of floras. Unfortunately, only a part of the plants is preserved in fossil floras. In addition, floras reflecting the vegetation of the past are confined to deposits that are locally represented and do not always contain plant remains. Therefore, it is impossible to fully apply the approaches used in floristic zoning to fossil floras. However, studying their interaction in time and space allows us to understand the general patterns of florogenesis.

In palaeobotany, a clear idea of the heterogeneity of the Mesozoic floras of Eurasia was first presented by Krystofovich (1939). The systematic composition of angiosperms, which were intensively introduced into plant communities throughout the Northern Hemisphere during the first half of the Upper Cretaceous was quite uniform (Krystofovich 1955, Vakhrameev 1957a,b) and, in general, characterized the predominantly evergreen flora in Western Europe and the Platanaceae–Trochodendraceae broadleaved forest flora within the northern part of Eurasia. Vakhrameev (1957a,b) identified two floristic regions for the beginning of the Upper Cretaceous, the boundary between which ran mainly in the latitudinal direction. Krystofovich (1955, 1957), systematizing palaeobotanical data for the entire Upper Cretaceous, noted the relative monotony of the flora, represented by coniferous-broadleaved and broadleaved forests, distributed throughout the Northern Hemisphere. Characterizing the Late Cretaceous flora, Krystofovich (1957) noted that the same relatively uniform vegetation continued to develop, in which representatives of angiosperms quickly spread throughout the globe. Vakhrameev (1957a,b, 1958, 1964b) showed that the floras of Western Europe, the southern regions of the USSR, India and South China belong to a single palaeofloristic region. The main features of the region are the abundance of cycads and bennettites, the widespread distribution of ferns from the families Marattiaceae, Matoniaceae and Dipteridaceae and conifers with scaly or awl-shaped needles (*Araucarites*, *Brachyphyllum*, *Elatocladus*, *Pagiophyllum*). Within this region, he identified four provinces. Baikovskaya (1956) combined all the available palaeobotanical data on the Late Cretaceous floras on extratropical Asia and outlined a belt of coniferous-deciduous forests that covered Siberia, the Urals and most of Kazakhstan, which were replaced to the south by a belt of subtropical vegetation with evergreen broadleaved species. The boundary between the belts passed approximately at the same latitudes as the boundary between the Gelinden and Greenland botanical-geographical provinces established by Krystofovich (1955) for the early Paleogene. Takhtajan (1966) proposed a zoning of the Late Cretaceous flora of the entire Holarctic, distinguishing boreal and ancient Mediterranean phytochores for this time. The boundary between them also emphasizing the inheritance of the boundaries of the early Paleogene botanical-geographical provinces from the Late Cretaceous.

A new direction in the analysis of the geography of Late Cretaceous floras appeared in connection with the development of palynological studies. The relatively poor list of known species of Late Cretaceous floras of Eurasia was significantly expanded and taken out of the framework of the natural system into the group of taxa of the artificial system. This mainly concerned angiosperms, the complex of which had previously seemed to be quite uniform. The first attempt to identify floristic differentiation in the territory of the USSR based on palynological data was undertaken by Boitsova et al. (1960). For the Early Cretaceous, the authors proposed to distinguish two floristic regions. For the Late Cretaceous, Boitsova et al. (1960) identified two floristic regions in the Asian part of the USSR. Zaklinskaya (1962) used palynological data for Eurasia to establish the stages and phases of angiosperm development from the Albian to the early Paleogene inclusive, noted their significant floristic differences in the European and Asian parts of the continent, and identified two palaeofloristic provinces. The flora of the European province from the polar latitudes to the Mediterranean is characterized by the participation of plants producing pollen belonging to the morphogenetic stem Normapolles. The flora of the Eastern Siberian province is distinguished by the abundance of species of Proteaceae, Lorantaceae, and other angiosperms, the pollen of which is grouped into the formal genus *Aquilapollenites* and others united into the morphological subgroup *Triprojectacites*. The boundary between the outlined palaeofloristic provinces passed in the meridional direction approximately between 70 and 80°E. At the same time, the closest connection of the *Normapolles* flora with the Late Cretaceous floras of the Atlantic, and the *Aquilapollenites*–Proteaceae flora with the flora of the Pacific coast of North America, as well as the florogenetic connections of the identified provinces with the continents of Africa, South America, Australia and New Zealand were noted. For Eurasia, differentiation of the Turkmen–Kazakhstan xerophytic province was also outlined, the flora of which was a mixture of "European" and "Asian" species and other taxa, and on the Pacific coast – some isolation of the flora based on the early appearance of representatives of the catkin-like plants. Later, this circumstance allowed Zaklinskaya (1967) to identify an independent Primorsko–Sakhalinskaya province. Later, the ideas about the floristic zoning of the USSR territory in the Cretaceous period based on palynological data were refined and significantly modified. Zaklinskaya (1963, 1966, 1970, 1977), Samoylovich (1966, 1977) and Pokrovskaya (1967) proposed several variants of palaeofloristic zonation based on palynological data. Chlonova (1971a, 1974) interprets palaeofloristic differentiation in Northern Asia from the point of view of the possible position of the degree grid in the Late Cretaceous. Vakhrameev (1970) proposed schemes of palaeofloristic zonation of Eurasia in the Early and Middle Cretaceous based on the study of large-sized plant remains. The composition of palynofloras and their changes during the Cretaceous were traced in Siberia and the Far East of Russia (Chlonova 1971b, 1974). Floristic provinces of the Cretaceous of the USSR and adjacent regions of East Asia were identified by Chlonova (1980) based on palynological data. The meridional orientation of the geographical regions of the Late Cretaceous was substantiated later (Zaklinskaya 1963, 1967, Pokrovskaya 1965, Samoylovich 1966, Goczan et al. 1967).

A number of works by Vakhrameev (1957a, 1966) are devoted to clarifying the connections between the history of climate development, the evolution of terrestrial floras, and changes in botanical and geographical zonality. Vakhrameev (1966), analyzing the Late Cretaceous vegetation of the Pacific coast, noted that in this territory, due to a more humid climate, mesophytic relics (some ferns, Czekanowskiaceae, *Nilssonia*) were preserved for a very long time, which gave him grounds to distinguish two provinces in the east of the USSR.

For the Paleocene, Krystofovich (1955) identified two botanical-geographical provinces of the Northern Hemisphere: Greenland and Gelinden, essentially corresponding to the temperate zone of the northern hemisphere and the tropical zone. The boundary between them essentially divided the temperate (without palms) flora of the Holarctic from the flora of the subtropics (with palms). The vastness of the identified provinces emphasized the limitations of the available data and the caution of the author, who did not consider it possible to make a more detailed zonation.

According to the concept of the Arcto-Tertiary geoflora (e.g. Chaney 1940, 1944, 1947, 1948, 1959, Axelrod 1966, 1983), the forests of eastern North America, eastern Asia, and western and central Europe represent relics of a temperate broadleaf deciduous forest of a particular floristic composition that developed at high northern latitudes in the Late Cretaceous and early Tertiary and, as the climate cooled, moved south across North America, Europe, and Asia, and by the Miocene had spread across the Northern Hemisphere. In response to climate cooling, this climax forest community migrated more or less intact to the middle latitudes in the Oligocene.

Some of the predictions of the Chaney hypothesis are as follows. Temperate climates prevailed in northern latitudes, and thus vicarious patterns should be found only in temperate taxa, such as the disjuncts between eastern Asia and eastern North America. Thus, cool temperate climates prevented the migration of tropical taxa between the Old and New Worlds. Neotropical Tertiary floras occurred south of the Arcto-Tertiary floras, and the main source of these tropical floras was South America. Land bridges (Beringia) between Eurasia and North America facilitated the exchange (or interchange) of predominantly temperate plants between these continents. The climatic tolerances of fossil floras were the same as those of modern analogues, i.e., the tolerances have not changed over geological time. This temperate broadleaved deciduous forest (i.e., fossil assemblage) closely resembled the North American eastern deciduous forest (many genera are the same) and was stable over a wide range of time and space (tens of millions of years and thousands of kilometers). A detailed description of the history and philosophy of the arctic-tertiary geoflora concept is given by Wolfe (1977).

Later, Wolfe (1994) and others showed the concept of Arcto-Tertiary geoflora to be invalid. To explain the floristic similarities between eastern North America, Europe, East Asia, and western North America, Wolfe (1975, 1977) and Tiffney (1985a, b) proposed a boreotropical hypothesis, given the boreal geography, near-tropical climate, and thermophilic affinities of many of the taxa comprising the flora. They based this hypothesis on the tropical taxa common to the Eocene floras of Europe and North America and the close taxonomic relationships of these floras to those extant in tropical southeast Asia and, to some extent, Central America and the Greater Antilles (Lavin & Luckow 1993). Thus, in contrast to the concept of the Arcto-Tertiary geoflora, the vegetation of the tropical climate in the Eocene extended to northern latitudes (Wolfe 1985), which allowed the exchange of tropical taxa through land bridges with the tropical flora of the Old World. According to this concept, a large number of modern taxa first appeared in the middle latitudes of the Northern Hemisphere in the early Tertiary (late Paleocene–Eocene) and spread via the Bering and North Atlantic land bridges and the shores of the Tethys Seaway. The Tethys Passage was important for the dispersal of plants across Eurasia (Wolfe & Leopold 1967, Tiffney 1985a, b) and for the dispersal of tropical, subtropical, and warm temperate plants between Southeast Asia and the southeastern United States (Dilcher 2000). Accordingly, the assertion of the Arcto-Tertiary geoflora concept that many lineages of this flora arose in the Arctic in the Late Cretaceous is invalid. Thus, according to Spicer et al. (1987), the first appearance of the clade (woody angiosperms) present in the Late Cretaceous–early Tertiary floras is consistently later in Alaska than in mid-latitudes. That is, the lineages first appeared in the low and mid-latitudes and then in the

Arctic (Spicer et al. 1987). Angiosperm migration was poleward (Axelrod 1959, Hickey & Doyle 1977). Wolfe (1994) stated that some Arcto-Tertiary lineages (e.g., *Ginkgo* and *Metasequoia* lineages) may even have a history, as suggested by Chaney (1938) the taxa appeared in high northern latitudes in the Late Cretaceous and early Cenozoic, and as the climate cooled, moved south through North America, Europe, and Asia, and during the Miocene had spread across the Northern Hemisphere.

In this paper, we aim to study the floristic background and taxonomical inventory of the early Paleogene palaeobotanical record of East Asia using quantitative techniques. The record comprises 110 micro- and macrofloras from the Eastern Siberia, Russian Far East (RFE), China, and Japan compiled from literature. The same floras were recently employed for detailed palaeoclimate and -vegetation reconstructions (Bondarenko & Utescher 2022, 2024a,b,c), thus providing a framework for the present floristic analysis. Our results shed light on the floristics in the eastern part of Eurasia and the dynamics and evolution succeeding the disruptions at the K/T boundary.

MATERIAL AND METHODS

Floral record

The palaeobotanical records on the Pacific side of Eurasia studied herein originate from 73 localities (Fig. 1, Supplementary electronic information 1 and 2). The early Paleogene deposits of China are widely distributed and generally represent terrestrial facies conditions. The early Paleogene deposits of the Eastern Siberia and RFE are also widely distributed, and are dominated by non-marine facies. For details on the Paleogene strata of the study area, the reader is referred to Bondarenko & Utescher (2022). We use regional stratigraphic schemes to allocate the palaeobotanical sites to a three time slices. The stratigraphic correlation chart is combined from Grinenko et al. (1997) for the continental part of the Eastern Siberia and north RFE, Kezina (2005), Pavlyutkin & Petrenko (2010) for the continental part of the south RFE, Gladenkov et al. (2005) for the Kamchatka Peninsula, Gladenkov et al. (2002) for Sakhalin Island, and Quan et al. (2012a) for China. 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 (Supplementary electronic information 1). The stratigraphic schemes of the Eastern Siberia and RFE have been tied to the International Stratigraphic Chart (Cohen et al. 2013, Gladenkov et al. 2002, 2005, Grinenko et al. 1997, Kezina 2005, Pavlyutkin & Petrenko 2010) and allow for dating the flora-bearing horizons at the stage level. For some of the floras, stratigraphic ages are constrained by radiometric dating (cf. Supplementary electronic information 2).

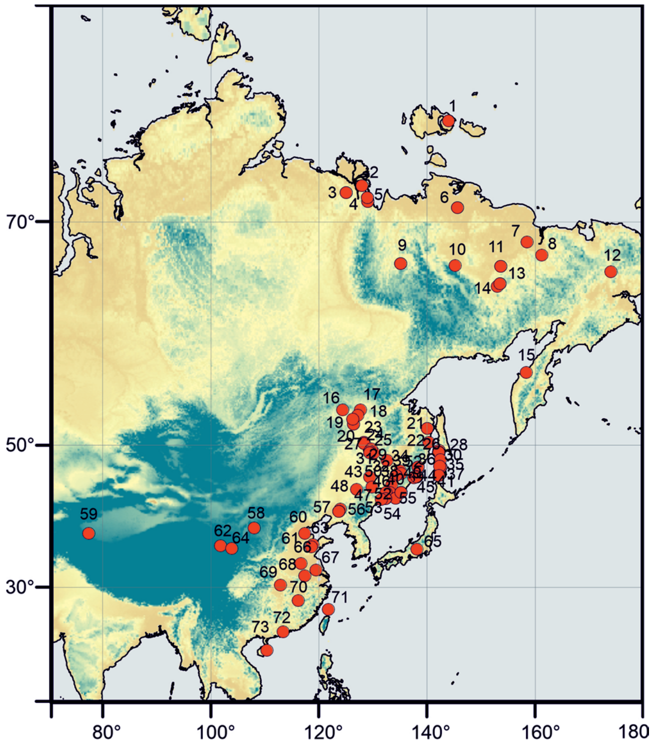

Figure 1 Map showing the location of the early Paleogene sites studied in East Asia

In this study, all palaeofloras considered were carefully re-evaluated regarding the validity of taxonomic identifications and Nearest Living Relatives (NLRs) of the fossil taxa. We analysed 110 floras including 79 palynofloras (PF), 30 leaf floras (LF) and one carpoflora (CF) with respect to the taxonomy of their palaeobotanical content considering three time slices, namely the early Paleocene, late Paleocene, and early Eocene. The floras cover a total time-span of ca. 17 myr, ranging from the Danian to Ypresian. The assignment of the palaeofloras to the three time slices considered here is based on stratigraphic information available in above cited literature and compiled in Supplementary electronic information 1. In many cases, flora-bearing horizons originate from longer successions that are tied to regional stratigraphy and partly cover the early Paleocene to early Eocene (e.g., Kolyma1, Slezovka15, Erkovtsy, etc.) thus facilitating a consistent sample selection. The single floras are listed in Supplementary electronic information 2 together with information on basin provenience, type of flora, stratigraphic age, method of dating, and references.

