Paleocene and Eocene floristic and climatic change in Russia and Northern Kazakhstan

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Paleocene and Eocene floras of Russia and adjacent regions are reviewed with an interpretation of climatic conditions under which they developed. Floristic and climatic changes in western and central regions of Russia in the Paleocene and in the first part of the Eocene were caused by the dynamics and rearrangement of the systems of marine seaways: a longitudinal seaway, which connected the Arctic basin with the marginal seas of Northern Peri-Tethys (Turanian, South Russian and others), and a latitudinal seaway, which connected the marginal seas of Northern Peri-Tethys with the Atlantic Ocean. As these systems were progressively reduced, the climate in the middle latitudes changed from paratropical (like in West and Central Europe) to a subtropical monsoon climate with wet summers (Late Ypresian to Lutetian), and later to a climate with wet winters (Late Lutetian to the first part of the Priabonian). Floristic changes reflect these climatic trends. In the Paleogene, cold currents constantly influenced the climate of regions of the northwestern Pacific and facilitated development of a warm-temperate mesophilic flora. A warmer episode took place in the Early Eocene. At this time thermophilic plants (*Sabal*, Myrtaceae and Lauraceae) reached Koryakia, North Western Kamchatka, probably as a result of northward migration. Some subtropical plants existed near the Recent Polar circle. The subtropical Raichikha-type Flora lost temperate elements and, by ecological and climatic types, it is more similar to the Recent flora of South-West and South China. • Key words: flora, palaeoclimate, Paleocene, Eocene, Russia.

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The quality of information about the Paleocene and Eocene floras in Russia is very variable. Little is known about the floras from the northern and central parts of the East European and Siberian platforms. Most localities are distributed along the coast of the Northern Peri-Tethys seas (South Russian, Turanian, West Siberian) and along the West Pacific periphery. Plant macrofossils are usually preserved in lacustrine and alluvial sediments of coastal plains or, more rarely, in intermontane coal-bearing sedimentary basins as well as around volcanic structures. Figs 1–4 show the main localities yielding plant macrofossils. Seas, straits and key palaeogeographic areas are named in Fig. 2.

Danian floras (Fig. 1)

At the K/T boundary, a transition to the warm temperate Tsagayan flora was first studied from the Tsagayan Series of the Zeya-Bureya sedimentary basin (Fig. 1, locs 5, 6) that developed on the continental boundary of the Western Pacific. *Onoclea*, *Osmunda*, *Ginkgo*, Taxodiaceae, Cupressaceae, *Trochodendroides*, Cornaceae, Hamamelidaceae, Nyssaceae (Akhmetiev *et al*. 2002) and some other taxa are the most typical members of this flora. *Trochodendroides* is a key indicator taxon for these floras (Fig. 1 – Tr). To date, at least 70 species of the Tsagayan flora have been recognized. Contemporary floras of the Tsagayan ecotype are known from areas adjacent to the Amur River Area: southern Primorye, Sakhalin, Sikhote-Alin volcanic belts (Malo-Mikhailovka and Takhobe localities), Kamchatka and Koryakia (Fig. 1, locs 7–10). These floras are discussed in the final section of this paper.

At high latitudes, the warm temperate humid flora migrated westward along the northern boundary of the West Siberian plate and in the Danian reached the northern and Middle Urals (Lozva flora, Fig. 1, loc. 1). The same type of the Danian flora occupied the Arctic region: Spitzbergen, Greenland, North Canada, Alaska and northern Siberia – many localities at the Lena River Mouth area and Kharaulakh ridge (Bykov arm of the Lena River, Kengdey and Kungi grabens) (Budantsev 1983). Tsagayan plants

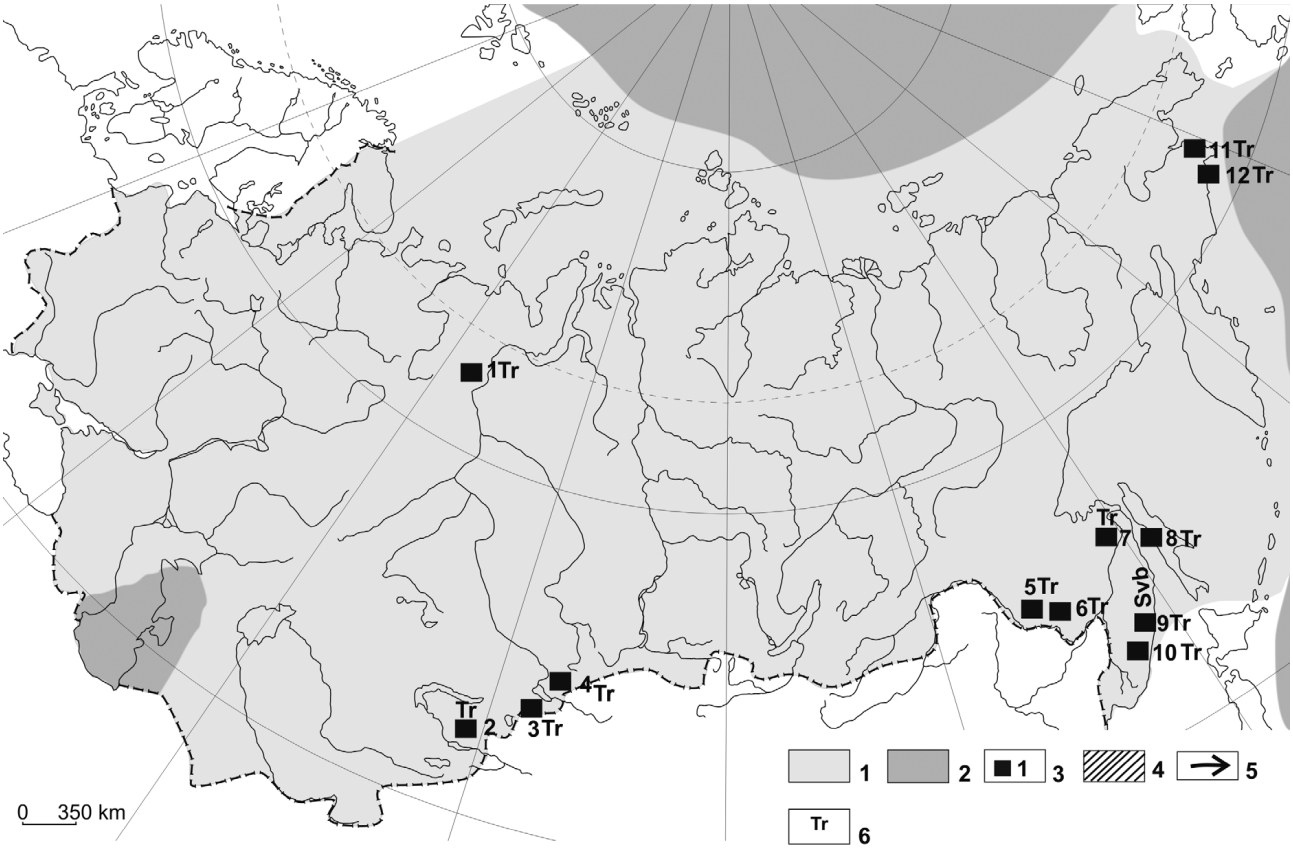


Figure 1–4. Palaeogeographic maps and main localities for Paleocene and Eocene floras (within the boundaries of the former USSR). Legend (see Fig. 1): 1 – land, 2 – sea, 3 – locality and its number on maps, 4 – areas of bauxitization, 5 – direction of sea currents, 6 – plant indicators: Tr – *Trochodendroides*, U – *Ushia*, S – *Sabal*, N – *Nypa*, P – *Palibinia.* All geographical and paleogeographical elements are shown in Fig. 2.

Figure 1. Early Danian. Localities: 1 – Lozva (western border of Western Siberian Plate) (Tr), 2 – Ulken-Kalkan (Ili River Basin, Kazakhstan) (Tr), 3 – Taizhusgen (Zaissan Lake basin) (Tr), 4 – Kara Biryuk (Zaissan Lake basin) (Tr), 5 – Raichikha coal field and Belaya Mount (Tsagayan flora – type locality) (Tr), 6 – Arkhara-Bouguchan coal field (Tr) (locality 5 and 6 – Zeya-Bureya sedimentary basin, Amur River Area), 7 – Malo-Mikhailovka (Lower Amur Area) (Tr), 8 – Kama River Area (Western Sakhalin) (Tr), 9 – Sobolevka (= Takhobe) (Eastern Sikhote-Alin) (Tr), 10 – Zerkalnaya (= Tadushi) (Eastern Sikhote-Alin) (Tr), 11 – Rarytkin Ridge (Northern Koryakia) (Tr), 12 – Beringovsky (Beringian sea, Anadyr Bay) (Tchukotskaya Formation) (Tr), Svb – Sikhote-Alin volcanic belt.

migrated westward along the mid-latitude tracts from the Amur River system and reached Mongolia, Dzhungarian Alatau, Ili River area (Ulken Kalkan), Semipalatinsk district on the Irtysh River area and the Zaissan Lake basin (South Eastern Kazakhstan) (Fig. 1, locs 2–4). In the Danian the Kara-Biryuk flora (Fig. 1, loc. 4) in the Zaissan Lake basin includes typical Tsagayan plants: *Taxites olrikii*, *Trochodendroides arctica*, *Nyssa bureica, Platanus raynoldsii, Porosia* and others.

In the Zeya-Bureya sedimentary basin (area of localities 5 and 6 in Fig. 1), the Tsagayan flora went through three stages of evolution from Middle Tsagayan to Kivda time (early Danian–?Selandian) (Kivda Flora see Fig. 1, loc. 5). The youngest flora of the Tsagayan ecotypes is characterized by various new members initially Myricaceae and Betulaceae as well as Ulmaceae. It should be noted that no principal changes in composition of the Tsagayan flora took place in the Danian and possibly, in the Late Paleocene. For each stage, only five to seven new taxa (up to 10% of total) appeared, and approximately the same number of taxa disappeared.