Taxonomic and floristic analyses

To apply taxonomic analysis, all known NLRs of the fossil taxa recorded were assigned to a family and, if possible, to a genus (Supplementary electronic information 2). Quantitative data are given in Table 1. Total diversity and classification of family members are given in Table 2. The total diversity and presence of families in different time slices and corresponding vegetation types of the early Paleogene of East Asia are listed in Table 3. Genus diversity of the early Paleogene floras of East Asia is shown in Table 4.

To interpret the taxonomic diversity of the fossil sites in terms of floristic analysis, multivariate classical clustering was performed (Fig. 2) using a data matrix with presence/absence of all families (PAST 4.03 program package; single linkage between groups; squared Euclidean distance measure). Characteristics of groups established for the early

Table 1. Number of fossil taxa.

Locality name	Microfloras				Macrofloras			
	Fossil taxa	Families	with NLRs, %	NLRs unknown, %	Fossil taxa	Families	with NLRs, %	NLRs unknown, %
Early Eocene								
1. Novosibirskie Islands	36	17	91.7	8.3	35	21	100	0
2. Bykovskaya Channel	63	38	95.2	4.8	19	11	100	0
3. Kengdei	61	31	96.7	3.3	20	16	95.0	5.0
4. Kunga	66	29	86.4	13.6	–	–	–	–
5. Kunga	68	31	88.2	11.8	22	14	100	0
6. Tastakh Lake	97	42	91.8	8.2	16	9	100	0
7. Diring-Yuryue15	52	23	94.2	5.8	–	–	–	–
8. Shamanikha	48	22	89.6	10.4	–	–	–	–
9. Medvezhye ozera	56	28	94.6	5.4	–	–	–	–
10. Snezhnegorskoe	43	21	97.7	2.3	–	–	–	–
11. Ushumunskii5	37	24	100	0	–	–	–	–
12. Bukhta Siziman	–	–	–	–	45	28	100	0
13. Erkovtsy	47	29	100	0	21	18	100	0
14. Raichikhinsk	74	41	95.9	4.1	69	49	100	0
15. Svobodnoe53	46	21	89.1	10.9	–	–	–	–
16. Snezhinka	18	10	94.4	5.6	34	22	97.1	2.9
17. Birofel'd	38	23	94.7	5.3	–	–	–	–
18. Krasnoyarka	15	11	93.3	6.7	39	18	92.3	7.7
19. Ozero Toni	32	15	100	0	44	18	100	0
20. Alchan	38	24	94.7	5.3	–	–	–	–
21. Bikin	58	32	96.6	3.4	–	–	–	–
22. Kril'on	33	20	93.9	6.1	–	–	–	–
23. Luchegorsk540/541	58	28	93.1	6.9	12	8	100	0
24. Yilan	53	32	88.7	11.3	–	–	–	–
25. Krylovskii524	59	31	96.6	3.4	–	–	–	–
26. Hualin	27	17	100	0	–	–	–	–
27. Shulan	36	24	94.4	5.6	–	–	–	–
28. Kluch Tuyanov	–	–	–	–	62	31	100	0
29. Arsen'evka	57	27	91.2	8.8	–	–	–	–
30. Rettikhovska	56	24	89.3	10.7	–	–	–	–
31. Kluch Ugolnyi	19	8	84.2	15.8	20	12	100	0
32. Smolyaninovo	56	25	92.9	7.1	42	22	100	0
33. Tavrichanka9142	58	27	91.4	8.6	–	–	–	–
34. Fushun	38	21	86.8	13.2	–	–	–	–
35. Fushun	21	13	100	0	–	–	–	–
36. Etuoke	18	10	83.3	16.7	–	–	–	–
37. Huanghua	51	30	88.2	11.8	–	–	–	–
38. Shache	11	9	81.8	18.2	–	–	–	–
39. Changle	32	21	96.9	3.1	–	–	–	–
40. Wutu	38	25	92.1	7.9	–	–	–	–
41. Xining	23	15	82.6	17.4	–	–	–	–
42. Lanzhou	26	20	88.5	11.5	–	–	–	–
43. AS_Japan	–	–	–	–	40	31	100	0
44. Luanchuan	34	21	85.3	14.7	–	–	–	–
45. Gaoyou	70	32	80.0	20.0	–	–	–	–
46. Hefei	38	26	97.4	2.6	–	–	–	–
47. Jianghan	65	36	84.6	15.4	–	–	–	–
48. Qingjiang	55	43	92.7	7.3	–	–	–	–
49. Donghai	36	21	88.9	11.1	–	–	–	–
50. Zhujiang	27	21	88.9	11.1	–	–	–	–
51. Changchang	42	29	83.3	16.7	–	–	–	–
mean	**44.4**	**24.3**	**91.7**	**8.3**	**33.8**	**20.4**	**99.0**	**1.0**
min	**11**	**8**	**80.0**	**0**	**12**	**8**	**92.3**	**0**
max	**97**	**43**	**100**	**20.0**	**69**	**49**	**100**	**7.7**
Late Paleocene								
52. Sogo	41	17	78.0	22.0	–	–	–	–
53. Sogo	42	20	95.2	4.8	–	–	–	–
54. Kolyma1	32	16	93.8	6.2	–	–	–	–
55. Yarovaya91	90	40	82.2	17.8	–	–	–	–
56. Diring-Yuryue15	26	14	88.5	11.5	–	–	–	–
57. Slezovka15	32	12	84.4	15.6	–	–	–	–
58. Shamanikha	53	25	88.7	11.3	–	–	–	–
59. Tigil'	72	32	86.1	13.9	–	–	–	–
60. Urkan	46	26	84.8	15.2	–	–	–	–
61. Ushumunskii5	41	21	90.2	9.8	–	–	–	–
62. Erkovtsy154	58	24	87.9	12.1	31	18	100	0
63. Raichikhinsk	47	27	89.4	10.6	–	–	–	–
64. Svobodnoe53	75	42	90.7	9.3	–	–	–	–
65. Snezhinka	–	–	–	–	21	14	95.2	4.8
66. Arkharo-Boguchan	–	–	–	–	19	11	89.5	10.5
67. Krasnoyarka	–	–	–	–	23	15	100	0
68. Kluch Kedrovyi	37	17	97.3	2.7	–	–	–	–
69. Kluch Stolbikova	–	–	–	–	14	8	100	0
70. Ustinovka	–	–	–	–	25	12	100	0
71. Fushun	38	19	92.1	7.9	–	–	–	–
mean	**48.7**	**23.5**	**88.6**	**11.4**	**22.2**	**12.8**	**97.5**	**2.5**
min	**26**	**12**	**78.0**	**2.7**	**14**	**8**	**89.5**	**0**
max	**90**	**42**	**97.3**	**22.0**	**31**	**18**	**100**	**10.5**

Paleogene floras of East Asia are given in Table 5. Considering "key" families, a 2-sided multivariate classical clustering was performed (Fig. 3) using a data matrix with diversity data of 55 families (PAST 4.03 program package; single linkage between groups; squared Euclidean distance measure). The characteristics of groups established for the early Paleogene floras of East Asia are given in Table 6.

To visualize the results, a series of palaeogeographic maps is provided and discussed below. The maps allow to trace the spatial distribution of floristic groups and single taxa throughout the early Paleogene (Figs. 3). For the technical preparation of the maps, ArcMAP 10.4 was used. We use rotated coordinates (using ODSN Plate Reconstruction Service for 55 Ma and hotspot reference frame I) for the palaeosites (Figs 3), because the palaeogeographic situation did not undergo any significant changes during the time-span regarded here.

RESULTS

Floristic content

To apply taxonomic and floristic analyses, 110 floras in total were analyzed (Supplementary electronic information 1 and 2). In the microfloras, the number of fossil taxa ranges from 11 to 97, the number of families – from 8 to 43, while in the macrofloras the number of fossil taxa varies from 12 to 69, the number of families – from 8 to 49 (Table 1). In general, the diversity of East Asian flora in the early Paleogene is represented by 578 genera (334 genera are formal or extinct) and 132 families (Table 2).

The NLRs of fossil taxa belong to 9 Divisions (Table 2). In total, Pterido-

Table 1. Continued.

Locality name	Microfloras: Fossil taxa	Microfloras: Families	Microfloras: with NLRs, %	Microfloras: NLRs unknown, %	Macrofloras: Fossil taxa	Macrofloras: Families	Macrofloras: with NLRs, %	Macrofloras: NLRs unknown, %
Early Paleocene								
72. Sakan'ya272-1	52	26	76.9	23.1	–	–	–	–
73. Slezovka15	41	22	82.9	17.1	–	–	–	–
74. Koluchinskaya guba	66	34	83.3	16.7	–	–	–	–
75. Pikanskii	42	22	73.8	26.2	–	–	–	–
76. Tygda245	37	16	86.5	13.5	–	–	–	–
77. Malomikhailovka	24	13	87.5	12.5	24	11	95.8	4.2
78. Erkovtsy154	47	27	87.2	12.8	15	9	100	0
79. Darmakan	–	–	–	–	47	31	97.9	2.1
80. Avgustovka	46	21	87.0	13.0	22	15	100	0
81. Svobodnoe53	48	23	87.5	12.5	–	–	–	–
82. Kama	–	–	–	–	29	14	93.1	6.9
83. Snezhinka	17	11	52.9	47.1	–	–	–	–
84. Snezhinka	19	8	73.7	26.3	19	10	94.7	5.3
85. Baishantou	82	36	78.0	22.0	34	19	82.4	17.6
86. Shakhtnyi	46	20	76.1	23.9	–	–	–	–
87. Naiba	46	20	76.1	23.9	–	–	–	–
88. Kril'on	37	22	89.2	10.8	–	–	–	–
89. Sobolevka	–	–	–	–	63	33	98.4	1.6
90. Ustinovka	–	–	–	–	31	16	96.8	3.2
91. Fushun	45	22	84.4	15.6	–	–	–	–
mean	**43.4**	**21.4**	**80.2**	**19.8**	**31.6**	**17.6**	**95.5**	**4.5**
min	**17**	**8**	**52.9**	**10.8**	**15**	**9**	**82.4**	**0**
max	**66**	**36**	**89.2**	**47.1**	**47**	**33**	**100**	**17.6**

Note: References and complete flora lists including Nearest Living Relatives are given in Supplementary electronic information 1 and 2.

phytes (including Bryophyta, Lycopodiophyta, Marchantiophyta and Polypodiophyta) are represented by 28 families, i.e. they account for 21.2 % of the total diversity. Gymnosperms (Cycadophyta, Ginkgophyta, Gnetophyta and Pinophyta) are represented by 10 families, i.e. they account only for 7.6 % of the total diversity. Angiosperms (Magnoliophyta), with two large classes – Eudicots and Monocots, are represented by 94 families, i.e. they account only for 71.2 % of the total diversity. Eudicots account for 82 families (62.1 %), while Monocots account for only 12 families (9.1 %).

Regarding the changes in the ratio of different groups, in the early Paleocene the mean value for Pteridophytes is 21.6 %, for Gymnosperms – 19.3 % and for Angiosperms – 59.2 %. In the late Paleocene the mean value for Pteridophytes is 19.4 %, for Gymnosperms – 19.9 % and for Angiosperms – 60.6 %. In the early Eocene the mean value for Pteridophytes is 14.6 %, for Gymnosperms – 15.2 % and for Angiosperms – 70.3 %.

Regarding the diversity of genera, the Cupressaceae and Malvaceae families are the richest, with 12 and 11 genera, respectively (Table 4). At the same time, 67 families are represented by only one genus, 31 taxa are assigned only at the high taxonomic rank of the family.

Spatio-temporal floristic patterns

For the early Paleocene, 25 floras were utilized, all originating from a relatively narrow latitudinal range from 41.50 to 67.06°N. In the 16 micro- and 9 macrofloras allocated to the early Paleocene members of 78 families are represented (Table 3). Members of the families Betulaceae, Cupressaceae, Myricaceae and Ulmaceae are found in 15 out of 16 microfloras. Slightly less frequently, in 14 out of 16 microfloras, members of the Juglandaceae and Pinaceae families are found. In 10 out of the 16 microfloras, members of the families Polypodiaceae, Osmundaceae, Podocarpaceae, Fagaceae, Ginkgoaceae and Lycopodiaceae are found. In all early Paleocene macrofloras, members of the families Cercidiphyllaceae and Cupressaceae are found. In 5 or more of the 9 macrofloras, members of the families Betulaceae, Equisetaceae, Ginkgoaceae, Malvaceae, Pinaceae, Platanaceae, Poaceae, Ulmaceae and Vitaceae are found.

For the late Paleocene, the compilation comprises 21 floras ranging from 41.50 to 71.50°N. In the 15 micro- and 6 macrofloras of the late Paleocene, members of 74 families are represented (Table 3). Members of the families Betulaceae, Cupressaceae and Pinaceae are found in 14 out of 15 microfloras. Slightly less frequently, in 13 out of 15 microfloras, members of the families Juglandaceae, Myricaceae, Podocarpaceae and Polypodiaceae are found. In 10 or more of the 15 microfloras, members of the families Osmundaceae, Ulmaceae and Fagaceae are found. In all late Paleocene macrofloras, members of the families Cercidiphyllaceae, Cupressaceae, Malvaceae, and Platanaceae are found. In 3 or more out of the 6 macrofloras, members of the families Betulaceae, Equisetaceae, Ginkgoaceae, Rhamnaceae, Ulmaceae and Vitaceae are found.

The early Eocene record includes 64 floras covering the widest latitudinal range, from 19.38 to 75.53°N. In 48 micro- and 16 macrofloras, members of 131 families are represented (Table 3). Members of the families Juglandaceae, Cupressaceae and Pinaceae are found in 40 or more out of the 48 microfloras. Slightly less frequently, in 35 or more out of the 48 microfloras, members of the families Altingiaceae, Betulaceae and Ulmaceae are found. In 30 or more out of the 48 microfloras, members of the families Polypodiaceae, Podocarpaceae, Anacardiaceae and Malvaceae are found. In 10 or more out of the 16 early Eocene macrofloras, members of the families Betulaceae, Cercidiphyllaceae, Cupressaceae, Equisetaceae, Ulmaceae and Vitaceae are present.

Based on cluster analysis performed on presence/absence data of all families in the single macro- and microfloras, four major groups are established (Fig. 2). The grouping reveals a clear separation of micro- and macrofloras. Details on the characteristics of the established groups regarding climatic envelope and reconstructed vegetation type are given in Table 5.

To study spatial floristic patterns and affinities of taxonomic units, a 2-sided cluster analysis is performed using

Table 2. Total diversity and classification of family members in the early Paleogene floras of East Asia (by alphabet).

Division
  Class
    Order
      Family

- **I Bryophyta**
  - Sphagnopsida
    - Sphagnales
      - 1 Sphagnaceae Dumort.
- **II Cycadophyta**
  - Cycadopsida
    - Cycadales
      - 2 Cycadaceae Pers.
- **III Ginkgophyta**
  - Ginkgopsida
    - Ginkgoales
      - 3 Ginkgoaceae Engl.
- **IV Gnetophyta**
  - Gnetopsida
    - Ephedrales
      - 4 Ephedraceae Dumort.
    - Gnetales
      - 5 Gnetaceae Blume
- **V Lycopodiophyta**
  - Lycopodiopsida
    - Lycopodiales
      - 6 Lycopodiaceae P.Breauv. ex Mirb.
    - Selaginellales
      - 7 Selaginellaceae Willk.
- **VI Magnoliophyta**
  - Eudicots
    - Apiales
      - 8 Apiaceae Lindl.
      - 9 Araliaceae Juss.
    - Aquifoliales
      - 10 Aquifoliaceae DC. ex A.Rich.
    - Asterales
      - 11 Asteraceae Bercht. et J.Presl
      - 12 Menyanthaceae Dumort.
    - Boraginales
      - 13 Boraginaceae Juss.
    - Brassicales
      - 14 Brassicaceae Burnett
    - Buxales
      - 15 Buxaceae Dumort.
    - Caryophyllales
      - 16 Amaranthaceae Juss.
      - 17 Droseraceae Salisb.
      - 18 Nyctaginaceae Juss.
      - 19 Polygonaceae Juss.
    - Celastrales
      - 20 Celastraceae R.Br.
    - Ceratophyllales
      - 21 Ceratophyllaceae Gray
    - Cornales
      - 22 Cornaceae Bercht. et J.Presl
    - Cucurbitales
      - 23 Cucurbitaceae Juss.
    - Dipsacales
      - 24 Caprifoliaceae Juss.
      - 25 Viburnaceae Raf.
    - Ericales
      - 26 Actinidiaceae Gilg et Werderm.
      - 27 Cyrillaceae Lindl.
      - 28 Ebenaceae Gürke
      - 29 Ericaceae Juss.
      - 30 Primulaceae Batsch et Borkh.
      - 31 Sapotaceae Juss.
      - 32 Styracaceae Dumort.
      - 33 Symplocaceae Jacq.
      - 34 Theaceae Mirb.
    - Fabales
      - 35 Fabaceae Lindl.
    - Fagales
      - 36 Betulaceae Gray
      - 37 Casuarinaceae R.Br.
      - 38 Fagaceae Dumort.
      - 39 Juglandaceae DC. ex Perleb
      - 40 Myricaceae A.Rich. ex Kunth
      - 41 Nothofagaceae Kuprian.
      - 42 Polygalaceae Hoffmanns. et Link
    - Garryales
      - 43 Eucommiaceae Engl.
    - Gentianales
      - 44 Apocynaceae Juss.
      - 45 Gentianaceae Juss.
      - 46 Rubiaceae Juss.
    - Icacinales
      - 47 Icacinaceae Miers
    - Lamiales
      - 48 Bignoniaceae Juss.
      - 49 Lamiaceae Martinov
      - 50 Oleaceae Hoffmanns. et Link
      - 51 Paulowniaceae Nakai
    - Laurales
      - 52 Lauraceae Juss.
    - Magnoliales
      - 53 Magnoliaceae Juss.
    - Malpighiales
      - 54 Euphorbiaceae Juss.
      - 55 Salicaceae Mirb.
    - Malvales
      - 56 Malvaceae Juss.
    - Myrtales
      - 57 Lythraceae J.St.-Hil.
      - 58 Myrtaceae Juss.
      - 59 Onagraceae Juss.
    - Nymphaeales
      - 60 Nymphaeaceae Salisb.
    - Pandanales
      - 61 Pandanaceae R.Br.
    - Piperales
      - 62 Saururaceae Martynov
    - Proteales
      - 63 Nelumbonaceae A.Rich.
      - 64 Platanaceae T.Lestib.
      - 65 Proteaceae Juss.
      - 66 Sabiaceae Blume
    - Ranunculales
      - 67 Menispermaceae Juss.
      - 68 Ranunculaceae Juss.
    - Rosales
      - 69 Cannabaceae Martinov
      - 70 Elaeagnaceae Juss.
      - 71 Moraceae Gaudich.
      - 72 Rhamnaceae Juss.
      - 73 Rosaceae Juss.
      - 74 Ulmaceae Mirb.
      - 75 Urticaceae Juss.
    - Santalales
      - 76 Loranthaceae Juss.
      - 77 Olacaceae R.Br.
      - 78 Santalaceae R.Br.
    - Sapindales
      - 79 Anacardiaceae (R.Br.) Lindl.
      - 80 Meliaceae Juss.
      - 81 Rutaceae Juss.
      - 82 Sapindaceae Juss.
      - 83 Simaroubaceae DC.
    - Saxifragales
      - 84 Altingiaceae Lindl.
      - 85 Cercidiphyllaceae Engl.
      - 86 Haloragaceae R.Br.
      - 87 Hamamelidaceae R.Br.
    - Trochodendrales
      - 88 Trochodendraceae Takhtajan ex Cronquist
      - Vitales
      - 89 Vitaceae Juss.
  - Monocots
    - Alismatales
      - 90 Alismataceae Vent.
      - 91 Araceae Juss.
      - 92 Hydrocharitaceae Juss.
      - 93 Potamogetonaceae Rchb.
    - Arecales
      - 94 Arecaceae Bercht. et J.Presl
    - Liliales
      - 95 Liliaceae Juss.
      - 96 Smilacaceae Vent.
    - Poales
      - 97 Cyperaceae Juss.
      - 98 Poaceae Barnhart
      - 99 Typhaceae Juss.
    - Zingiberales
      - 100 Strelitziaceae Hutch.
      - 101 Zingiberaceae Martinov
- **VII Marchantiophyta**
  - Marchantiopsida
    - Sphaerocarpales
      - 102 Riellaceae Engl.
- **VIII Pinophyta**
  - Pinopsida
    - Araucariales
      - 103 Araucariaceae Henkel et W.Hochstetter
      - 104 Podocarpaceae Endl.
    - Cupressales
      - 105 Cupressaceae Bartlett
      - 106 Taxaceae S.F.Gray
    - Pinales
      - 107 Pinaceae Lindl.
      - 108 Sciadopityaceae Luerss
- **IX Polypodiophyta**
  - Polypodiopsida
    - Cyatheales
      - 109 Cyatheaceae Kaulf.
      - 110 Dicksoniaceae Bower.
    - Equisetales
      - 111 Equisetaceae Michx. ex DC.
    - Gleicheniales
      - 112 Gleicheniaceae (R.Br.) C.Presl
      - 113 Matoniaceae C.Presl
    - Hymenophyllales
      - 114 Hymenophyllaceae Link
    - Marattiales
      - 115 Marattiaceae Kaulf.
    - Ophioglossales
      - 116 Ophioglossaceae Martinov
    - Osmundales
      - 117 Osmundaceae Martinov
    - Polypodiales
      - 118 Aspleniaceae Newm.
      - 119 Athyriaceae Alston
      - 120 Blechnaceae Newman
      - 121 Dennstaedtiaceae Lotsy
      - 122 Dryopteridaceae Herter
      - 123 Onocleaceae Pic.Serm.
      - 124 Polypodiaceae J.Presl et C.Presl
      - 125 Pteridaceae E.D.M.Kirchn.
      - 126 Thelypteridaceae Ching ex Pic. Serm.
      - 127 Woodsiaceae Herter
    - Salviniales
      - 128 Marsileaceae Mirb.
      - 129 Salviniaceae Martinov
    - Schizaeales
      - 130 Anemiaceae Link
      - 131 Lygodiaceae C.Presl
      - 132 Schizaeaceae Kaulf.

Table 3. Presence/absence of family members in different age and types of the early Paleogene floras of East Asia.