There is the typical Danian Flora in the central part of the Rarytkin Ridge (North Koryakia, Fig. 1, loc. 11) and a similar flora from Sakhalin (Kama River beds, Fig. 1, loc. 8) (Kodrul 1999).

Later Paleocene and Eocene floras of Northern Central Eurasia

Two main marine systems influenced the development of the Paleogene flora and vegetation in European Russia and Siberia. 1) A meridional system that connected the Tethys with the Arctic Basin via the West Siberian epicontinental sea and the Turgai strait. 2) A latitudinal system that connected the East Peritethys with the Atlantic Ocean through

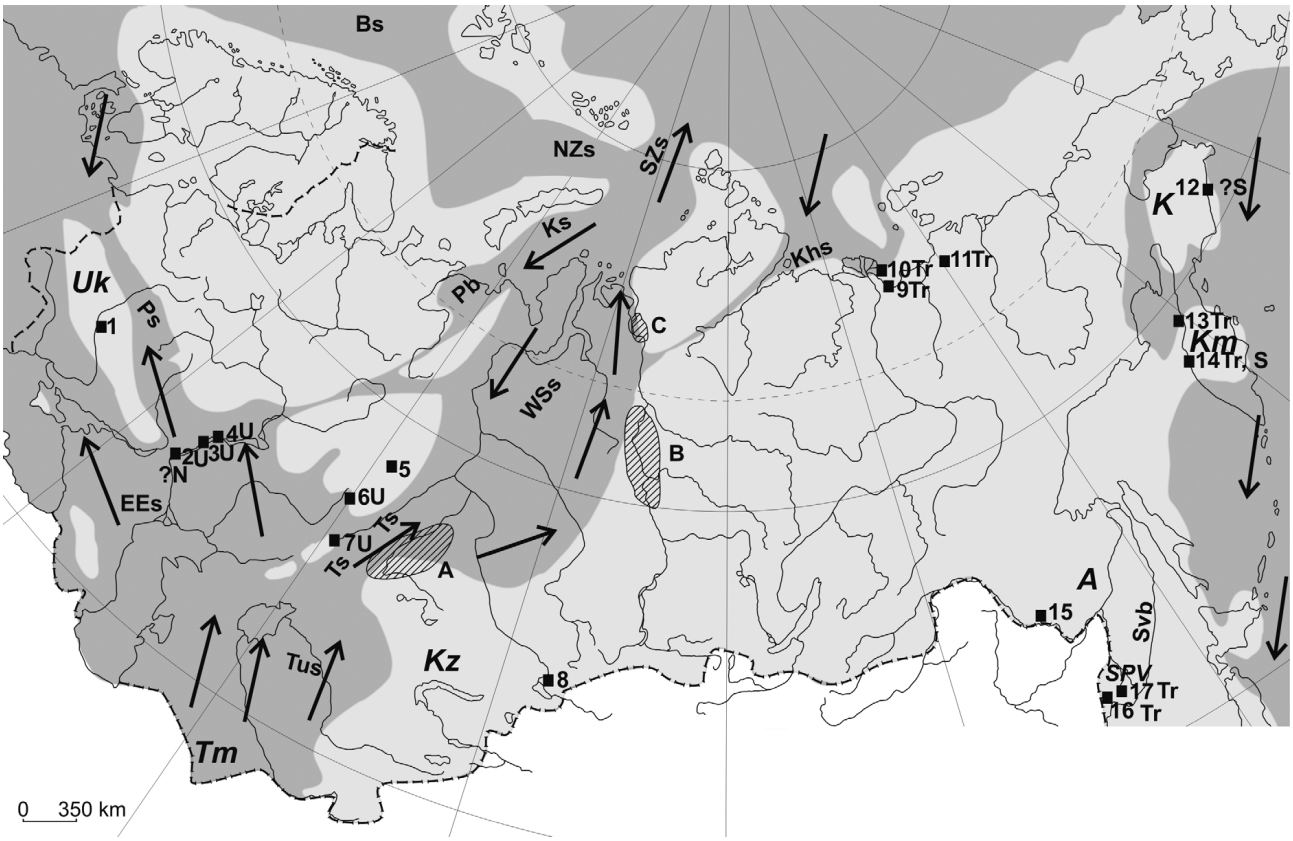


Figure 2. Late Thanetian–Early Ypresian (including the PETM Episode). Localities: 1 – Kanev (Dnieper River Area, Southern Kiev), 2 – Kamyshin (Volga River Area (U, ?N), 3 – Nikulino-Privolsk (Volga River Area, northern of Saratov) (U), 4 – Akshuat – Tashly (northern of Saratov) (U), 5 – Smolino (South Ural, near Tchelyabinsk), 6 – Romankol (Or River Area, Northern Kazakhstan) (U), 7 – Tykbutak (Mugodzary Mounntain, Northern Kazakhstan) (U), 8 – Kiin-Kerish (Zaissan Lake Basin, brown clays "flora"), 9 – Kengday and Kunga troughs (Lower Lena River Area) (Tr), 10 – Bykovo channel (Lower Lena River Area) (Tr), 11 – Tas-Takh Lake (northern part of Siberian platform) (Tr), 12 – Beringovsky (Beringian Sea, Anadyr Bay) (Sandstones Member with ?*Sabal*), 13 – Tchemurnaut (Western Kamchatka) (Tr), 14 – Rebro Cape (Western Kamchatka) (Tr, S), 15 – Raichikha (Raichikhinsk coal field, Zeya – Bureya sedimentary basin), 16 – Rechnoi peninsula (northern of Vladivostok), Lower coal-bearing Member (Tr), 17 – Maikhe coal-bearing field (eastern of Vladivostok) (Tr).
Areas of bauxitization: A – Arkalyk, B – Yenisei-Angara Area, C – Lower Yenisei River Area.
Uk – Ukraine, *Kz* – Kazakhstan, *K* – Koryakia, *Km* – Kamchatka, *SPV* – South Primorie, Vladivostok, *A* – Amur River basin, *Tm* – Turkmenia. Bs – Barents sea, NZs – "Novaya Zemlya" strait, SZs –"Severnaya Zemlya" strait, Khs – Khatanga strait, WSs – West Siberian sea, Ks – Kara sea, Pb – Pechora bay, Ts – Turgayan strait, EEs – Eastern European sea, Tus – Turanian sea. Ps – Pripyat strait, Svb – Sikhote-Alin volcanic belt.

the Dnieper-Donetsk Sea and western (Pripyat and Polish) straits (Akhmetiev & Beniamovski 2006).

Paleocene and Early Eocene evergreen thermophilic flora west of the Urals (Fig. 2, localities 1–4) and Kazakhstan (Fig. 2, localities 6–8)

Since the Danian, a Tethys Gelinden ecotype thermophilic flora, with mostly evergreen aspects, developed to the west of the Ural mountain range under a humid "paratropical" climate.

During the Selandian and the Thanetian the core of the paratropical flora was formed by the *Ushia* assemblage (Fig. 2 – localities with U) with *Chamaecyparis*, *Ushia*, *Dewalquea*, *Macclintockia*, *Dryophyllum* and Lauraceae. This assemblage was found in several localities from the Volga basin in the Ulyanovsk and Saratov districts (Fig. 2, locs 2–4). The Kamyshin Flora contains *Ushia* in different morphotypes, which are described as species: *Ushia kamyschinensis* (Goepp.) Kolakovsky, *U. alnifolia* Makulbekov, *U. janishevskii* Makulbekov, *etc.*) as well as Lauraceae (*Daphnogene lanceolata* Ung., *Litsea* sp., *Ocotea* sp., *Persea paleomorpha* Sap., *P. enormis* (Krasnov) Makulbekov, *Dewalquea gelindensis* Sap. & Mar., *Oxycarpia bifaria* Tautsch., *Ficus murczisonii* Makulbekov, *Viburnum volgensie* Krasnov, and others (Krasnov 1910, Makulbekov 1977, Mai 1995). In the Late Paleocene the *Ushia*-type flora spread to North Kazakhstan. The Romankol flora (Fig. 2, loc. 6) from the Paleocene-Eocene transition (corresponding with climatic optimum – PETM)