No	Family	early Paleocene		late Paleocene		early Eocene	
		PF	**LF**	**PF**	**LF**	**PF**	**LF**
1	Actinidiaceae Gilg et Werderm.	–	–	–	1	–	2
2	Alismataceae Vent.	–	–	–	–	1	–
3	Altingiaceae Lindl.	2	1	9	–	37	5
4	Amaranthaceae Juss.	–	–	–	–	5	–
5	Anacardiaceae Lindl.	3	3	3	1	30	4
6	Anemiaceae Link	–	–	–	–	–	2
7	Apiaceae Lindl.	–	–	–	–	8	1
8	Apocynaceae Juss.	–	–	–	–	1	–
9	Aquifoliaceae DC ex. A.Rich.	–	–	4	–	23	–
10	Araceae Juss.	–	1	–	–	3	2
11	Araliaceae Juss.	–	2	2	1	13	3
12	Araucariaceae Henkel et W. Hochst.	4	2	5	–	11	–
13	Arecaceae Bercht. et J.Presl	2	–	5	–	13	1
14	Aspleniaceae A.B. Frank	–	1	–	–	2	2
15	Asteraceae Juss.	–	–	–	–	1	–
16	Athyriaceae Alston	–	–	–	–	1	2
17	Betulaceae Gray	15	7	15	4	35	13
18	Bignoniaceae Juss.	–	–	–	–	2	–
19	Blechnaceae Newman	–	2	–	1	–	3
20	Boraginaceae Juss.	–	–	–	–	–	1
21	Brassicaceae Burnett	–	–	–	–	1	–
22	Buxaceae Dumort.	3	–	–	–	2	–
23	Cannabaceae Martinov	2	–	–	–	3	2
24	Caprifoliaceae Juss.	–	–	–	–	16	1
25	Casuarinaceae R.Br.	5	–	4	–	2	–
26	Celastraceae R.Br.	–	–	–	–	–	1
27	Ceratophyllaceae Gray	–	–	–	–	–	3
28	Cercidiphyllaceae Endl.	1	9	2	5	–	13
29	Cornaceae Bercht. et J.Presl	6	5	6	1	22	6
30	Cucurbitaceae Juss.	–	–	–	–	1	–
31	Cupressaceae Gray	15	9	15	5	43	15
32	Cyatheaceae Holub	5	–	6	–	12	–
33	Cycadaceae Pers.	4	–	3	–	5	–
34	Cyperaceae Juss.	–	3	–	–	1	3
35	Cyrillaceae Endl.	–	–	–	–	2	–
36	Dennstaedtiaceae Lotsy	–	2	–	–	1	3
37	Dicksoniaceae Bower	1	–	2	–	5	–
38	Droseraceae Salisb.	–	–	–	–	–	1
39	Dryopteridaceae Herter	–	2	–	–	–	4
40	Ebenaceae Gurke	–	–	–	–	–	2
41	Elaeagnaceae Adans.	–	–	–	–	4	–
42	Ephedraceae Dumort.	4	–	4	–	20	–
43	Equisetaceae Mchx. ex DC	–	6	–	3	–	10
44	Ericaceae Juss.	4	–	6	–	10	2
45	Eucommiaceae Endl.	–	–	2	–	10	1
46	Euphorbiaceae Juss.	–	–	–	–	10	4
47	Fabaceae Lindl.	2	2	2	1	10	6
48	Fagaceae Dumort.	10	3	10	–	47	9
49	Gentianaceae Juss.	–	–	–	–	8	–
50	Ginkgoaceae Endl.	10	6	9	2	16	7
51	Gleicheniaceae C. Presl	7	1	8	–	13	–
52	Gnetaceae Lindl.	1	–	–	–	–	–
53	Haloragaceae R.Br.	–	–	1	–	–	–
54	Hamamelidaceae R. Brown	6	2	8	1	26	4
55	Hydrocharitaceae Juss.	–	–	–	–	2	–
56	Hymenophyllaceae A.B. Frank	–	–	–	–	4	2
57	Icacinaceae Miers	–	–	–	1	–	–
58	Juglandaceae A. Richard ex Kunth	14	4	14	2	47	8
59	Lamiaceae Lindl.	–	–	–	–	2	1
60	Lauraceae Juss.	–	2	2	1	3	6
61	Liliaceae Juss.	1	–	2	–	4	–
62	Loranthaceae Juss.	8	–	4	–	24	–
63	Lycopodiaceae P.Beauv. ex Mirb.	10	–	7	–	18	–
64	Lygodiaceae C.Presl	9	–	7	1	21	3
65	Lythraceae J.St.-Hil.	–	1	1	–	1	2
66	Magnoliaceae Juss.	7	2	8	1	26	6
67	Malvaceae Juss.	3	5	7	5	34	10
68	Marattiaceae Kaulf.	–	–	–	–	1	–
69	Marsileaceae Mirb.	–	–	–	–	–	2
70	Matoniaceae C.Presl	4	–	–	–	1	–
71	Meliaceae Juss.	–	–	–	–	7	–
72	Menispermaceae Juss.	6	4	7	–	7	8
73	Menyanthaceae Dumort.	–	–	–	–	–	1
74	Moraceae Link	7	1	5	–	15	2
75	Myricaceae Blume	15	2	14	1	27	4
76	Myrtaceae Juss.	–	–	2	–	16	–
77	Nelumbonaceae A.Rich.	–	–	–	–	1	4
78	Nothofagaceae Kuprian	3	–	2	–	2	–
79	Nyctaginaceae Juss.	–	–	–	–	–	1
80	Nymphaeaceae Salisb.	–	3	–	2	3	1
81	Olacaceae Mirbel ex Candolle	6	–	6	–	6	–
82	Oleaceae Hoffmanns. et Link	3	1	2	–	12	2
83	Onagraceae Juss.	–	–	–	–	6	–
84	Onocleaceae Pic.Serm.	–	3	1	–	2	2
85	Ophioglossaceae Agardh	3	–	2	–	5	–
86	Osmundaceae Berch.	11	2	13	2	27	5
87	Pandanaceae R.Br.	–	–	1	–	–	–
88	Paulowniaceae Nakai	–	–	–	–	–	1
89	Pinaceae Lindl.	14	6	15	2	43	8
90	Platanaceae T. Lest. ex Dumort.	4	7	5	5	8	13
91	Poaceae Barnh.	–	5	1	2	5	4
92	Podocarpaceae Endl.	11	2	14	–	32	1
93	Polygalaceae Hoffmanns. et Link	–	–	–	–	1	–
94	Polygonaceae Juss.	–	–	–	–	3	–
95	Polypodiaceae Bercht. et J. Presl	12	–	14	–	34	–
96	Potamogetonaceae Rchb.	–	–	–	–	4	1
97	Primulaceae Batsch ex Borkh.	–	–	–	1	–	1
98	Proteaceae Juss.	6	–	1	–	11	–
99	Pteridaceae E.D.M.Kirchn.	5	–	4	1	13	3
100	Ranunculaceae Juss.	–	–	–	–	2	–
101	Rhamnaceae Juss.	1	2	1	2	6	5
102	Riellaceae Endl.	–	–	–	–	1	–
103	Rosaceae Juss.	3	3	5	1	5	5
104	Rubiaceae Juss.	–	–	–	–	1	–
105	Rutaceae Juss.	–	1	2	–	15	1
106	Sabiaceae Blume	–	–	–	–	–	2
107	Salicaceae Mirb.	3	4	5	2	20	7
108	Salviniaceae Martinov	1	–	2	–	2	3
109	Santalaceae R. Brown	1	–	–	–	3	–
110	Sapindaceae Juss.	7	3	7	2	15	8
111	Sapotaceae Juss.	–	–	–	–	6	–
112	Saururaceae Martynov	–	–	–	–	–	1
113	Schizaeaceae Kaulf.	8	2	3	–	7	–
114	Sciadopityaceae Luerss.	5	–	5	–	11	1
115	Selaginellaceae Willk.	3	–	4	–	6	1
116	Simaroubaceae DC	–	–	–	–	2	1
117	Smilacaceae Vent.	–	–	–	–	1	1
118	Sphagnaceae Dumort.	7	–	7	–	13	–
119	Strelitziaceae Hutch	–	–	–	–	–	1
120	Styracaceae Dumort.	–	–	–	–	1	1
121	Symplocaceae Desf.	3	–	–	–	4	–
122	Taxaceae Gray	1	2	1	–	1	2
123	Theaceae Mirb.	–	–	–	–	1	1
124	Thelypteridaceae Pic. Serm.	–	–	–	–	–	3
125	Trochodendraceae Eichler	6	2	5	–	13	1
126	Typhaceae Juss.	2	–	5	–	7	3
127	Ulmaceae Mirb.	15	7	11	4	45	12
128	Urticaceae Juss.	–	–	–	–	–	1
129	Viburnaceae Raf.	–	5	2	–	1	8
130	Vitaceae Juss.	–	5	–	4	1	13
131	Woodsiaceae Herter	1	–	–	–	2	–
132	Zingiberaceae Lindl.	–	1	–	1	–	1
	Total diversity	**77**		**73**		**128**	

family diversity (number of genera) data and focusing on 55 frequently occurring families. As a result, six major groups are established and interpreted in terms of palaeofloristic zonation (Fig. 3). The characteristics of established groups of floras and their spatio-temporal distribution are given in Table 6. There is a clear division of micro- and macrofloras into separate groups (Fig. 3G). Microfloras are combined into four groups – 1, 3, 5 and 6 (Table 6). In the early Paleocene (Fig. 3C,F), group 6 was widespread. Occasionally, in the mid-latitudes (~50–60° palaeolatitude), groups 1, 3 and 5 are found. In the late Paleocene (Fig. 3B,E), group 6 was also widespread. However, group 3 was more widespread towards higher latitudes compared to the early Paleocene (~50–70° palaeolatitude). Group 5 slightly expanded its distribution area in the mid-latitudes. In the early Eocene (Fig. 3A,D), the floristic pattern changed distinctly. Group 6 significantly reduced its distribution area to a few floras in the middle and lower latitudes. At the same time, groups 1, 3 and 5 became widespread. Group 3 was widespread in high and middle latitudes, group 5 – in middle and lower

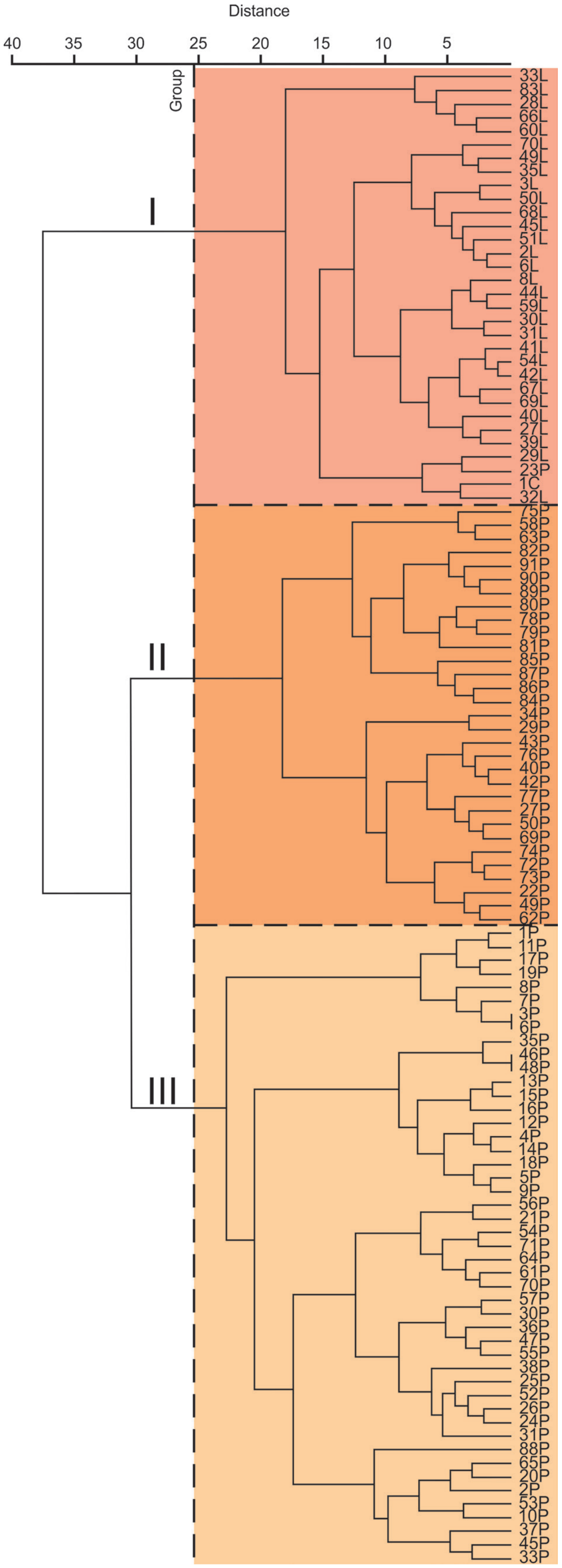

Figure 2 Clustering based on presence/absence of all families

latitudes and mainly in the eastern part (i.e. on the western coast of the Pacific Ocean). Group 1 was less common and was distributed at lower latitudes, but in the western part (i.e. on the coast of the Paratethys). Most of the macrofloras (Fig. 3D–F) are combined into one cluster (group 2), with the exception of 6 floras (group 4).

DISCUSSION

Taxonomic diversity

The taxonomic diversity in the study area demonstrates significant changes throughout the early Paleogene. In the early Paleocene, the floras comprise members of 77 families, in the late Paleocene – 73 families, while in the early Eocene – 128 families are recorded. In general, the diversity of East Asian flora in the early Paleogene is represented by 132 families (Tables 2 and 3). The plot of the number of fossil taxa vs. number of families (Fig. 4) implies that the actual number of families was distinctly larger compared to what was detected because the correlation does not show any asymptotic behavior. The total diversity of genera is 578, however only 244 genera are represented by modern ones (e.g. *Abies*, *Betula*, *Ulmus*, etc.), other 334 genera are formal or extinct. These formal taxa, in additional to genus like *Alnus*, also include genera like *Alnipollenites*, *Alnites* and *Alnuspollenites*, therefore, the total number of genera maybe overestimated. In our records 1119 species are accounted for East Asia in the early Paleogene, but the total diversity of fossil species may also be slightly overestimated.

Considering modern vegetation, we would have expected an increasing trend of taxonomic diversity towards lower latitudes. However, based on the actual palaeofloras in the record, there are no distinct latitudinal or longitudinal gradients of the diversity and number of families observed (Fig. 5). Maybe, the minor temporal diversity increase along the early Paleogene, was possibly related to rising temperatures. According to Stebbins (1947), the predominance of subtropical forest vegetation and the development of Hymenoptera determined the nature of the first, Mesozoic stage of angiosperm evolution, when, with relative uniformity of growth forms, there was an increased diversification of reproductive structures and the main families quickly formed.

The statistics (Fig. 6, Table 3) show a fairly high percentage of common early Paleogene taxa, but at the same time there is a noticeable jump in diversification in the early Eocene leading to almost doubling of the number of families. In addition, a gradual decrease of formal taxa and/or taxa with unknown nearest living relatives is observed (Table 1), both in micro- and macrofloras. According to Krystofovich (1933), who summarized all materials on the stratigraphy and floras of the continental deposits of the Jurassic and Cretaceous of the Asian part of the USSR, the list of all Mesozoic plants contained about 190 species known at that time from the Upper Triassic, Jurassic and Lower Cretaceous deposits of Central Asia and Siberia. This is five times less than the number of fossil species in the early Paleogene of East Asia. The mass extinction event started at the end of the Cretaceous (66.02 Ma), known as the Cretaceous – Paleogene boundary (KPB). By Vakhromeev et al. (1970), the reorganization of the entire previously developing complex of plant communities that had taken root on Eurasia was expressed primarily in the extinction of a large group of plants that produced pollen

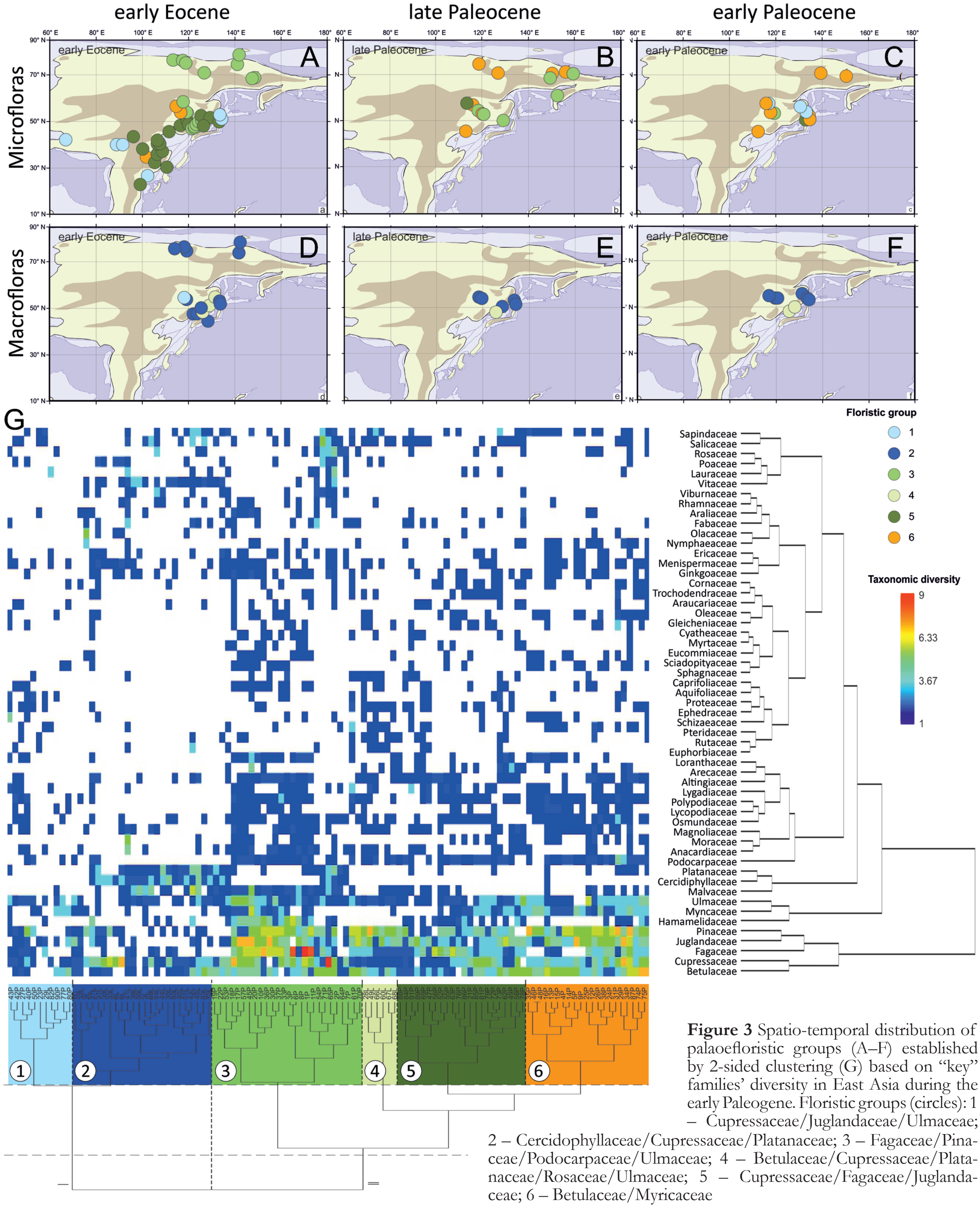

Figure 3 Spatio-temporal distribution of palaeofloristic groups (A–F) established by 2-sided clustering (G) based on "key" families' diversity in East Asia during the early Paleogene. Floristic groups (circles): 1 – Cupressaceae/Juglandaceae/Ulmaceae; 2 – Cercidophyllaceae/Cupressaceae/Platanaceae; 3 – Fagaceae/Pinaceae/Podocarpaceae/Ulmaceae; 4 – Betulaceae/Cupressaceae/Platanaceae/Rosaceae/Ulmaceae; 5 – Cupressaceae/Fagaceae/Juglandaceae; 6 – Betulaceae/Myricaceae

of the *Aquilapollenites* morphological type. The *Normapolles* clan, which represented a stable phylogenetic branch of true angiosperms, the descendants of which extended into the Paleogene and Neogene, disappeared from the Paleogene floras in stages and gradually. By Krassilov (1970), the Cretaceous extinction affected primarily the bennettites, the most xerophilic and photophilic plants of the Mesozoic. The Caytoniaceae and Czekanowskiaceae, whose ovules were located inside capsules similar to ovaries, also became extinct.

According to Vakhrameev et al. (1970), in areas with a stable humid climate, located both within the tropical and moderately warm zones, the evolution of floras occurred gradually. In the Paleogene and Neogene, Southeast Asia was such a region: here the relict forms were preserved the

Table 4. Genus diversity of the early Paleogene floras of East Asia.

Family	Number of genera	Genus diversity
Cupressaceae Gray	12	*Chamaecyparis* Spach., *Cryptomeria* D. Don, *Cunninghamia* R. Brown ex Rich. et A. Rich., *Cupressus* L., *Glyptostrobus* Endl., *Juniperus* L., *Libocedrus* Endl., *Metasequoia* Hu et W.C. Cheng, *Sequoia* Endl., *Taiwania* Hayata, *Taxodium* Rich., *Thuja* L.
Malvaceae Juss.	11	*Ayenia* L., *Craigia* Smith et Evans, *Diplodiscus* Turcz., *Dombleya* Cav., *Grewia* L., *Hibiscus* L., *Kleinhovia* L., *Pterospermum* Schreb., *Reevesia* Lindl., *Sterculia* L., *Tilia* L.
Juglandaceae DC. ex Perleb	9	*Alfaroa* Standl., *Carya* Nutt., *Cyclocarya* Iljinsk., *Engelhardia* Lesch. ex Blume, *Juglans* L., *Oreamunoa* Oerst., *Platycarya* Siebold et Zucc., *Pterocarya* Kunth, *Rhoiptelea* Link
Pinaceae Lindl.	8	*Abies* Mill., *Cedrus* Trew, *Keteleeria* Carr., *Larix* Mill., *Picea* A.Dietr., *Pinus* L., *Pseudolarix* Gord., *Tsuga* Carr.
Rosaceae Juss.	7	*Crataegus* L., *Physocarpus* (Camb.) Rafin., *Prunus* L., *Rubus* L., *Sorbaria* (Sering.) A. Brown, *Sorbus* L., *Spiraea* L.
Fagaceae Dumort.	6	*Castanea* Mill., *Castanopsis* (D. Don) Spach, *Cyclobalanopsis* Oerst., *Fagus* L., *Lithocarpus* Blume, *Quercus* L.
Hamamelidaceae R. Brown	6	*Chunia* H.T.Chang, *Corylopsis* Siebold et Zucc., *Fothergilla* Murr., *Hamamelis* L., *Parrotia* C.A. Mey., *Sycopsis* Oliv.
Lauraceae Juss.	6	*Cinnamomum* L., *Laurus* L., *Lindera* Thunb., *Neolitsea* (Benth. et Hook. f.) Merr., *Ocotea* Aubl., *Sassafras* J. Presl
Anacardiaceae Lindl.	5	*Cotinus* Mill., *Mangifera* L., *Pistacia* L., *Rhus* L., *Schinus* L.
Betulaceae Gray	5	*Alnus* Mill., *Betula* L., *Carpinus* L., *Corylus* L., *Ostrya* Scop.
Fabaceae Lindl.	5	*Caesalpinia* (Plum.) L., *Dalbergia* L., *Pueraria* Candl., *Robinia* L., *Wisteria* Nutt.
Araceae Juss.	4	*Epipremnum* Schott, *Lemna* L., *Peltandra* Rafin., *Spirodela* Schleid.
Cornaceae Bercht. et J.Presl	4	*Alangium* Lam., *Cornus* L., *Davidia* Baill., *Nyssa* L.
Ericaceae Juss.	4	*Andromeda* L., *Leucothoe* D. Don, *Rhododendron* L., *Vaccinium* L.
Rhamnaceae Juss.	4	*Gouania* Jacq., *Paliurus* Mill., *Rhamnus* L., *Ziziphus* Mill.
Vitaceae Juss.	4	*Ampelopsis* Michx., *Cissus* L., *Parthenocissus* Planch., *Vitis* L.
Arecaceae Bercht. et J.Presl	3	*Nypa* Steck, *Phoenix* L., *Sabal* Adans. ex Guer.
Cannabaceae Martinov	3	*Celtis* L., *Humulus* L., *Trema* Lour.
Caprifoliaceae Juss.	3	*Diervilla* (Tourn.) Mill., *Lonicera* L., *Weigela* Thunb.
Lythraceae J.St.-Hil.	3	*Decodon* J. F. Gmelin, *Sonneratia* L.f., *Trapa* L.
Magnoliaceae Juss.	3	*Delavaya* Franch., *Liriodendron* L., *Magnolia* L.
Moraceae Link	3	*Ficus* L., *Morus* L., *Maclura* Nutt.
Pteridaceae E.D.M.Kirchn.	3	*Acrostichum* L., *Adiantum* L., *Pteris* L.
Sapindaceae Juss.	3	*Acer* L., *Aesculus* L., *Koelreuteria* Laxm.
Taxaceae Gray	3	*Cephalotaxus* Siebold et Zucc. ex Endl., *Taxus* L., *Torreya* Arnott
Ulmaceae Mirb.	3	*Planera* Gmelin, *Ulmus* L., *Zelkova* Spach
Altingiaceae Lindl.	2	*Altingia* Noronha, *Liquidambar* L.
Araliaceae Juss.	2	*Aralia* L., *Fatsia* Decne et Planch.
Buxaceae Dumort.	2	*Pachysandra* Mich., *Sarcococca* Lindl.
Dennstaedtiaceae Lotsy	2	*Dennstaedtia* Bernh., *Leptolepia* Prantl
Menispermaceae Juss.	2	*Cocculus* Candolle, *Menispermum* L.
Myricaceae Blume	2	*Comptonia* L'Her. ex Aiton, *Myrica* L.
Oleaceae Hoffmanns. et Link	2	*Fraxinus* L., *Ligustrum* L.
Podocarpaceae Endl.	2	*Dacrydium* Sol. ex G. Forst., *Podocarpus* L'Her. ex Pers.
Salicaceae Mirb.	2	*Salix* L., *Populus* L.
Salviniaceae Martinov	2	*Azolla* Lam., *Salvini*a Seguier
Typhaceae Juss.	2	*Typha* L., *Sparganium* L.

longest. Particularly indicative in this regard are the regions of Asia adjacent to the Pacific Ocean, which were least subject to climatic drying (Scheinmann 1954) during the epochs of great aridization. Here it was *Cordaites* survived until the beginning of the Jurassic (Vietnam), *Nilssonia* – until the beginning of the Paleogene (Sakhalin, Primorye), and *Metasequoia* and *Ginkgo* – until the present.

The most complex stage in the history of the formation and development of the Earth's Cenozoic flora, according to Vakhrameev et al. (1970), characterized by the intensive introduction of angiosperms into all types of vegetation and then their complete dominance in the plant world, is associated with the late Cretaceous and early Paleogene (Paleocene – early Eocene). Based on molecular data, Ramrez-Barahona et al. (2020) showed that although angiosperms were phylogenetically diverse, geographically widespread, and involved in complex ecological interactions by the mid-Cretaceous, the diversification of families into the modern diversity was somehow delayed until the Paleocene. This occurred against a backdrop of profound changes in terrestrial ecosystems, including a well-documented trend of global warming during the Paleocene and Eocene.

According to Collinson & Hooker (2003), the Paleocene floras are characterized by deciduous angiosperms (especially plants with the *Trochodendroides* and *Corylites* leaf types) and taxodioid conifers. Associated with these floras is

Table 5. Characteristic of groups established for the early Paleogene floras of East Asia based on presence/absence of all families.

Group	Characteristic	Climate means (Bondarenko & Utescher 2022, 2024b)	Vegetation types (Bondarenko & Utescher 2024a)
I	**All macrofloras** (30LF, 1CF) and 1PF, 32 floras in total. **In 50 % floras and higher** present Betulaceae, Cercidiphyllaceae, Cupressaceae, Equisetaceae, Ginkgoaceae, Malvaceae, Pinaceae, Platanaceae, Ulmaceae, Vitaceae. **In 30 % and higher** present Cornaceae, Fagaceae, Juglandaceae, Lauraceae, Menispermaceae, Osmundaceae, Poaceae, Rhamnaceae, Salicaceae, Sapindaceae, Viburnaceae.	MAT 17.0/13.1–19.2°C CMMT 7.8/5.4–9.6°C WMMT 25.3/22.8–27.7°C MAP 1185/886–1422 mm	BLDF BLDF/MMF MMF Gl or St
II	**31 microfloras**. **In 50 % floras and higher** present Altingiaceae, Anacardiaceae, Betulaceae, Cupressaceae, Ephedraceae, Fagaceae, Juglandaceae, Pinaceae, Salicaceae, Ulmaceae. In 30 % floras and higher present Aquifoliaceae, Arecaceae, Caprifoliaceae, Cannabaceae, Euphorbiaceae, Magnoliaceae, Malvaceae, Myricaceae, Osmundaceae, Podocarpaceae, Polypodiaceae, Proteaceae, Pteridaceae, Rutaceae, Sapindaceae.	MAT 17.3/14.2–20.2°C CMMT 8.7/2.4–13.2°C WMMT 25.0/22.9–26.0°C MAP 1199/1004–1650 mm	BLDF BLDF/MMF MMF MMF/BLEF BLEF OWl Gl or ST
III	**47 microfloras.** In all floras present Pinaceae. In 50 % floras and higher present Altingiaceae, Betulaceae, Cornaceae, Cupressaceae, Fagaceae, Ginkgoaceae, Hamamelidaceae, Juglandaceae, Loranthaceae, Lycopodiaceae, Lygodiaceae, Magnoliaceae, Malvaceae, Myricaceae, Osmundaceae, Podocarpaceae, Polypodiaceae, Sphagnaceae, Ulmaceae. In 30% floras and higher present Anacardiaceae, Aquifoliaceae, Araucariaceae, Cyatheaceae, Ericaceae, Gleicheniaceae, Menispermaceae, Moraceae, Olacaceae, Sapindaceae, Schizaeaceae, Sciadopityaceae, Trochodendraceae.	MAT 16.6/15.1–19.0°C CMMT 9.0/6.8–10.4°C WMMT 24.9/22.2–26.1°C MAP 1215/1126–1407 mm	BLDF/MMF MMF MMF/BLEF OWl

Note: Established group are given in Figure 2.

a fern undergrowth which includes *Osmunda*, *Onoclea*, *Woodwardia* and the extinct *Coniopteris*. In the Greenland region (Greenland, Spitsbergen, Ellesmere Island, Scotland), far eastern and northern mainland Russia and Sakhalin the floras are characterized by the *Trochodendroides*/*Corylites*/*Metasequoia* association (Budantsev 1994, 1997, Herman 1993, Herman & Spicer 1996, Golovneva 1994, 2000). This contrasts with the *Taxodium*/*Trochodendroides* association in Kazakhstan, regions of Amur in Russia and Mongolia (Golovneva 1996). In the Eocene, the macrofloras are dominated by evergreen Fagaceae and Lauraceae (Collinson & Hooker 2003). Key members include species of Fagaceae, Altingiaceae, Myrtaceae and Lauraceae (Mai 1995, Wilde 1995, Walther 1994). Sterculiaceae, Icacinaceae, Sapotaceae, Menispermaceae, Vitaceae, Nyssaceae, Apocynaceae, Arecaceae and Symplocaceae are also recorded in the macrofloras (Mai 1995, Wilde 1989, 1995). Ferns such as *Lygodium* are common. Juglandaceae (especially *Platycarya* and *Engelhardia*) are also recorded in macrofloras (Manchester 1987, Mai 1995). Eocene macrofloras also contain a diverse and abundant collection of taxa whose nearest living relatives are found in paratropical forests (Collinson 1983, 2000, Collinson & Cleal 2001, Tiffney 1994, Mai 1970, 1989, 1995). These members include members of Arecaceae, Anacardiaceae, Anonnaceae, Burseraceae, Cornaceae, Dilleniaceae, Icacinaceae, Lauraceae, Menispermaceae, Sabiaceae, Sapindaceae and Vitaceae.