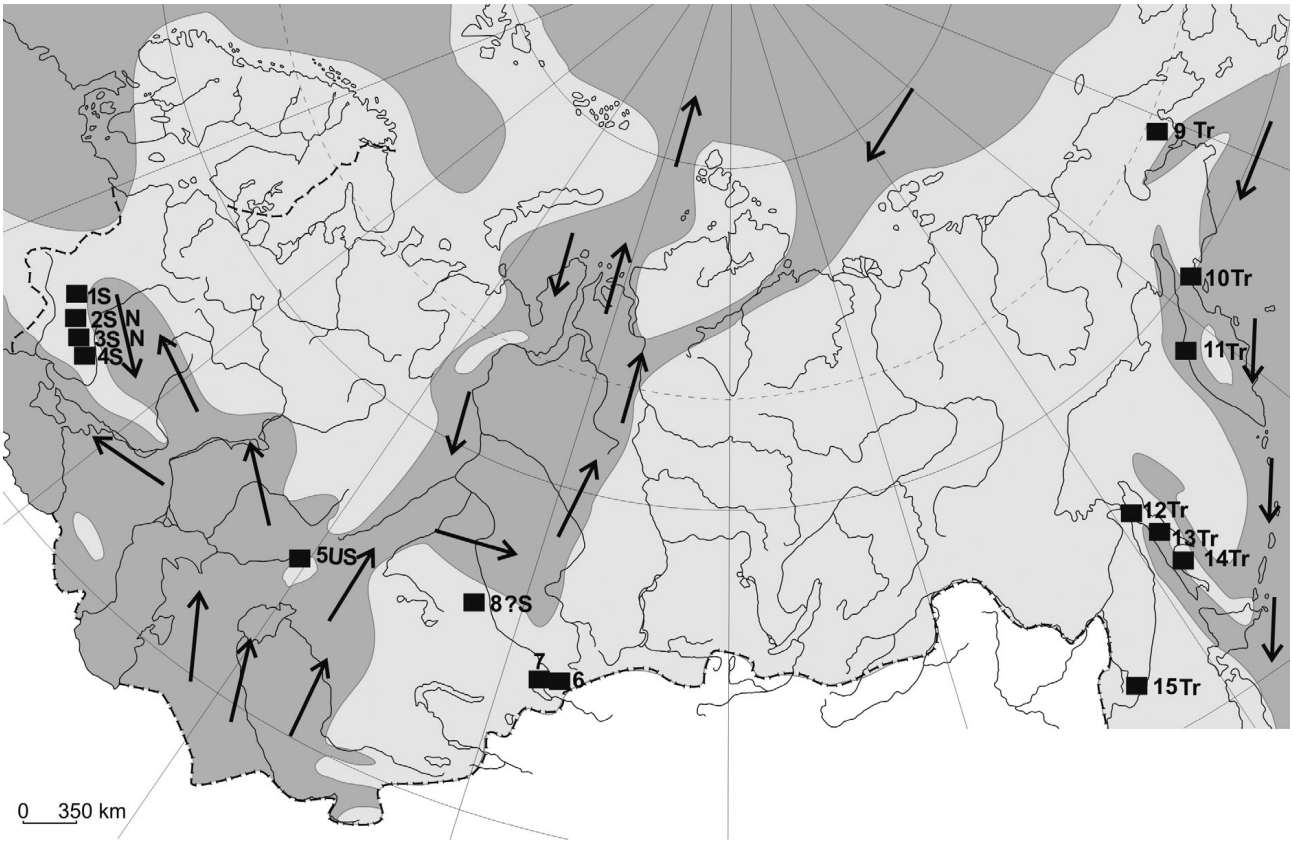


Figure 3. Late Ypresian–Early Lutetian. Localities: 1 – Mogilno (western of Kiev) (S), 2 – Kremyanka (western of Kiev) (S), 3 – Zvenigorodka (Yekaterinopolye, Dniper River Area, south-eastern of Kiev), (Bouchak Formation) (S), 4 – Adzhamka (Dnieper River Area, south-eastern of Kiev) (Bouchak Formation) (S), 5 – Karakol (Mugodzhary Mountain, Northern Kazakhstan) (U), 6 – Chakelmes (Zaissan Lake Basin), 7 – Kershi (Zaissan Lake Basin), 8 – Karasor (North-Western Kazakhstan, Irtysh River Area) (?S), 9 – Northern Koryakia (Circus Mount) (Tr), 10 – Kangpil Cape (Penzhinsky Bay) (Tr), 11 – Snatol (Palana) (Western Kamchatka) (Tr), 12 – Due (Western Sakhalin) (Conglomerate and Lower Due formations) (Tr), 13 – Snezhinka (Lower Snezhinka Subformation) (Western Sakhalin) (Tr), 14 – Krasnoyarka River (Naibuti Formation) (South-Eastern Sakhalin) (Tr), 15 – Artyem Coal field (north-western of Vladivostok) (Uglovoye Formation) (Tr).

included *Ushia* and various evergreen plants belonging to Moraceae (*Artocarpus*, *Ficus*), Proteaceae (*Dryandra*), Magnoliaceae, Lauraceae (6 genera), Euphorbiaceae, Elaeocarpaceae, Sterculiaceae, Combretaceae, Myrtaceae, Theaceae, Melastomataceae, Araliaceae, Sapotaceae (*Sideroxylon*), Symplocaceae, Apocynaceae *etc*. (Makulbekov 1977, Baikovskaya 1984, Akhmetiev 2007).

The Tykbutak locality (Fig. 2, loc. 7, Mugodzary Mountain, Northern Kazakhstan) was studied by N.M. Makulbekov (1977). The fossils were collected from the Tykbutak Formation. This formation consists of alternate sands, sandstones (predominate), sandy clays, and a form of chert (a fine grained porous siliceous sedimentary rock with small proportions of sand) [the Russian term for the latter is opoka or gaises which seems to have no exact English equivalent]. Most of the leaves have entire margins and belong to subtropical or tropical genera and families: *Quasisequoia couttsiae* (Heer) Kunzmann, *Glyptostrobus* sp., *Magnolia embica* Makulbekov, different Lauraceae (dominants, belong to *Persea*, *Litsea*, *Laurus*, *Laurophyllum*, *Apollonias*, *Daphnogene*, *Phoebe*), *Ficus* sp., *Ushia* sp. (several morphotypes), *Myrica banksiaefolia* Ung., *Leucothoë protogaea* (Ung.) Schimp., *Bumelia oblongifolia* Ett., *Mimosites* sp., *Callistemophyllum melaleucaeforme* Ett., *Sapindus* sp., *Aralia venulosa* Sap. & Mar., *Celastrophyllum* sp., (?)*Dryandra karakulensis* Baranova, Poaceae gen., *Dewalquea gelindensis* Sap. & Mar. and others.

Locality 8 (Fig. 2) is situated on the northern Zaissan Lake, on the western part of the Kiin-Kerish hill. Iljinskaya (1963), Romanova (1970) and Akhmetiev (1985) studied "Brown clays flora" at the base of the North-Zaissan Group. The composition of this flora changed from base to top of the sequence. Near the base aquatic or semi-aquatic plants predominated, such as *Peltandra, Zingiberopsis, Nelumbo, Salvinia, Anoectomeria brongniartii* Sap., *Nymphaea polyrhiza* Sap., *Carex* sp., *Cyperacites* sp., *Poacites* sp., *Phragmites* sp. The rarer *Protoacerophyllum perfoliatum* Romanova is also found near the base. Some aquatic plants are like those from the Early Eocene Raichikha flora

Amur River basin (*Salvinia*, *Peltandra*, *Zingiberopsis*, *Nelumbo*, *Nymphaea*). Both floras are characterized by reduction in conifers. This is a typical oxbow-lake assemblage. To the top of the section aquatic or semi-aquatic plants are reduced and different narrow leaved angiosperms appear, some of them endemics: "*Begonia*" *vachrameevii* Romanova, "*Oxicarpia*" *microcarpa* Romanova, *Protophyllum zaissanicum* Romanova, *Arthollia* (*Zaissania*) spp. Among narrow-leaved endemic species there are *Dryophyllum curticellense* (Wat.) Sap. & Mar., *Lindera vassilenkoi* Iljinskaya, Lauraceae gen., *Apocynophyllum iljinskajae* Romanova and others.

In Western Ukraine the Kanev Formation (Fig. 2, loc. 1) included clays and marls with rich Early Ypresian microfossil assemblages (planktonic foraminifera, nannoplankton, dinocysts) distributed along the Dnieper valley from South to North Kiev. A.N. Kryshtofovich described several species: *Posidonia parisiensis* (Desm.) Frittel, *Arunidites roginei* (Wat.) Frittel, *Macclintockia kanei* (Heer) Sap., *Hakea spathulata* Schmal., two small leaves similar to Lauraceae genera and *Andromeda* sp. (*Leucothoë* sp.) (see Baranov 1959, p. 71).

Bauxite (another indicator of warm wet subtropical climate) occurs in the Early Eocene in different areas of Kazakhstan and Siberia (Fig. 2). These include the areas near the Turgai-Arkalyk district of North Kazakhstan, along the Siberian platform (right side of the Yenisey River valley) from south to east along the south part of the Yenisey ridge (60° north latitude) up to 67° N. Some studies show that the ore was found near the Yenisey River mouth (70° N) (Bushinsky 1958).

Late Ypresian subtropical humid forests, central Eurasia (Fig. 3, locality 5)

By the Late Ypresian the central Eurasian paratropical climate changed to a summer-wet monsoon-type of subtropical climate. This change was probably connected with interrupted latitudinal communications between the western and eastern North Peri-Tethys seas. A land barrier was formed on the Pripyat strait (Akhmetiev & Beniamovski 2006). By the Early Lutetian the inner marine seas began to shallow and showed signs of reduction of the longitudinal straits connecting the Arctic basin with the Tethys through theTurgai strait and West Siberian Sea. The Orsk-Ayat strait in the southern Ural disappeared. The West Siberian Sea also reduced, but southern transfer of heat and moisture continued elsewhere. Seasonal redistribution of precipitation took place. Early Paleogene paratropical forests changed to subtropical humid forests as a result of the onset of a monsoon summer-wet climate. These forests included Lauraceae (*Persea*, *Litsea*, *Daphnogene*) and Fagaceae, especially *Castanopsis*, and also *Lithocarpus*, *Dryophyllum* and large-leaved *Quercus* predominated and also *Magnolia*, *Sterculia*, *Leguminophyllum* and other woody elements. Such assemblages were documented by Makulbekov (1972, 1977) at Karakol (Cis-Irtysian) (about 50% *Castanopsis*) and Sarkol (Mugodzhary) (both Fig. 3, loc. 5). Floristic layers with *Castanopsis* overlap with the Lower Member of the Tykbutak Formation with *Ushia*.

Late Ypresian–Lutetian, Ukraine (Fig. 3, localities 1–4), North-Eastern Kazakhstan (Fig. 3, locality 8), Zaissan Lake Basin (Fig. 3, localities 6, 7)

To the west in Ukraine a large-leaved flora similar to that in Central Eurasia was described from the coal-bearing Buchak Formation (Lutetian). Most localities are concentrated south of Kiev, Volynian (Mogilno locality, Fig. 3, loc. 1), and Dnieper River areas [Kremyanka (Fig. 3, locs 2–4) (N), Jablontsy localities and others] (Schmalhausen 1883–1884, Kryshtofovich 1927, Pimenova 1937, Stanislavsky 1950, Zhilin 1986). *Sabal* (Fig. 3 – S) is an important consituent of these floras. The main components of these floras were Lauraceae (*Daphnogene*, *Cinnamomophyllum*, *Laurus*, *Persea*), Fagaceae (*Dryophyllum*, *Eotrigonobalanus*, *Lithocarpus*, *Castanopsis*), evergreen plants represented by *Ficus*, Palmae (*Sabal* and *Nypa*), *Magnolia*, *Myrtophyllum*, *Myrsine*, *Pittosporum etc*. Ferns (*Lygodium*) and conifers (*Doliostrobus*, *Quasisequoia*) were very rare. Early Lutetian clays with *Spondylos* can be followed along the right side of the Dniper Valley from Kiev to Yekaterinopolye (Fig. 3, loc. 3). Several localities with *Nypa burtinii* occur in this zone together with the typical mangrove fern *Acrostichum*.

Two localities with Late Ypresian–Early Bartonian floras were found near the Zaissan Lake (South-Eastern Kazakhstan). The first of them is Chakelmes hill (Fig. 3, loc. 6). Dominants of the Chakelmes flora are Taxodiaceae, *Dryophyllum curticellense* (Wat.) Sap. & Mar., *D. dewalquei* Sap. & Mar., *D. kryshtofovichii* Iljinskaya, different Lauraceae (dominant, more then 80% specimens, determined by epidermal investigation) and *Zingiberopsis* sp. More rarely encountered are *Sequoia* sp., *Taxodium dubium* (Sternb.) Heer, *Glyptostrobus* sp., *Cryptomeria* sp., *Magnolia* sp., *Populus kryshtofovichii* Iljinskaya, *Lindera* sp., *Apocynophyllum* sp. and others (Iljinskaya 1986, Akhmetiev 1993).

The second flora is from Kershi (a small hill in the northern Zaissan Lake area) (Fig. 3, loc. 7). This is a typical sclerophyllous subtropical-type flora. E.V. Romanova and I.A. Iljinskaya recognized more than ten species: *Liquidambar kazakhstanica* Romanova, *Ficus* sp., *Coccoloba* sp., *Sterculia* sp., *Cassia* sp., *Eugenia kirshiensis* Romanova,

Idesia romanovii Iljinskaya, *Ungnadia kryshtofovichii* Iljinskaya and others (Iljinskaya 1986).

The typical monsoon-type subtropical flora is found in Karasor (North Eastern Kazakhstan, Irtysh River area) (Makulbekov 1972) (Fig. 3, loc. 8). The main components of this flora are Fagaceae, especially *Castanopsis* (more than 50% *C. kazachstanensis* Makulbekov and *C. pavlodarensis* Makulbekov), *Quercus kornilovae* Makulbekov, *Q. irtyshensis* Makulbekov, *Quercus* spp., *Dryophyllum curticellense* (Wat.) Sap. & Mar., *Dryophyllum dewalquei* Sap. & Mar. More rarely found are "*Podocarpus*" *eocenica,* Lauraceae (*Persea, Cinnamomum, Litsea*), *Myrica* spp., *Leucothoe protogaea* (Ung.) Schimp., *Diospyros* sp., *Sterculia kalkamanica* Makulbekov, Leguminosae gen., *Eugenia haeringiana* Ung., *Lomatia macrophylla* Makulbekov, *Echitonium* sp., *Palmophyllum* sp. and others.

Late Eocene, mixed evergreen deciduous, amber flora, Sambian peninsula, Baltic Region (Fig. 4, locality 22)

The Late Eocene flora of the Sambian peninsula (Baltic Region, Kaliningrad district) is unusual. It is represented by equal amounts of evergreen and deciduous plants. It is preserved in pieces of amber as inclusions of flowers, fruits and fragments of leaves. Fossil plant remains belong, besides angiosperms, to mosses, ferns, *Pinus* needles and reproductive organs, Cupressaceae and rare Taxodiaceae. About two hundred species of angiosperms (especially fruits and seeds) were described including evergreen Fagaceae, Lauraceae, Anacardiaceae, Hamamelidaceae, Araliaceae and others (Conwents 1886, 1890). This flora characterizes an ecotonal zone between the Boreal and Tethys realms.

Bartonian, sclerophyllous flora, Ukraine to Kazakhstan (Fig. 4, localities 5–9, 12, 13), and Turkmenia (Fig. 4, localities 10, 11)

A xerophytic Bartonian flora is distributed in the latitudinal zone from northern Ukraine through the Voronezh anticline, southern Ural and Mugodzhary to eastern Kazakhstan (Pavlodarian Irtysh River area). The localities often contain *Palibinia* (Fig. 4 – P) as an important indicator taxon. Plant remains are preserved in red cavernous quartzite sandstones and represent mostly chaotically twisted small and narrow sclerophyllous leaves of angiosperms and conifers. Empty holes in the rock resulted after plant tissues of trunks and branches decayed after being covered by eolian sands and dust-like particles. The quartzite sandstones are younger than the Late Lutetian just after the meridional marine communication between the Tethys and Arctic basins ceased. The warm current continued from Tethys to the surviving large West Siberian marine gulf separated by a land barrier from the Arctic Basin. The climate changed and monsoon summer-wet climate was replaced by seasonal winter-wet climate, similar to that of the present region of the Mediterranean.

The floral lists herein are based on (i) the author's own collection of the xerophytic flora from the Baky locality (Fig. 4, loc. 5), southern Ural, (ii) the author's revisions of other collections from Baky made by M.D. Usnadze-Dgebuadze and N.M. Makulbekov and (iii) the author's revisions of collections from neighboring areas: Mugadzhary, Emba River area and Pavlodar district (Cisirtysh area), which were studied by A.N. Kryshtofovich, V.I. Baranov, L.Y. Budantsev, I.V. Vassiliev and V.S. Kornilova during the 1950–1970s.

After the revision, the flora contains some conifers ("*Sequoia*", "*Podocarpus*") and angiosperms, such as *Macclintockia* (= *Majanthemophyllum*), some Myricaceae, Fagaceae and Fabaceae. The typical Baky flora and other floras of the same composition from the Or' – Ilek watershed (Romankol, upper floristic layers, Zharlykap, Fig. 4, loc. 6 with *Sabal*, Fagaceae gen. (evergreen), *Leucothoë*, *Palibina* and others) and Or' River, South Urals (Fig. 4, loc. 7) with Cupressaceae and small sclerophyllous leaves Angiospermae), Mugodzhary, Pavlodar district [Takyrsor (Fig. 4, loc. 13), Zhaman Tuz (Fig. 4, loc. 12 – Makulbekov 1972] include *Athrotaxis*, ?*Doliostrobus*, Cupressaceae gen. indet, *Laurophyllum*, *Myrica*, *Rhodomyrtophyllum*, *Quercus*, *Eotrigonobalanus*, *Leucothoë*, *Majanthemophyllum*, *Leguminophyllum* (different species), *Echitonium etc*. This list can be complemented by plants which are not represented in our collection: *Palibinia* (small sclerophyll narrow lobed leaves similar to those of *Comptonia* or *Dryandra)*, *Sabal* and some others (data from N.D. Vassilevskaya). Southern Uralian and Mugodzharian species of *Palibinia* match the Badkhys *Palibinia* that Korovin (1932, 1934) described from the Bartonian Turkestan regional stage.

The Akar-Cheshme flora (Western Badkhyz, Turkmenia) (Fig. 4, loc. 10) with *Palibinia,* was discovered by N.D. Vassilevskaya (1957). Fossil plants are concentrated in thin ash layers (Andesite-dacite tuffaceus Member) underlying and overlapping marine clays with Bartonian planktonic foraminifera and nannoplankton assemblages. The Akar-Cheshme assemblage consists of different endemic ferns and angiosperms conifers are absent. There were determined by N.D.Vassilevskaya: *Blechnum akartscheschmens* Vassilevskaya, *Lastraea badchyzica* Vassilevskaya, *Polypodites nepphrotiopsis* Vassilevskaya, *Myrica dilodendrofolia* Vassilevskaya (dominant), *Carya typica* Vassilevskaya, *Banksia myricifolia* Vassilevskaya, Lauraceae (*Ocotea, Laurus*), *Amygdalus turcmenensis* Vassilevskaya, Leguminosae gen., *Anacardites badchyzicus*