So, our data on the Early Paleogene of East Asia generally do not contradict or refute previous results, they complement and detail them. Some minor differences or disagreements are due to the fact that the above mentioned data are based only on macrofloras and the idea of taxa dominance is most likely based on the abundance of leaf impressions and is blurred by taphonomic factors. Our results are based on integrated data from both micro- and macrofloras and are not based on abundance data, but only on the presence or absence of taxa.

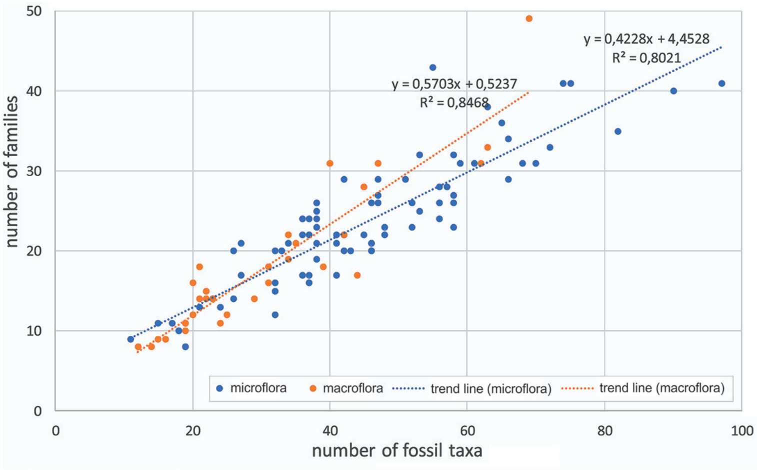

Figure 4 Chart showing number of fossil taxa vs. number of families

Comparison with modern floristic zonation

Today, the Holarctic Kingdom is the largest of all floristic kingdoms and occupies more than half of the entire landmass. It covers all of Europe, extratropical North Africa, all of extratropical Asia and almost all of North America. Despite the enormous extent of the territory of this kingdom, the floras of its individual regions are closely related to each other and have much in common (Takhtajan 1986). As can be seen in Figure 2, all early Paleogene floras are united into one large cluster, which is divided into 3 closely related groups. The Holarctic flora includes more than 30 endemic families of vascular plants (Takhtajan 1986). All these families are small; the vast majority of them consist of only one genus, often monotypic. The early Paleogene

Table 6. Characteristic of groups established for the early Paleogene floras of East Asia based on "key" families.

Group	Includes	Characterized by	Temporal distribution	Spatial distribution
1 Cupressaceae/ Juglandaceae/ Ulmaceae	11 floras (10 micro- and 1 macroflora). From 7 to 10 families (mean 11) in each flora.	Present in all floras – no family. Present in 50% floras and higher – Betulaceae, Cupressaceae, Fagaceae, Juglandaceae, Myricaceae, Pinaceae, Ulmaceae. Absent in all floras – Araucariaceae, Arecaceae, Caprifoliaceae, Cercidiphyllaceae, Cornaceae, Ericaceae, Eucommiaceae, Moraceae, Myrtaceae, Nymphaeaceae, Rhamnaceae, Sciadopityaceae, Viburnaceae, Vitaceae.	mainly early Eocene	22–53°N
2 Cercidiphyllaceae/ Cupressaceae / Platanaceae	24 floras (all macrofloras). From 5 to 27 families (mean 13) in each flora.	Present in all floras – no family. Present in 50% floras and higher – Betulaceae, Cercidiphyllaceae, Cornaceae, Cupressaceae, Ginkgoaceae, Malvaceae, Pinaceae, Platanaceae, Ulmaceae, Viburnaceae, Vitaceae. Absent in all floras – Aquifoliaceae, Cyatheaceae, Ephedraceae, Loranthaceae, Lycopodiaceae, Myrtaceae, Polypodiaceae, Proteaceae, Sphagnaceae.	Paleocene and early Eocene	36–75°N
3 Fagaceae/Pinaceae/ Podocarpaceae/ Ulmaceae	26 floras (all microfloras). From 13 to 33 families (mean 25) in each flora.	Present in all floras – Fagaceae, Pinaceae, Podocarpaceae, Ulmaceae. Present in 50% floras and higher – Altingiaceae, Anacardiaceae, Aquifoliaceae, Betulaceae, Cornaceae, Cupressaceae, Ginkgoaceae, Gleicheniaceae, Hamamelidaceae, Juglandaceae, Loranthaceae, Lycopodiaceae, Lygodiaceae, Magnoliaceae, Malvaceae, Moraceae, Myricaceae, Osmundaceae, Polypodiaceae, Sphagnaceae. Absent in all floras – Cercidiphyllaceae, Euphorbiaceae.	mainly early Eocene	43–75°N
4 Betulaceae/ Cupressaceae/ Platanaceae/ Rosaceae/Ulmaceae	6 floras (all macrofloras). From 11 to 29 families (mean 19) in each flora.	Present in all floras – Betulaceae, Cupressaceae, Platanaceae, Rosaceae, Ulmaceae. Present in 50% floras and higher – Anacardiaceae, Cercidiphyllaceae, Fagaceae, Ginkgoaceae, Juglandaceae, Lauraceae, Malvaceae, Menispermaceae, Osmundaceae, Pinaceae, Poaceae, Rhamnaceae, Salicaceae, Sapindaceae, Viburnaceae, Vitaceae. Absent in all floras – Altingiaceae, Aquifoliaceae, Arecaceae, Caprifoliaceae, Cyatheaceae, Ephedraceae, Ericaceae, Eucommiaceae, Gleicheniaceae, Loranthaceae, Lycopodiaceae, Myricaceae, Myrtaceae, Nymphaeaceae, Polypodiaceae, Proteaceae, Rutaceae, Sciadopityaceae, Sphagnaceae.	Paleocene and early Eocene	44–50°N
5 Cupressaceae/ Fagaceae/ Juglandaceae	22 floras (all microfloras). From 8 to 27 families (mean 19) in each flora.	Present in all floras – no family. Present in 50% floras and higher – Altingiaceae, Betulaceae, Cupressaceae, Ephedraceae, Fagaceae, Juglandaceae, Lygodiaceae, Magnoliaceae, Malvaceae, Osmundaceae, Pinaceae, Podocarpaceae, Polypodiaceae, Salicaceae, Ulmaceae. Absent in all floras – Lauraceae, Nymphaeaceae, Viburnaceae, Vitaceae.	mainly early Eocene	19–54°N
6 Betulaceae/ Myricaceae	21 floras (all microfloras). From 12 to 30 families (mean 19) in each flora.	Present in all floras – Betulaceae, Myricaceae. Present in 50% floras and higher – Cupressaceae, Fagaceae, Juglandaceae, Loranthaceae, Lycopodiaceae, Magnoliaceae, Osmundaceae, Pinaceae, Podocarpaceae, Polypodiaceae, Sapindaceae, Ulmaceae. Absent in all floras – Poaceae, Vitaceae.	mainly Paleocene	30–71°N

Note: Groups are named based on dominated families. Established groups are given in Figure 3. Spatial distribution of established groups is shown in Figure 3.

floras of East Asia include representatives of 10 of the 30 endemic families that make up the Holarctic flora, namely Ginkgoaceae, Cephalotaxaceae (now included in Taxaceae), Trochodendraceae, Tetracentraceae (now included in Trochodendraceae), Cercidiphyllaceae, Platanaceae, Eucommiaceae, Rhoipteleaceae, Davidiaceae (now included in Cornaceae), Adoxaceae (now called Viburnaceae). According to Takhtajan (1986), Magnoliaceae, Lauraceae, Ranunculaceae, Berberidaceae, Fagaceae, Juglandaceae, Caryophyllaceae, Chenopodiaceae, Polygonaceae, Plumbaginaceae, Theaceae, Salicaceae, Brassicaceae, Ericaceae, Primulaceae, Malvaceae, Euphorbiaceae, Thymelaeaceae, Rosaceae, Fabaceae, Cornaceae, Araliaceae, Apiaceae, Rhamnaceae, Gentianaceae, Boraginaceae, Scrophulariaceae, Lamiaceae, Campanulaceae, Asteraceae, Liliaceae s.l., Iridaceae, Orchidaceae, Juncaceae, Cyperaceae and Poaceae are currently richly represented in the Holarctic flora. Among conifers there are many species of Pinaceae and Cupressaceae. Ferns are represented mainly by Aspleniaceae and Polypodiaceae. Only 9 of the above listed families (Berberidaceae, Caryophyllaceae, Plumbaginaceae, Thymelaeaceae, Scrophulariaceae, Campanulaceae, Iridaceae, Orchidaceae, Juncaceae) are not represented in the early Paleogene floras of East Asia at least in our records (Table 3).

For East Asia, two large floristic regions are identified (Circumboreal and Eastern Asiatic Regions by Takhtajan 1986, Krestov 2006, or Boreal and East Asian Subkingdoms by Kamelin 2017, 2022).

The Circumboreal Region is the largest floristic region, a significant part of which is located on the territory of Russia. In the flora of the Circumboreal Region there are

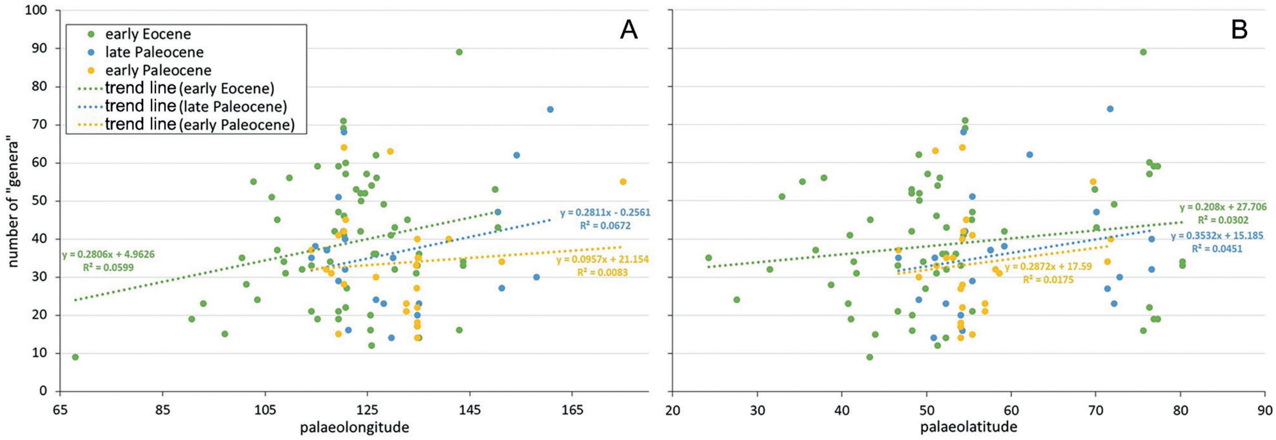

Figure 5 Changes of fossil taxa diversity along the palaeolongitude (A) and palaeolatitude (B)

no endemic families and the number of endemic genera is relatively small, but there is a very large number of common endemic genera with the Eastern Asiatic Region. Most endemic genera of the Circumboreal Region are concentrated in the Pyrenees, Alps and Caucasus. The Pyrenees, Alps, Carpathians, Caucasus, mountains of Siberia and Canada are richest in endemic species. Among the conifers, the most typical species for the region are *Pinus*, *Picea*, *Abies* and *Larix*, in Canada also *Tsuga* and *Thuja*. Among the numerous broadleaved species, the most common are *Acer*, *Alnus*, *Betula*, *Carpinus*, *Celtis*, *Cornus*, *Fagus*, *Fraxinus*, *Juglans*, *Ostrya*, *Populus*, *Quercus*, *Salix*, *Tilia*, *Ulmus*. Among other woody plants, species of *Crataegus*, *Lonicera*, *Malus*, *Prunus*, *Pyrus*, *Rhamnus*, *Rhododendron*, *Sambucus*, *Sorbus*, *Spiraea*, *Staphylea*, *Vaccinium*, *Viburnum* are also common. Along with broadleaved and coniferous forests, meadows are widespread, which turn into steppe in the southern regions of the European part of Russia and Siberia. The northern regions are characterized by extensive swamps and tundra. In the mountains, forest vegetation forms belts, of which the upper usually consists of coniferous forests. Above the forest belt there is a belt of high-mountain (subalpine and alpine) vegetation, very rich in endemic taxa. The vast Circumboreal Region is divided into a number of more or less clearly defined provinces (15 provinces according to Takhtajan 1986). According to our data, the Circumboreal Region is not distinguished in the early Paleogene of East Asia. All genera cited above are also present in our record, but at the same time many southern genera and families are present in the early Paleogene records and totally absent in the region today.