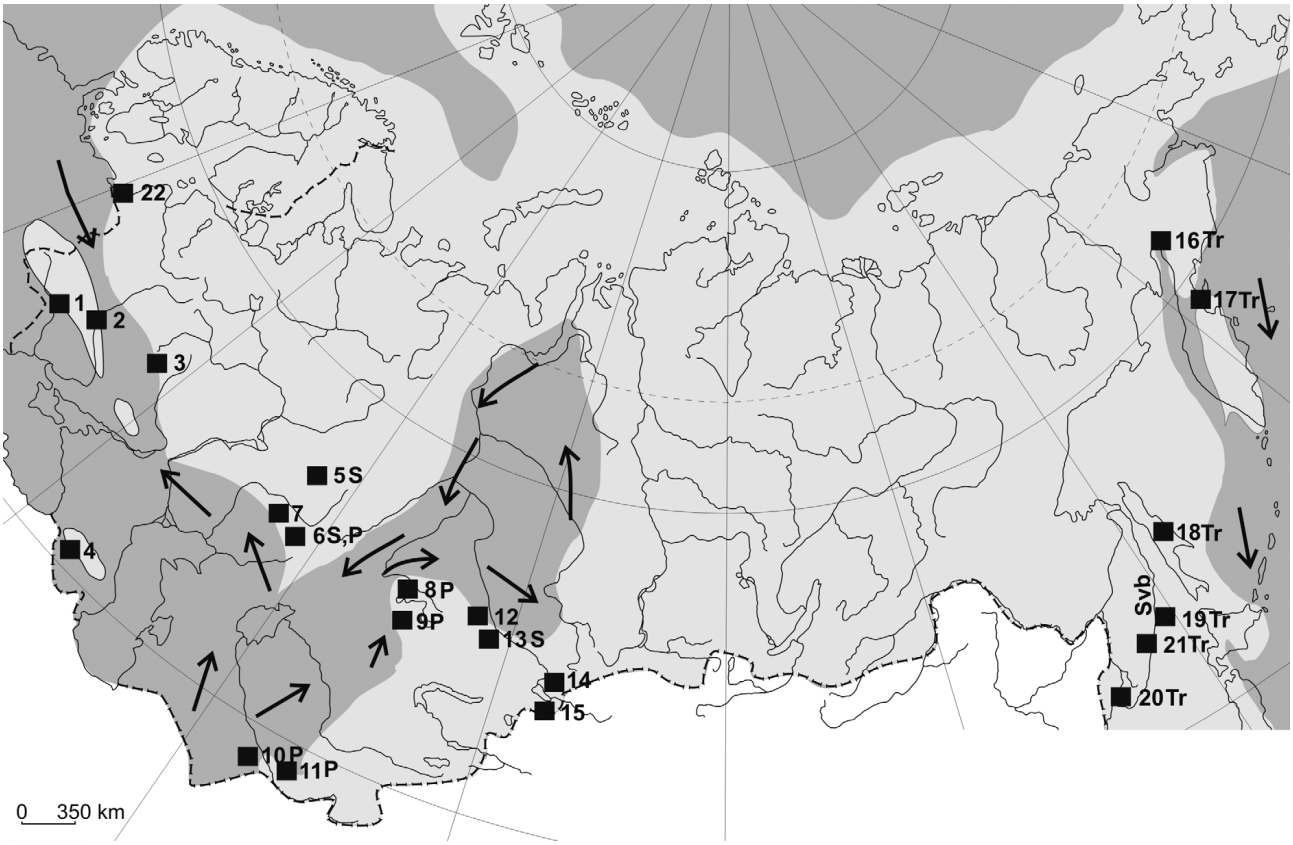


Figure 4. Late Lutetian–Bartonian. localities: 1 – Volyantschina (west of Kiev), 2 – Kiev (Lower Kiev Subformation) (N), 3 – Putivl (east of Kiev) (N), 4 – Akhaltsikhe (Georgia), 5 – Baky (Southern Ural) (S), 6 – Zharlykap (Or River Area, Southern Ural) (S, P), 7 – Or (Or River) (Southern Ural), 8 – Zhaman-Kaindy (Turgai District, Northern Kazakhstan) (P), 9 – Tortmolla (Turgai District, Northern Kazakhstan) (P), 10 – Akar-Cheshne (Western Badkhys, Turkmenia) (P), 11 – Er Oilan-Duz, Kushka district, Turkmenia) (P), 12 – Zhaman Tus (Irtysh River Area, North Western Kazakhstan), 13 – Takyrsor (Irtysh River Area, North Western Kazakhstan) (S), 14 – Tuzkabak (Zaissan Lake Basin), 15 – Kalmakpai (Zaissan Lake Basin) (Sargamyss Formation), 16 – Shestakovo (Penzhina Bay) (Tr), 17 – Podkagernaya (Western Kamchatka) (Irgirnin Formation) (Tr), 18 – Snezhinka (Western Sakhalin) (Upper Snezhinka Subformation), 19 – Sonye (Eastern Sikhote-Alin volcanic belt) (Tr), 20 – Rechnoi peninsula (northern of Vladivostok) ("Nadezhdinskaya" Formation) (Tr), 21 – Svetlovodnaya (Eastern Sikhote-Alin volcanic belt), 22 – Sambian peninsula, Prussian Formation, amber flora, Late Eocene, Svb – Sikhote-Alin volcanic belt.

Vassilevskaya, *Rhus* sp., *Zizyphus* spp., *Tetracera* sp., *Melastomites* sp., *Diospyros* sp. *Palibinia* is one of the dominant plants in this assemblage.

The Er Oilan-Duz flora (Kushka district, Turkmenia, Fig. 4, loc. 11) has the same stratigraphical position. The main components of this flora are *Palibinia* Korovin (several species), *Rhus turkomanica* (Krysht.) Korovin and *Cinnamomum* sp. Leaves of *Rhus* sp., *Zizyphus and Diospyros* were also found. Both of the Bartonian Turkmenian floras have small- and sclerophyllous leaves.

The age of some Turgaian Paleogene floras, *e.g*. the Tortmolla flora (Fig. 4, loc. 9) with *Palibinia* and *Rhus turcomanica* and the Zhaman-Kaindy flora (Fig. 4, loc. 8), originally dated to Early Oligocene (Zhilin 1989), has been revised. Zhilin (2005) changed his opinion and dated the Tortmolla flora to the Late Eocene. It is now possible to determine more precisely the stratigraphical position of the Tortmolla floristic layers. These layers overlap with Middle Eocene marine deposits with rich dinocyst assemblage (N.I. Zaporozhets, personal communication). Fossil plants are concentrated in fossil soil horizons on a red-orange crust of weathering over marine deposits. The Oligocene clays with *Chalicotherium* (V.Y. Reshetov, personal communication) overlap and cross-cut the soil horizon. Therefore, the Tortmolla flora with *Quasisequoia couttsiae*, *Palibinia*, *Rhus turcomanica*, *Leucothoë*, *Echitonium*, *etc*. is probably of Middle or Late Eocene age. The Tortmolla flora (only microphyllous) is a more xeromorphic type than the South Uralian and Cisirtyshian floras [see Fig. 2, loc. 5 – Smolino (with *Oxycarpia*), loc. 6 – Romankol, loc. 7 – Tykbutak; Fig. 3, loc. 5 – Karakol; Fig. 4, loc. 5 – Baky, loc. 6 – Zharlykap, loc. 7 – Or (All South Ural and Mugodzhary), loc. 8 – Zhaman-Kaindy, loc. 10 – Tortmolla (both of Turgai, North Kazakhstan)]. Judging according to the distribution of recent vegetation analogues of the Bartonian xerophytic plant assemblages,

the precipitation was 200–600 mm per year, and the mean summer temperatures were 22–26 °C. Zonal types of vegetation north of the Peritethys coastal plane and southern coast of the West Siberian sea were sclerophyllous woodlands with different major components and rich in shrubs (like recent maquis) with narrow-leaved Ericaceae, Myricaceae, Fagaceae, Fabaceae, Myrtaceae, and sclerophyllous conifers.

Late Eocene freshening of sea surface waters

At this time, the partly isolated West Siberian marine basin opened to the Tethys. One of the main groups for biostratigraphic dating is organic-walled phytoplankton indicating a mid to late Eocene age at the Bartonian-Priabonian transition. At the beginning of the Late Eocene surface waters of the West-Siberian inner sea and Turanian sea on the North-Eastern Peri-Tethys margin were freshened after a continental bridge formed at the southern Arctic interrupting the Arctic/Tethys connection. This process was repeated several times. At the first stage layers with *Pediastrum* were formed there, in the second stage layers with *Hydropteris indutus,* and in the third stage layers with *Azolla* (megaspores and leaves) (Akhmetiev *et al.* 2004a, b; Akhmetiev & Zaporozhets, personal observations). During the last century also impressions of leaves of *Azolla vera* Krysht. were recovered in the lower parts of the Chegan and Tavda formations (Bartonian-Priabonian transition) at many localities (Aral sea cliffs, Turgai and Irtysh areas in western Pavlodar escarpments of cuestas, West Siberia, and in South Siberian boreholes samples).

Middle and Late Eocene, mixed deciduous and evergreen floras, Zaissan Lake Basin (Fig. 4, localities 14, 15)

The Middle and Late Eocene floras of the Zaissan Lake basin are characterized by a mixture of evergreen and deciduous elements. The climate was more humid, but seasonal. Three localities of Bartonian age are known in this area: the Kalmakpai (Fig. 4, loc. 15) and Kiin-Kerish hills (same area as locality 8 in Fig. 2 with a continuous section from Late Paleocene to Oligocene) and the Tuskabak depression area (Fig. 4, loc. 14) around the Zaissan Lake. Plant remains are concentrated in variegated clays between two red weathering clayey crusts. The main components of the Mid to Late Eocene Kiin-Kerish flora (I.A. Iljinskaya and Akhmetiev, personal observations) are "*Hibiscus*" *neuburgae*, "*Hibiscus*" *kalmakpaica*, *Populus kryshtofovichii*, Fabaceae (leaves and fruits), rare *Comptonia*, small-leaved *Ulmus*, *Liquidambar*, *Celtis*, *Zelkova*, *Magnolia*, and *Ailanthus*. The richest is the Sargamyss Formation flora in the Kalmakpai area. It includes in addition *Salvinia natanella*, *Craigia*, *Lindera vassilenkoi*, and *Ungnadia*. The flora of the Tuskabak depression includes also *Dryophyllum*, *Nitophyllites* and *Alnus*.

The Late Eocene flora of the Turanga Formation (Kiin-Kerish hill) was studied by Iljinskaya (1963, 1986) and Akhmetiev (1985). Thin-bedded light yellow clays and thin sands (22–25 m) overlaid by variegated deposits with the Bartonian flora include three floristic layers of the Turanga flora (9, 12 and 20 m above the base of the Turanga Formation). Late Eocene swamp rhinoceros *Zaissanamynodon borissovii* and *Kiinkerishella zaissanica* (Arctocionidae) were found 2 m above the base of this section (7 m lower than the first floristic layer). In the lower floristic layer *Salvinia mildeana*, *Nelumbo*, *Zingiberites borealis* are dominant. "*Hibiscus*" *neuburgae* and *Ulmus* are rarer.

The next floristic layer (3 m further above) is formed by clays. This riparian assemblage consists of *Alnus*, *Ulmus*, *Populus arnaudii*, "*Hibiscus" neuburgae*, *Zelkova zelkovifolia*, rarely *Lindera* sp., *Myrica* sp., *Leguminosae* spp. (leaves and fruits), *Dryophyllum* spp., *Sterculia* sp., *Eucalyptus* sp. and *Apocynophyllum* sp. Several leaf beds were formed by *Ulmus* sp. and "*Hibiscus*" *neuburgae*.

The upper floristic horizon is formed by a lens of white clay just below the red soil horizon (first stage of originating crust of weathering). Fossil plants are sclerophyllous, of middle size, some also narrow-leaved. The following elements were determined: *Dryophyllum curticellense*, *D. dewalquei*, *D. krystofovichii*, *Myrica acuminata*, *Myrica* cf. *lignitum*, *Taxodium dubium*, *Lindera vassilenkoi*, *Zelkova zelkovifolia*, *Ampelopsis schischkinii*, *Fraxinus*, *Astronium ninae*, *Craigia, etc*.

Later Paleocene and Eocene floras in the Western Pacific Margin

The majority of the Western Pacific Paleogene plant localities are situated in intermontane coal bearing deposits in depressions, some of them occupying vast areas (*e.g.*, the Zeya-Bureya sedimentary basin, Amur River area) in marine coastal zones, and in sedimentary tuffaceous beds of the West Pacific volcanic belts.

The main characteristics of the East Asian floras and climate are principally different from contemporaneous floras and climate in Central and Western Russian Eurasia at middle latitudes. The East Siberian and Far East Paleogene floras belong to the Boreal realm. The composition of East Asian floras was influenced by a cold current running along the eastern coast from Beringia through Kamchatka, Sakhalin to Japan. The stability of this current was maintained by the long existing Bering Land Bridge.

Early Eocene floras of the high latitude Siberian Platform (Fig. 2, localities 9–11)

The Early Eocene climate at the northern margin of the Siberian platform was similar to the climate of the polar sea, where the surface-water temperature reached +20 °C (Backman *et al.* 2006). It was frostless or with episodic short cold winters. This is confirmed by some localities that are nowadays situated within the Arctic Circle, north of 70 N (grabens on the lower course of the Lena River (Fig. 2, locs 9, 10) and Lake Tastakh (Fig. 2, loc. 11) in the Yana and Indigirka interfluve). These floras contain remains of gymnosperms (*Ginkgo*, Pinaceae, *Taxodium*, *Metasequoia, etc.*), both deciduous broad-leaved trees (*Trochodendroides*, Platanaceae, Ulmaceae, *etc.*) and thermophilic southern migrants, such as Myrtaceae and *Liquidambar* represented by leaves and reproductive organs (Ozerov *et al.* 2006), leaves of *Magnolia*, Palmae (pollen), Loranthaceae (pollen), and Hamamelidaceae (Kulkova 1973).

Early Paleogene floras of North East Russia (Fig. 2, localities 12–14, Fig. 3, locality 11), Sakhalin (Fig. 1, locality 8) and South Primorie (Fig. 2, localities 16, 17)

The early Paleogene floras of northern Russia, like the preceding Late Cretaceous flora, were broad-leaved and existed under conditions of limited day-light during short winter days within the Arctic Circle. L.Y. Budantsev (1983, 1986, 2006) described three stages of floral evolution in the Early Paleogene of the western Kamchatka Peninsula (which he referred to as the Beringian Province of the Boreal Realm), (i) Khulgun (Paleocene), (ii) Tchemurnaut (Fig. 2, loc. 13) (Early and Early Middle Eocene) and (iii) Irgirnin (Late Eocene according to Budantsev, Middle-Late Eocene transition according to Zaporozhets *et al.* (2006) based on a dinoflagellate assemblage at the base of the Ratygin Formation which conformably overlies the plant-bearing Irgirnin Coal Formation).

The Khulgun-type flora (Palana locality, near Snatol) (Fig. 3, loc. 11) was rich with more than 70 species two thirds of which appear for the first time (Budantsev 2006). These include *Osmundastrum*, *Dennstaedtia*, *Ginkgo*, *Magnolia*, *Lindera*, *Tetracentron*, *Betula*, *Corylus*, *Alnus*, *Carpinus*, *Myrica*, *Juglans*, *Pterocarya*, *Acer*, *Hydrangea* and others. The same type of Paleocene flora is known on Sakhalin (Kama beds) containing Taxodiaceae, Ulmaceae, *Craigia*, *Trochodendroides arctica* and others (Kodrul 1999). The Tchemurnaut stage coincides with the Early Eocene major global warming. The Tkapravajam Formation flora (Budantsev 2006) includes at least 40% entire-margined leaves and a high diversity of thermophilic plants reaching 64%. Among them are *Lygodium*, *Ocotea*, *Cinnamomophyllum*, *Corylopsis*, *Platycarya*, *Camellia*, *Byttneria*, *Dombeya*, *Myrtophyllum*, Leguminosae (fruits and leaves), and others. Leaves of *Sabal* were discovered between the capes Rebro and Kengi (Fig. 2, loc. 14). A partial specimen of *Sabal* (lacking the rachis) was found by V. Volobuyeva in levels of the same age south of the mouth of the Anadyr River (North Koryakia) (Fig. 2, loc. 12). Unfortunately the specimen is now lost so the record is treated as ?*Sabal* on the map. During the Middle Eocene cooling most thermophilic plants disappeared and the Irgirnin flora corresponds to a temperate mesophilic type, with numerous conifers (*Pinus*, *Abies*, *Larix*, *Metasequoia*, *Taxodium*, *Cryptomeria*, *Cunninghamia*, *Sciadopitys*, *etc*). The appearance of *Fagus*, *Castanea* and some other modern genera, analogous to the Irgirnin flora, was recorded by the author from the Ust – Penzhina Formation (Penzhinskaya Bay, South Koryakia), in the central part of the Rarytkin Ridge (North Koryakia) (for location see Fig. 1, loc. 11 an area with both Danian and Early Eocene floras). T.M. Kodrul described a similar flora from Sakhalin (Kama River beds, Fig. 1, loc. 8) (Kodrul 1999).

In Northern Vladivostok an Early Eocene flora was found at the base of coal-bearing deposits on the Rechnoi peninsula (Uglovaya Formation, Taurichanka coal-field, Fig. 2, loc. 16). This is a typical *Metasequoia-Trochodendroides*-Platanaceae assemblage (Akhmetiev 1993). Most of the plants are concentrated in coal-bearing sandstones and silts (middle part of Uglovaya Formation). In addition to these dominants *Magnolia* sp., *Pterocarya* sp., *Zelkova kushiroensis* Oishi & Huzioka, *Nelumbo nipponica* Endo, *Hamamelis* sp., *Liquidambar* sp., *Rhus* sp. and *Plafkeria* sp. were identified.

In eastern Vladivostok in the Maikhe coal-bearing field (Fig. 2, loc. 17) some thermophillic plants [evergreen Fagaceae, Lauraceae and Leguminosae (Akhmetiev 1993)] were found at the base of the Uglovaya Formation.

Eocene warm temperate floras of the Russian Far East

The Far East flora remained warm-temperate, mesophilic and deciduous till the Late Eocene and retained some Early Paleogene morpho-genera like *Trochodendroides* or *Fagopsis*. Only during global warming at the Paleocene/Eocene boundary and in the Early Eocene did some evergreen immigrants invade into high latitudes. At that time, palms (*Sabal*) reached Western Kamchatka and Koryakia (as far as to 64° N). The boundary between the Boreal and Tethys realms was shifted northwards by 8–10° in the Far East (Akhmetiev *et al.* 2002, Budantsev 2006).

Eocene subtropical Raichikha flora (Fig. 2 locality 15, Figs 5–7)

The Lower Paleogene deposits of the Zeya-Bureya sedimentary basin include two types of floras: warm-temperate Tsagayan (Paleocene) (see section on Danian floras) and Raichikha (Eocene). The Early Eocene flora of the Raichikha coal-field (50° N) has a distinctive composition, with typically subtropical elements and including various evergreen plants (Figs 5–7). This flora was studied by T.N. Baikovskaya (1950). Later A.N. Krystofovich (1952) noticed the unusual composition of the flora. M.A. Akhmetiev (1969, manuscr.), V.V. Fedotov (1983, doctor thesis), and A.M. Kamaeva (1990) described many new taxa. The Raichikha and preceding Tsagayan floras have very few elements in common (except for some ferns, *Taxodium*, *Porosia* and Platanaceae). The Tsagayan-type flora could not be an ancestral assemblage to the Raichikha flora. The Raichikha flora includes southern elements which might have migrated from the low latitudes during the Early Eocene warming. Modern analogues of the Raichikha flora are widespread through South China and also Japan (30° N). The Raichikha flora lacks palms, but it is characterized by diverse ferns, various evergreen and deciduous angiosperms. This flora is composed of one member of Hepaticopsida, one *Equisetum*, 10 ferns, one conifer, more than 70 species of dicots (of which 44.6% have entire margined leaves) and 6 monocots. Betulaceae and *Trochodendroides* were not recovered.

Especially in aquatic and helophytic assemblages the Raichikha flora is similar to that of the Paleocene and Early Eocene Zaissan Lake basin (South East Kazakhstan) (Fig. 2, loc. 8). The Raichikha assemblage includes (Figs 5–7) *Marchantites*, *Cyclosorus*, *Osmunda*, *Woodwardia*, *Salvinia*, *Regnellidium*, *Taxodium*, *Nelumbo*, *Nuphar*, *Hibiscus*, *Limnobiophyllum*, *Zingiberopsis*, *Peltandra*, *Typha*, Lauraceae and Fabaceae along with Rhamnaceae (*Guoania*, *Ziziphus*). The Raichikha flora occupied more elevated habitats too, accompanied by ferns, such as *Lygodium* and *Anemia*. The flora includes many evergreen plants (*Magnolia*, *Ocotea*, *Neolitsea*, *Ficus*, some Fabaceae, *Myrtophyllum*, *Delavaya*, *etc*.) (see Figs 5–7).

The Raichikha flora arose in the northern part of the subtropical realm of Eastern Eurasia. In the Early Eocene the Raichikha flora suggests that the northern boundary of the subtropical zone migrated at least 20° further north relative to its present position. The Early Eocene climate was subtropical monsoon (summer wet). This is confirmed for the Raichikha Formation by active kaolinization.