The East Asia Region includes the Eastern Himalayas (approximately east of 83°E), parts of the northeastern regions of India, mountainous Northern Burma, mountainous Northern Tonkin, much of mainland China and the island. Taiwan, the Korean Peninsula, Japan, the southern islands of the Kuril Archipelago, the southern and central parts of Sakhalin south of 51°30'N, Primorye and a significant part of the Amur river basin, as well as the southeastern part of Transbaikalia and a section in the northeast and extreme east of Mongolia. The flora of the East Asia Region is extremely rich and unique, and has 14 endemic families and more than 300 endemic genera, not to mention a huge number of endemic species (Takhtajan 1986). These endemic genera belong to a wide variety of families, both primitive and advanced. Characteristically, many endemic genera belong to the primitive subclasses Magnoliidae, Ranunculidae and Hamamelididae (Takhtajan 1986). The early Paleogene floras of East Asia include members of 8 of the 14 endemic families of the Eastern Asiatic Region, namely Ginkgoaceae, Cephalotaxaceae (now included in Taxaceae), Trochodendraceae, Tetracentraceae (now included in Trochodendraceae), Cercidiphyllaceae, Eucommiaceae, Rhoipteleaceae, Davidiaceae (now included in Cornaceae). Of the large number of endemic genera in the early Paleogene floras of East Asia, 24 genera are represented: *Cephalotaxus*, *Cercidiphyllum*, *Corylopsis*, *Cryptomeria*, *Cunninghamia*, *Cyclocarya*, *Davidia*, *Delavaya*, *Disanthus*, *Eucommia*, *Fatsia*, *Ginkgo*, *Keteleeria*, *Metasequoia*, *Paulownia*, *Phellodendron*, *Platycarya*, *Pseudolarix*, *Sciadopitys*, *Taiwania*, *Tetracentron*, *Trochodendron*, *Weigela*.

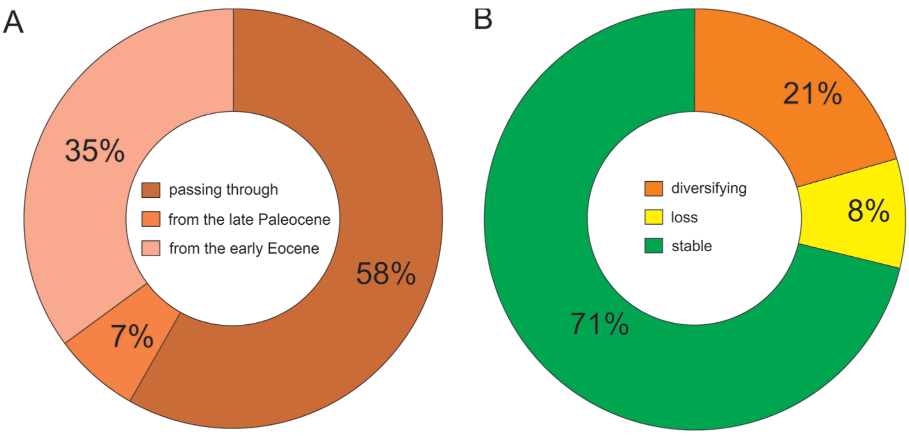

Figure 6 Proportion of families (A) and changes of genera number in families (B) of the early Paleogene floras of East Asia

Takhtajan (1986) emphasizes the exceptional antiquity of the East Asia flora and bases his conclusion on the large number of ancient relict endemics of different taxonomic ranks, including ancient endemic families and even orders. Our data support the conclusion that the East Asia flora is older than the Circumboreal flora. At least in the early Paleogene of East Asia, all analyzed floras are similar to the East Asia flora. It seems that the Holarctic Kingdom had almost formed, but there are still members of families (Araucariaceae, Arecaceae, Nothofagaceae, Pandanaceae, Proteaceae, etc.) from other, more southern Kingdoms such as Palaeotropical and Neotropical. The East Asia Region was just forming in the early Paleogene, while the Circumboreal Region was completely absent.

Today, two large floristic regions within East Asia are bordering and partially overlapping at approximately 50°N (Takhtajan 1986, Krestov 2006, Kamelin 2017, 2022). In the Paleocene, in contrast, no distinct spatial pattern was found regarding changes in the floristic composition, while in the early Eocene some differences are observed between the northern and southern parts of the study area. Various members of the Asteraceae, Bignoniaceae, Chenopodiaceae, Euphorbiaceae, Meliaceae, Ranunculaceae, and Sapotaceae families appeared and are found only south of 50° palaeolatitude (Bondarenko & Utescher 2024c). Also, a significant positive correlation of the distribution of swamp taxa (*Glyptostrobus* and *Taxodium*) is reported in Bondarenko & Utescher (2024b), with a wetter climatic zone located to the north of 50°N palaeolatitude (Fig. 7). Moreover, the taxa demonstrate different patterns of spatio-temporal distribution: *Taxodium*/*Glyptostrobus* occurred from high to middle latitudes during the early Paleogene, while *Ephedra* was distributed in the mid-latitudes and occupied the lower latitudes in the early Eocene.

Palaeofloristic provinces

In the Maastrichtian, the boundary between the two main floristic regions, which Vakhrameev et al. (1970) called the European–Turanian and Siberian–Canadian, was finally differentiated; their boundary, according to the ratio of *Normapolles* and *Aquilapollenites* pollen, passed approximately between 70 and 80°E. The coastal-marine facies of the eastern edge of the lowland up to the valley of the Vasyugan River contains exclusively the *Aquilapollenites* flora, while its western limits, including the regions of the Taz Peninsula in the north and the entire region of the Irtysh syneclise in the south, abound in species of the *Normapolles* clan. In the vast territory of Asia, over the entire area from 70 to 80°E, forest flora with an abundance of plants producing pollen of *Aquilapollenites*, *Wodehouseia*, and some others, which gave a diverse complex of pollen of the type "Oculata", "Unica" and "Proteaceae" spread, by the Upper Cretaceous, a significant differentiation of plant communities occurred. In particular, representatives of the Proteaceae, and along with them many representatives of the typical humid tropical flora (Loranthaceae, Bombacaceae, *Myrica*, Santhalaceae) retreated to the south. This circumstance allowed Samoylovich (1966, 1967) to distinguish two provinces in Siberia: Khatanga–Lena, practically devoid of Proteaceae and distinguished by a comparatively moderate flora, and Yenisei–Amur, abundant in Proteaceae species (*Beaupreaidites*, *Proteaceaidites*), Loranthaceae (*Elythranthe*, *Gothanipollis*). The eastern boundaries of these provinces are currently difficult to establish precisely. It is possible that the Khatanga–Lena province extended all the way to the Pacific coast, where, according to palynological data, an independent province is distinguished – tentatively named Primorsko-Sakhalinskaya. The characteristics of the latter are: the absence of Proteaceae representatives, a poorer species composition of *Aquilapollenites*, the early appearance and abundance of *Triatriopollenites* and *Aquilapollenites* species (*Ulmoideipites*, *Alnus*, Betulaceae). The listed flora features characterize the regions of Primorye, Sakhalin and Japan.

In the Paleocene, after the disruptions at the K/T boundary, floristic composition became less diverse and more homogenous. Nevertheless, Krystofovich (1955) identified two provinces for the Paleocene: Greenland and Gelinden, which essentially correspond to the temperate and tropical zones of the Northern Hemisphere. By calling these zones provinces (not even regions!), he wanted to emphasize the absence of sharp differentiation of the vegetation cover in the Paleocene. Regarding our data, the spatial distribution of the groups based on “key” families’ diversity for microfloras shows some very clear patterns during the early Paleogene (Fig. 3). In the early Paleocene, the group Betulaceae/Myricaceae was widespread, while other groups occurred occasionally, and only in the middle latitudes (~50–60° palaeolatitude). In the late Paleocene (Fig. 3B,E), in addition to the group Betulaceae/Myricaceae, the group Fagaceae/Pinaceae/Podocarpaceae/Ulmaceae became more widespread in the high latitudes compared to the early Paleocene (~50–70° palaeolatitude). Unfortunately, due to the lack of palaeofloras south of 40° N, it is impossible to say whether other groups were distributed at lower latitudes in the Paleocene. In our data, *Aquilapollenites* pollen was found in 12 of 16 early Paleocene microfloras, and in 8 of 15 late Paleocene microfloras of East Asia. Moreover, this pollen is found in 9 of 48 early Eocene microfloras from 71 to 26°N.

Researches for floristic provinces of East Asia in the Eocene are absent. According to our results, in the early Eocene (Fig. 3A,D), the floristic pattern changed dramatically in comparison with the Paleocene. The group 6 significantly reduces its distribution area to a few floras in the middle and lower latitudes. At the same time, the groups 1, 3 and 5 become widespread. The group 3 is widespread in high and middle latitudes, the group 5 – in middle and low latitudes and mainly in the eastern part (i.e. on the western coast of the Pacific Ocean). The floristic composition of macrofloras demonstrates striking homogeneity. Most macrofloras were included in the group Cercidiphyllaceae/Cupressaceae/Platanaceae, which was distributed throughout Asia during the early Paleogene (Fig. 3), with the exception of 6 floras (group Betulaceae/Cupressaceae/Platanaceae/Rosaceae/Ulmaceae). Floras included in group 4 are localized throughout the early Paleogene in the region of the Sikhote-Alin mountain system and most likely reflect a very local, mountain flora.

According to vegetation and plant biomes data (Bondarenko & Utescher 2024a,c), the early Paleogene vegetation cover in the study area fundamentally differed from mo-

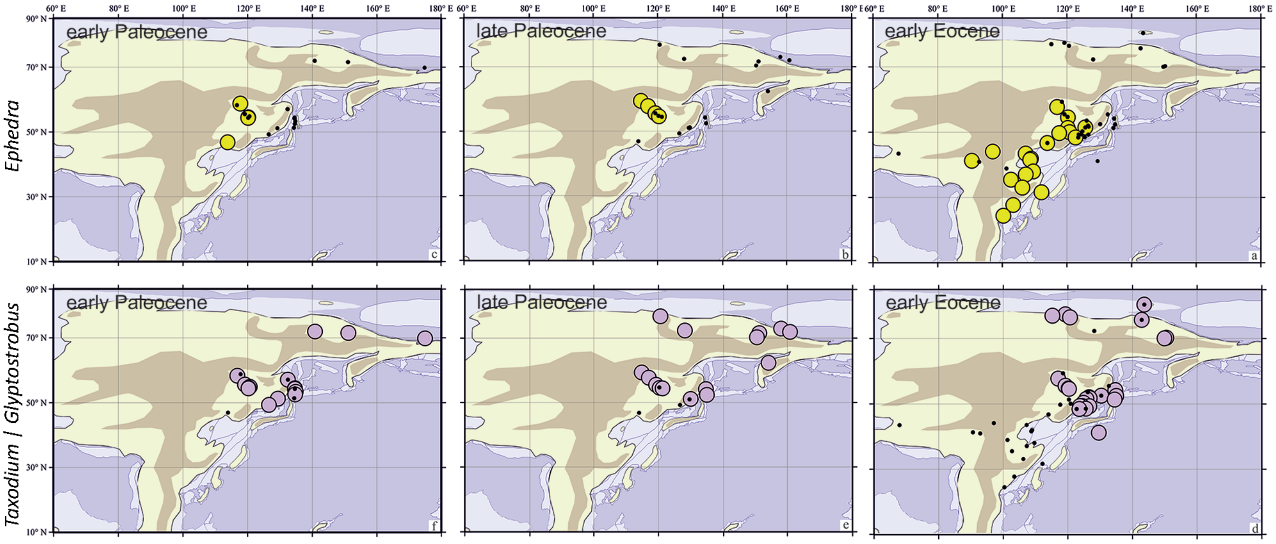

Figure 7 Spatio-temporal distribution of Ephedra and Taxodium/Glyptostrobus in East Asia during the early Paleogene (from Bondarenko & Utescher 2024b)

dern and was much more homogeneous compared to the modern one. Using Integrated Plant Record (IPR) vegetation analysis, Bondarenko & Utescher (2024a), mixed mesophytic zonal vegetation dominated on the Pacific side of Eurasia during the early Paleogene. Thermophilous mixed mesophytic forests were distributed even at very high latitudes, but at the same time, ecotone between the mixed mesophytic/broadleaved evergreen forests and broadleaved evergreen forest were confined to regions south of 50°N. Using Plant Functional Type (PFT) approach, Bondarenko & Utescher (2024c) demonstrate that in the early Paleocene, the dominant type of vegetation is typical mixed mesophytic forest (MMF). In the late Paleocene, a pronounced zone of MMF with diverse conifers appeared in high latitudes, the middle latitudes occupied by evergreens and typical MMF. In the early Eocene, MMF with diverse broadleaved evergreens and typical MMF are widespread and dominant. Early Eocene microfloras differ from Paleocene microfloras in the higher participation of warm temperate trees and higher contents in tropical PFTs.

Correlation with climate zonation

Krassilov (2014) suggests that rhythmic climate changes are directly related to both extinction and typogenesis. According to Vakhromeev et al. (1970), palaeofloristic zoning is closely related to the climatic assessment of the identified phytochores. Without such an assessment, an analysis of the spatial distribution of taxa alone does not yet provide a true zoning. There are no two identical floras, and a simple listing of the established differences, without identifying the trends determined primarily by climate change, will inevitably lead to an unjustifiably large number of regions, provinces, and districts. Palaeoclimatic reconstructions based on fossil plant complexes are, of course, very complex.