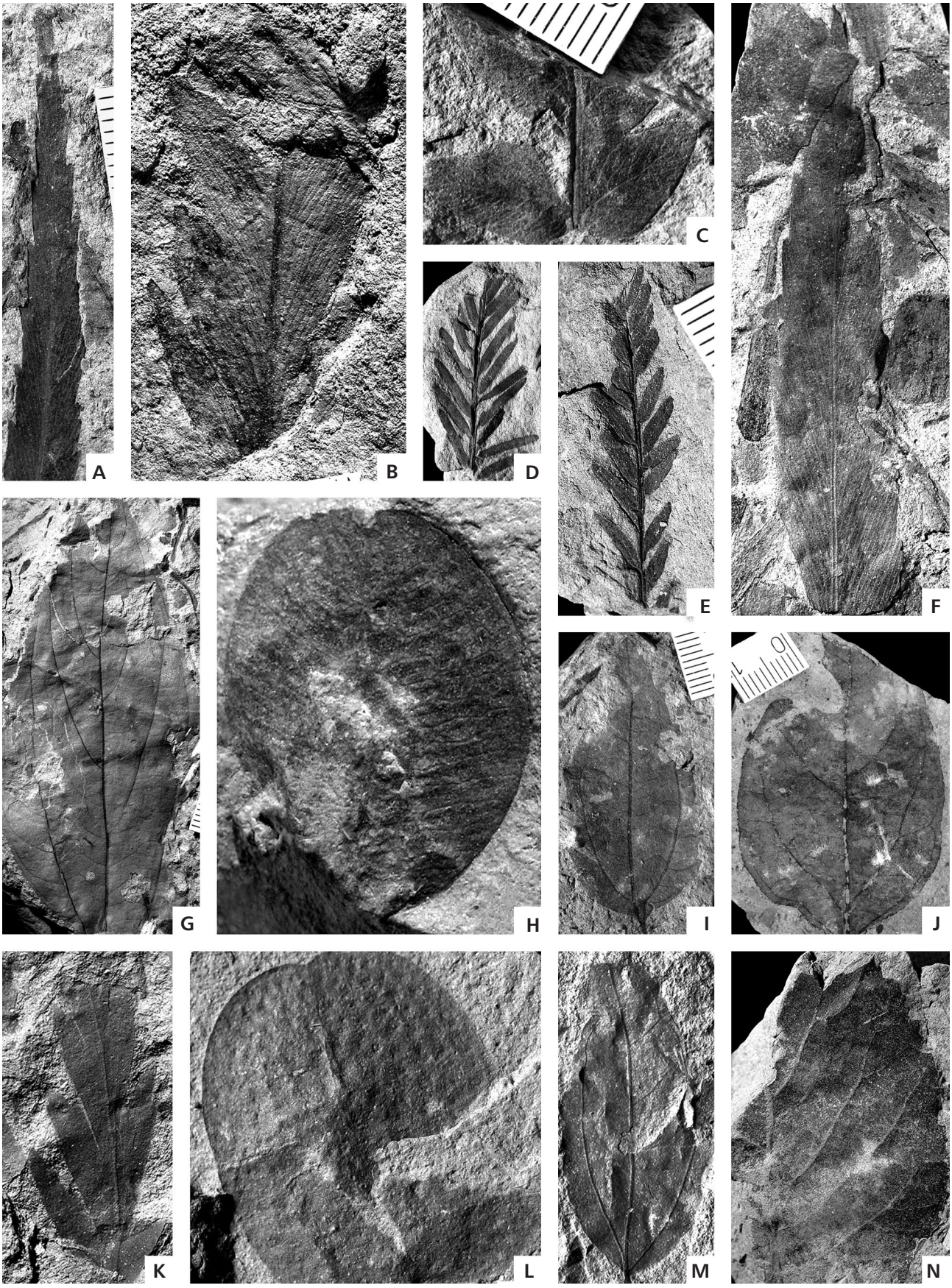
Late Ypresian and Lutetian floras of the North-Western Pacific coast (Fig. 3, localities 9–11), Sakhalin (Fig. 3, localities 12–14), Primorie (Fig. 3, locality 15)

The floras of the localities of the North-Western Pacific: Circus Mount (North Koryakia, Fig. 1, loc. 9) (Akhmetiev 1993), Kangpil Cape (Penzinsky Bay, Fig. 3, loc. 10) (Akhmetiev 1993) and Snatol River (Western Kamchatka, loc. 11) (Budantsev 1997, 2006) are similar and represent typical Late Ypresian–Early Lutetian assemblages with ferns (*Osmunda macrophylla* Penhallow, *Dennstaedtia americana* Knowlt., *Lygodium coloradense* Knowlt.), *Ginkgo kamtschatica* Budants., *Metasequoia occidentalis* (Newb.) Chaney, *Taxodium tinajorum* Heer, *Glyptostrobus europaeus* (Brongn.) Heer, *Magnolia basicordata* Fotjanova & O. Lavrenko, *Trochodendroides arctica* (Heer) Berry, *Nyssidium arcticum* (Heer) Iljinskaya, *Cocculus ezoanum* Tanai, *Nordenskioldia borealis* Heer, *Populus microdentata* Budants., *P. celastrophylla* (Baikovskaya) Sycheva, *Carpinus* ex gr. *C. japonica* Blume, *Alnus kushiroensis* Tanai, *Alnus* sp., *Fagopsis* sp., *Dryophyllum* sp., *Platanus* cf. *P. newberriana* Heer, *Craigia oregonensis* (Arn.) Kvaček, Bůžek & Manchester, "*Pterospermites*" *auriculaecordatus* Hollick, *Archeampelos acerifolia* (Heer) McIver & Basinger and others.

The flora from Due village (North-Western Sakhalin, Fig. 3, loc. 12) was first described by Kryshtofovich (1936) and Borsuk (1956). The fossils belong to the Conglomerate Formation, but mainly the Lower Due Formation (conglomerates, sandstones, silts and coal). The main components of this flora are *Osmunda sachalinensis* Krysht, *Lygodium asiaticum* Borsuk, *Ginkgo adiantoides* (Ung.) Heer, *Metasequoia occidentalis* (Newb.) Chaney, *Taxodium dubium* (Sternb.) Heer, *Glyptostrobus europaeus* (Brongn.) Ung., *Trochodendroides arctica* (Heer) Berry, various Amentiflorae (*Populus celastrophylla* Baikovskaya & Sycheva, *Myrica ovalifolia* Borsuk, *Castanea longifolia* Borsuk, *Quercus* spp., *Alnus onorica* Borsuk

Figure 5–7. Plant macrofossils showing the distinctive nature of the Early Eocene subtropical flora from Raichikha (Zeya-Bureya sedimentary basin, Amur River Area) (coll. No. 3816, Geological Institute RAS).

Figure 5. A, B, F, K – *Anemia elongata* (Newberry) Knowlton: A – No. 3816/36 (× 2), 2 – No. 3816/128 (× 2), F – No. 3816/426 (× 2), K – No. 3816/371 (× 2). • C – *Filices* sp., No. 3816/105 (× 2.5). • D, E – *Taxodium dubium* (Sternb.) Heer: D – No. 3816/59 (× 1), E – No. 3816/165 (× 2). • G – *Guoania grubovii* Fedotov, No. 3816/1996 (× 1). • H, L – *Salvinia praeaculeata* Berry: H – No. 3816/256 (× 5), L – No. 3816/27(× 5). • I, M – *Ziziphus raitschichensis* Fedotov: I – No. 3816/469 (× 1), M – No. 3816/113 (× 1). J – *Ocotea beringiana* Budants., No. 3816/345 (× 1). • N – *Morus* sp., No. 3816/150 (× 1).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and others), *Magnolia kryshtofovichii* Borsuk, *Platanus* spp., *Liquidambar europaea* A. Braun, *Vitis sachalinensis* Krysht. and others (*Sorbaria, Craigia, Zizyphus, Rhamnus, Viburnum,* Rosaceae, *Daphne, Vaccinium*). This assemblage consists of more then 40 species.

Two other floras (Western Sakhalin, Lower and Middle Snezhinka Subformations, Fig. 3, loc. 13 and South-Eastern Sakhalin, Naibuti Formation, Fig. 3, loc. 14) were studied by Sycheva (1977), Akhmetiev (1993) and Kodrul (1999). Both floras are the same age, probably Late Ypresian–Lutetian, but they are distinguished by ecological factors. The ferns are few (*Osmunda sachalinensis* Krysht., *Onoclea hesperia* R.W. Brown), gymnosperms are dominant, especially *Ginkgo adiantoides* (Ung.) Heer, *Glyptostrobus europaeus* (Brongn.) Heer, *Metasequoia occidentalis* (Newb.) Chaney, *Taxodium dubium* (Sternb.) Heer, more rarely *Pseudolarix, Sciadopitys,* Pinaceae and Cupressaceae are almost absent. The main components of angiosperms are Trochodendraceae, Platanaceae, Fagaceae, Betulaceae, Salicaceae, Ulmaceae: (*Trochodendroides arctica* (Heer) Berry*, Nordenskioldia borealis* Heer*, Platanus acutiloba* Borsuk, *P. mabuti* Oishi & Huzioka*, P. zhuravlevii* Medjul., *Castanea longifolia* Borsuk, *C. sachalinensis* Kodrul, *Fagopsis nipponica* Tanai, *Alnus ezoensis* Tanai, *A. hokkaidoensis* Tanai, *A. kushiroensis* Tanai, *Carpinus kushiroensis* Tanai, *Populus budantsevi* Ablaev, *P. celastrophylla* (Baikovskaya) Sycheva, *P. gigantophylla* Budants., *Ulmus ezoana* (Oishi & Huzioka) Kodrul, *U. harutoriensis* Oishi & Huzioka, *Zelkova kushiroensis* Oishi & Huzioka). Tiliaceae are represented by *Craigia oregonensis* (Arnold) Kvaček, Bůžek & Manchester, *Plafkeria basiobliqua* (Oishi & Huzioka) Tanai, various Rosaceae, Aceraceae, Anacardiaceae, Vitaceae (*Crataegus* sp., *Rubus fretalis* Borsuk, *Acer* cf. *kushiroanum* Tanai, *Acer* cf. *palaeoplatanoides* Endo*, Acer* spp. (fruits), *Cotinus* sp., *Rhus angustifolia* Kodrul, *Vitis sachalinensis* Krysht., *Vitis* spp.) and others (more than 100 species). More warmer elements of these floras are *Byttneria iizimae* Tanai, *Kleinhovia basitruncata* (Oishi & Huzioka) Tanai, *Ficus spiculifolia* Nagai, *Phytocrene* sp. A more ancient element of these floras is *Archeampelos acerifolia* (Heer) McIver & Basinger.