As is known, the temperature and seasonality of the climate affect the rate of mutation, the size and growth rate of organisms, the size of populations, which in turn affects the rate of spread of these mutations. Such general adaptations as photoperiodism in plants or warm-bloodedness in animals could develop only in a seasonal climate. In a seasonless climate, the population "seeks" to maximize fitness for any trait, while in a seasonal climate, fitness for the conditions of a particular season does not reach its maximum value, but remains high enough for both seasons (Timofeev-Ressovsky & Svirezhev 1970). Therefore, a seasonal climate favors species with a broad ecological niche ("generalists"), and a seasonless climate favors species with a narrow ecological niche ("specialists"). Using the Coexistence Approach, high temperatures are reconstructed in the early Paleogene in East Asia (Bondarenko & Utescher 2022), with a weakly expressed latitudinal gradient, amounting to only ≈ 1/3 of the modern (Wolfe 1978, Greenwood & Wing 1995) or even less (Bondarenko & Utescher 2022). Temperature data correlate well with high precipitation for high and middle latitudes of East Asia in the early Paleogene compared to the modern (Bondarenko & Utescher 2024b). Moreover, Bondarenko and Utescher (2024b) suggest that in the early Paleogene, the global atmospheric circulation consisted of two well-defined cells, Hadley and Ferrell, while the polar cell was either absent or located over the Arctic Ocean and was very weak. This hypothesis is supported by distinguishing two regional climatic zones are based on MAT and MAP values. The warm temperate climate zone (north of ~50° palaeolatitude) is characterized by lower values for temperature (14.2–16.2°C) and higher ones for precipitation (1158–1334 mm). The subtropical climate zone (south of ~50° palaeolatitude) is characterized by higher values for temperature (16.5–19.1°C) and lower for precipitation (874–1263 mm). Thus, the climate was very equable, especially during the Paleocene that is in line with our results showing the rich taxonomic diversity, wide spread of taxa, more homogenous floristic composition and, correspondently, only few floristic provinces. All temperature and precipitation data suggest seasonality of the early Paleogene climate over East Asia. The spatial patterns of mean annual ranges of temperatures (MART) and precipitations (MARP) apparently were quite uniform. Seasonality in the early Paleogene was distinctly lower compared to present-day. Based on the fact that the climate was seasonal and the taxa had a very wide distribution area, it is most likely that the species in the early Paleogene of East Asia were mainly "generalists". Moreover, ~50° palaeolatitude was very important. This latitude was main boundary for global atmospheric circulation, mean values of MAT and MAP, and distribution of taxa, vegetation types and floristic provinces. Today, two large floristic regions in East of Asia are also have boundary at ~50° N (cf. Takhtajan 1986, Krestov 2006, Kamelin 2017, 2022)

Arcto-Tertiary flora concept vs. Boreotropical flora hypothesis

According to the concept of the Arcto-Tertiary geoflora, Arcto-Tertiary floras once occupied large areas high latitudes of Northern Hemisphere during the Cretaceous and early Paleogene (Chaney 1947, Mai 1991), and this vegetation subsequently migrated south to mid-latitudes in Eurasia and North America (Sakai 1971). During such movements in space and time, many taxa became extinct or restricted to central and southern China and/or eastern/western North America. Various authors (e.g., Chaney 1940, 1944, 1947, 1948, 1959, Axelrod 1966, 1983) suggested that the forests of eastern North America, Eastern Asia, and western and central Europe represent relics of a temperate broadleaf deciduous forest of a particular floristic composition that developed at high northern latitudes in the Late Cretaceous and early Cenozoic and, as the climate cooled in the late Paleogene, moved south across North America, Europe, and Asia, and by the Miocene had spread across the Northern Hemisphere. In response to climate cooling, this climax forest community migrated more or less intact to the middle latitudes in the Oligocene.

To explain the floristic similarities between eastern North America, Europe, Eastern Asia, and western North America, a Boreotropical hypothesis was proposed, given the boreal geography, near-tropical climate, and thermophilic affinities of many of the taxa comprising the flora (Wolfe 1975, 1977, Tiffney 1985a,b). They based this hypothesis on the tropical taxa shared by the Eocene floras of Europe and North America and the close taxonomic relationships of these floras to those extant in tropical southeast Asia and, to some extent, Central America and the Greater Antilles (Lavin & Luckow 1993). Thus, in this hypothesis and in contrast to the concept of the Arcto-Tertiary geoflora, the vegetation of the tropical climate in the Eocene extended to northern latitudes (Wolfe 1985), which allowed the exchange of tropical taxa through land bridges with the tropical flora of the Old World. According to this concept, a large number of modern taxa first appeared in the middle latitudes of the Northern Hemisphere in the early Cenozoic (late Paleocene–Eocene) and spread via the Bering and North Atlantic land (NALB) bridges and the shores of the Tethys Seaway. The Tethys Passage was important for the dispersal of plants across Eurasia (Wolfe & Leopold 1967, Tiffney 1985a,b) and for the dispersal of tropical, subtropical, and warm temperate plants between Southeast Asia and the southeastern United States (Dilcher 2000). Accordingly, the assertion of the Arcto-Tertiary geoflora concept that many lineages arose in the Arctic in the Late Cretaceous is considered invalid (Baskin & Baskin 2016). According to Spicer et al. (1987), the first appearance of the clade (woody angiosperms) present in the Late Cretaceous – early Cenozoic floras is consistently later in Alaska than in mid-latitudes. That is, the lineages first appeared in the low and mid-latitudes and then in the Arctic (Spicer et al. 1987). Thus, a poleward migration of angiosperm taxa is assumed (Axelrod 1959, Hickey & Doyle 1977).

The boreotropical flora is thought to have had a diffuse origin, i.e., to have appeared in several places in the Northern Hemisphere. This flora arose from several separate sources and, therefore, did not originate exclusively in Southeast Asia (Tiffney 1985b). Southeast Asia (the Indo-malayan region) is considered a refugium for the boreotropical flora, not its centre of origin (Tiffney 1985a, Schuster 1972, 1976, Thorne 1999). Furthermore, this boreotropical flora was not homogeneous; it showed spatial and temporal variations in taxonomic composition, and its taxa appeared in the fossil record at different times and had different ecologies (Tiffney 1985a,b). The boreotropical flora existed in a warm, equable (paratropical) climate with MATs of 20–25°C and a low MART. This flora included a mixture of temperate, tropical, and paratropical genera, many of which have survived in or were associated with the mixed mesophytic forest of the later early and late Cenozoic; key genera were e.g. *Acer*, *Alangium*, *Betula*, *Calycocarpium*, *Carpinus*, *Carya*, *Celtis*, *Cercidiphyllum*, *Cladrastis*, *Cocculus*, *Fagus*, *Gordonia*, *Halesia*, *Hamamelis*, *Hydrangea*, *Juglans*, *Liquidambar*, *Liriodendron*, *Magnolia*, *Nyssa*, *Platanus*, *Pterocarya*, *Quercus*, *Tetracentron*, *Tilia*, *Ulmus*, and *Zelkova* (Wolfe 1977). These taxa still persist in mixed mesophytic forests of eastern Asia and/or eastern North America.

In contrast to the Arcto-Tertiary geoflora concept, the Boreotropical hypothesis views the mixed mesophytic forests of eastern Asia and eastern North America as having evolved independently after the geographic disruption of the boreotropical flora, rather than as direct relicts of broad-leaved deciduous forests that developed at high latitudes in the Northern Hemisphere and then migrated as an intact unit to mid-latitudes during the gradual climatic cooling of the Cenozoic. High-latitude (Laurasian) migration is an important and widely cited explanation for pantropical tree divergences (Lavin & Luckow 1993, Davis et al. 2002) via the two northern land bridges are Beringia and the NALB (Wolfe 1975). Because during the Paleocene the NALB was by ca. 10° lower in latitude than Beringia and contained more thermophilic flora, it is thought to have been more likely to have facilitated tropical biotic exchange between Eurasia and North America (Graham 2018). Today, the major part of the Northern Hemisphere harbours moist and temperate deciduous forests remaining from the fragmentation of this global forest are in Eastern Asia, Europe, and eastern North America. Tree species richness varies considerably among the three regions, with eastern Asia being higher than eastern North America, and eastern North America being higher than Europe (Latham & Ricklefs 1993, Guo et al. 1998, Svenning 2003). The Boreotropical hypothesis advanced to explain the patterns of East Asian/eastern North

American floristic disjunctions has been that a once continuous Arcto-Tertiary flora existed in the Northern Hemisphere during the Late Cretaceous and Paleogene, which was fragmented by the cooling-induced extinctions of the Neogene and Quaternary (Tiffney 1985a, Wen 1999, Tiffney & Manchester 2001, Milne & Abbott 2002). However, the wide range of divergence times estimated by molecular dating among disjunctive taxa between East Asia and North America suggests multiple and complex origins for the disjunctions in the Northern Hemisphere (Xiang et al. 2000). Many researchers (Takhtajan 1969, Latham & Ricklefs 1993, Li & Adair 1994, Qian 2001, Qian et al. 2003) have suggested that the flora of Eastern Asia is ancient, because a lot of living fossil plants today are found only in this region. Hence, it is considered the cradle of the North American, European floras, and even the modern flora of the Palaeotropics (Tang 2000, Wu et al. 2011). Furthermore, Eastern Asia has also been considered the center of origin and/or diversification of angiosperms (Qian 2001, Qian et al. 2003, Wu et al. 2011). Based on molecular data Chen et al. (2018), the median age of the Eastern Asian flora is 13.60 Ma (middle Miocene), with most clades of specimens appearing from 22.23 Ma (early Miocene), although several lineages are dated to the Oligocene, Eocene, or even older geological times. This suggests that the formation of the East Asian flora may have been greatly affected by environmental changes in the Neogene. During this period, the topography of Eastern Asia became closer to modern (Hsu 1983, Wang 2004), the major mountain range and drainage systems were formed (Zheng 2015), and the formation and development of the East Asian monsoon occurred (Zhang et al. 2007). According to Chen et al. (2018), available fossil data show that the first appearances of East Asian endemic genera in the flora date from the Late Jurassic to the Pleistocene, with most clades occurring from the Miocene. Among these fossils, gymnosperm fossils appear to be much older than angiosperm fossils. The first appearance of fossil gymnosperms that are members of the Eastern Asian flora can be dated to the Late Cretaceous, such as *Cathaya*, *Pseudolarix*, *Metasequoia*, or even the Late Jurassic (*Ginkgo*). Among the fossil angiosperms, the only genera that can be dated to the Eocene were *Eucommia* and *Sinomenium*. In our data, *Eucommia* occurred in the late Paleocene (Yarovaya91 and Raichikhinsk, see also Table 3).

Generally, our data support a diffuse origin of the early Paleogene floras of East Asia as suggested by Tiffney (1985b) and a lower to mid-latitudinal appearance of angiosperm taxa and a pole-ward migration thereafter as suggested by Axelrod (1959), Spicer et al. (1987), and Baskin & Baskin (2016). Our results demonstrate that the early Paleogene floras of East Asia are quite homogeneous, however show minor spatial and temporal variations in taxonomic composition, and some taxa appeared in the fossil record at different times and had different ecologies. According to our climate reconstructions (Bondarenko & Utescher 2022, 2024b), the early Paleogene floras of East Asia existed in a warm, equable climate. At the same time, our data do not support the existence of paratropical conditions in high and middle latitudes. The early Paleogene floras do include a mixture of temperate, tropical, and paratropical genera, many of which have survived in or were associated with the mixed mesophytic forest of the later early and late Cenozoic. Thus, our data support the Boreotropical hypothesis.

CONCLUSION

The analysis of our early Paleogene floral record of East Asia reveals a floristic diversity of 578 genera (334 formal genera) from a total of 132 families. Angiosperms represent the most diverse division accounting for over two-thirds of family diversity. The application of multivariate statistics provides insight into the floristic similarities of the single palaeofloras and the relation between taxonomic entities. Our analysis allows to trace the spatio-temporal distribution of six floristic groups characterised by taxonomic associations. It is shown that macro- and microfloras have a significantly differing representatives as regards taxonomic composition, so an integrative approach is useful when reconstructing palaeofloristics.

The floristic composition in the study area did not undergo any significant changes throughout the early Paleocene, but with 77 families present taxonomic diversity was already at a high level after the K/T boundary. The early Eocene saw a distinct increase, 128 families are recorded, mainly referable to a diversification of angiosperms. Thus, our data support the assumption of a Mesozoic origin for a large number of taxa, at the same time they underline the suggested diversification pulses occurring during the Cenozoic. The diversification observed in the early Eocene can possibly be related to the coeval warming trend.

Earlier palaeotemperature and precipitation reconstructions suggest a seasonal climate in the early Paleogene climate over East Asia, but seasonality was distinctly lower compared to present-day. The spatial patterns for temperature and precipitation seasonality apparently was quite uniform. Based on the fact that the climate was seasonal and the taxa had a very wide distribution area, it is most likely that the species in the early Paleogene of East Asia were mainly "generalists". Moreover, ~50° palaeolatitude was main boundary for global atmospheric circulation, mean values of MAT and MAP, and distribution of taxa, vegetation types and floristic provinces. At the same time, no distinct spatial patterns are found regarding changes in the Paleocene floristic composition, while in the early Eocene the floristic patterns changed dramatically exhibiting significant differences between the northern and southern parts of the study area. Various members of the Asteraceae, Bignoniaceae, Chenopodiaceae, Euphorbiaceae, Meliaceae, Ranunculaceae, and Sapotaceae families appeared and are found only south of 50° palaeolatitude.

Our data on the Early Paleogene of East Asia generally do not contradict or refute previous analyzes of the taxonomic diversity, they complement and detail them. Some minor differences or disagreements are due to the fact that the above mentioned data are based only on macrofloras and the idea of taxon dominance is most likely based on the abundance of leaf impressions. Our results are based on integrated data from both micro- and macrofloras and are not based on abundance data, but only on the presence or absence of taxa.

Our analysis of the Paleocene floras supports their continuity with Late Cretaceous floras, more homogeneity and only two floristic provinces, as suggested by Krystofovich (1955). However, our data demonstrate different boundaries for the floristic provinces and do not allow distinguish the tropical one. Previous researches on floristic provinces of East Asia in the Eocene are absent. According to our results, in the early Eocene the floristic pattern changed dramatically in comparison with the Paleocene. Based on microfloras, we suggest at least three floristic provinces in the early Eocene of East Asia.

Our results support a diffuse origin of the early Paleogene floras of East Asia and a lower to mid-latitudinal appearance of angiosperm taxa and a pole-ward migration thereafter, and generally can be interpreted as supported to the Boreotropical hypothesis. The early Paleogene floras of East Asia demonstrate some homogeneity, however show minor spatial and temporal variations in taxonomic composition, and some taxa appeared in the fossil record at different times and had different ecologies.

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