The flora from the lower part of the coal-bearing Uglovaya Formation (Artjem coal-field) (Fig. 3, loc. 15) consists of typical Early and Middle Eocene components (*Ginkgo,* Taxodiaceae, *Trochodendroides,* Platanaceae, Ulmaceae, ancient Amentiferae). There are more often Hamamelidaceae (*Hamamelis, Fothergilla, Corylopsis*), Lauraceae (*Sassafras, Daphnogene*) and Magnoliaceae (Akhmetiev 1993).

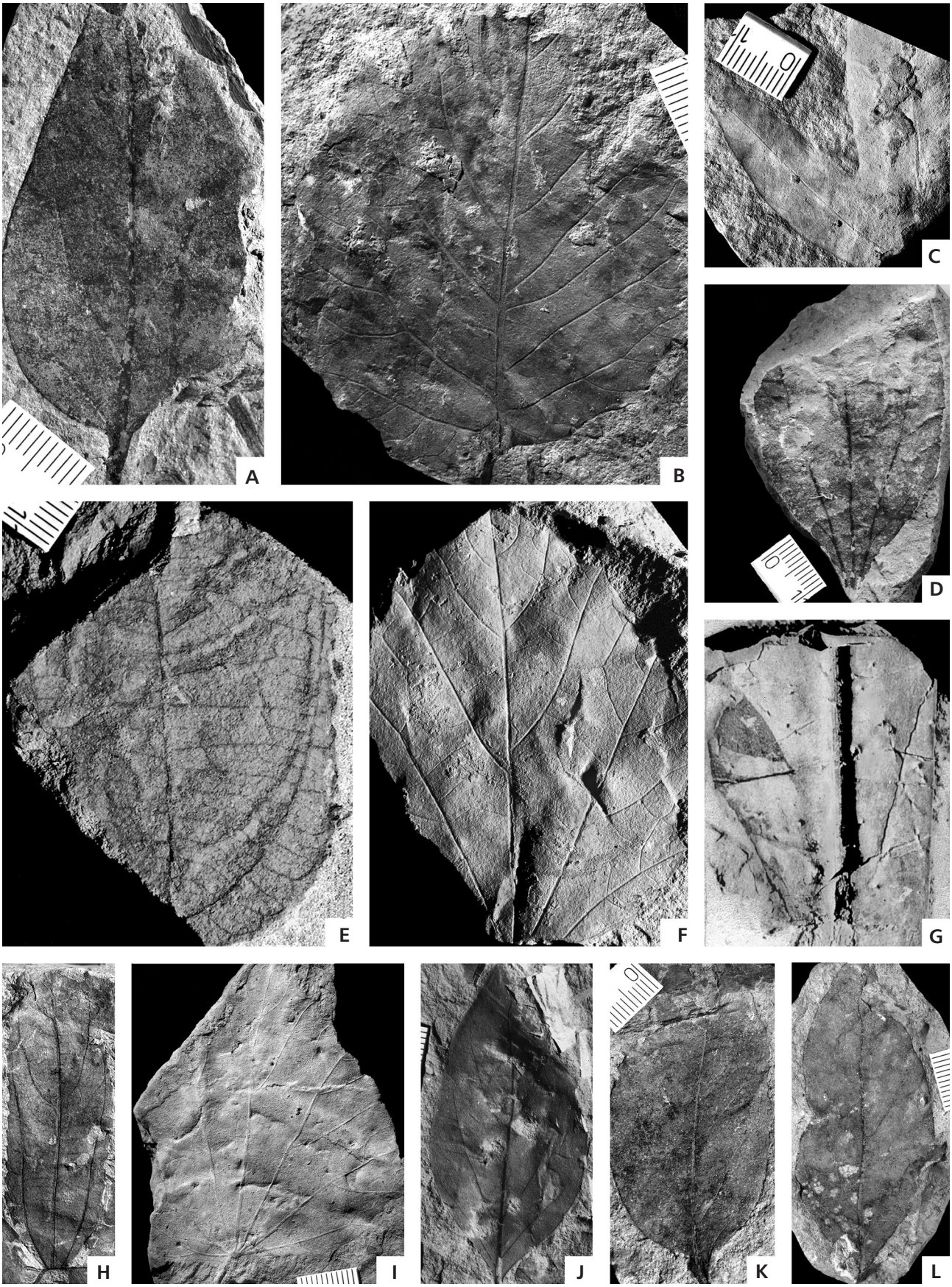
Late Lutetian–Bartonian warm temperate to temperate floras of the North-Western Pacific coast (Fig. 4, localities 16, 17), Sakhalin (Fig. 4, locality 18), South Primorie (Fig. 4, locality 20)

On the North-Western Pacific coast there are several localities. Shestakovo (Fig. 4, loc. 16) on the south coast of Penzhina bay is situated between the mouth of the Shestakovo River and Lovaty Creek. Plant fossiliferous strata contain interbedded silts and siltstones, coals and coaly silts, rare sandstones (300 m), thin coal and coaly clays lenses and diatomitic clays with marine diatoms, probably Middle Eocene. Coaly clays and silts include fossils (leaves, seeds, fruits, sometimes conifer woods).

This flora was studied by Kryshtofovich (1958), Ablaev (1985), and Akhmetiev & Bratsteva (1989). The authors collections include more than 20 species – typical elements of the Middle Eocene North-East Asia floras: *Equisetum arcticum* Heer, *Dennstaedtia americana* Knowlt., *Osmunda macrophylla* Penh., *Ginkgo* ex gr. a*diantoides* (Ung.) Heer, *Picea* sp. (seeds), *Pinus* sp. (leaves), *Pinus* sp. (seeds), *Pseudolarix* sp. (bractea), *Taxodium tinajorum* Heer, *Metasequoia occidentalis* (Newb.) Chaney*, Sequoia* sp., *Glyptostrobus europaeus* (Brongn.) Heer, Cupressaceae gen., *Magnolia praekobus* Budants., *Trochodendroides arctica* (Heer) Berry, *Nyssidium arcticum* (Heer) Iljinskaya, *Alnus protophylloides* Budants. & Golovneva, *Myrica beringiana* Budants., *Juglans pogozheviii* Chelebaeva, *Craigia oregonensis* (Arnold) Kvaček, Bůžek & Manchester, *Acer* sp., *Aesculus magnifica* (Knowlt.) Iljinskaya, *Archeampelos acerifolia* (Newb.) McIver & Basinger [= "*Acer*" *arcticum* (Heer) R.W. Brown], *Cissites ochotensis* Krysht.

The Irgirnin assemblage is very similar to that from Shestakovo. L.Y. Budantsev described the flora from Podkagernaya Bay on the coast (Fig. 4, loc. 17), but it is probably younger, late Middle Eocene–(?)Late Eocene. It includes *Cercidiphyllum intermedium* Budats., *Ulmus compacta* Fotjanova, *Liquidambar brevilobata* Budants., *Fagus napanensis* Fotjanova, *Castanea kamtschatica* Fotjanova, *Juglans protocinerea* Iljinskaya & Budants. Most of the components are the same as Shestakovo (*Equisetum arcticum, Dennstaedtia americana, Ginkgo* ex gr. *adian-*

Figure 6. A, J–L – *Ocotea beringiana* Budants.: A – No. 3816/571 (× 1.2), J – 3816/179 (× 1), K – No. 3816/387 (× 1), L – No. 3816/406 (× 1). • B – ?*Tilia* sp., No. 3816/486 (× 1). • C – *Lindera rajczichensis* Fedotov, No. 3816/215 (× 1). • D – *Neolitsea rajczichensis* Fedotov, No. 3816/443 (× 1). • E, H – Urticaceae gen. et sp. indet.: E – No. 3816/192 (× 1), H – No. 3816/201 (× 1). • F, I – *Hibiscus* sp.: F – No. 3816/276 (× 1.5), I – No. 3816/209 (× 1). • G – *Zingiberopsis magnifolia* (Knowlton) Hickey, No. 3816/101 (× 1).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toides (Ung.) Heer, *Metasequoia occidentalis, Glyptodtrobus europaeus, Trochodendroides* ex gr. *arctica, Alnus protophylloides* (Budantsev 1997).

The late Middle Eocene floristic section of Middle Sakhalin, situated near Uglergorsk town (Snezhinka River basin) (Fig. 4, loc. 18) is very important. The late Middle Eocene Upper Snezhinka subformation represents coals, coal bearing silt and siltstones and rare sandstones (300 m). The fossil leaves and fruits are smaller in size than in the Kamchatka-Koryakia region, but the taxonomic composition is similar (Akhmetiev 1993, Kodrul 1999). T.M. Kodrul described 36 species, mostly warm-temperate elements. There are 6 ferns: *Osmunda, Dennstaedtia, Dryopteris, Lastrea, Onoclea, Woodwardia.* Conifers (not more then 10% specimens) are represented by *Pseudolarix*, *Glyptostrobus*, *Metasequoia*, *Taxodium*. Angiosperms (more than 20 species) include *Trochodendroides arctica* (Heer) Berry, *Nyssidium arcticum* (Heer) Iljinskaya, *Platanus* sp., various Amentiferae (*Alnus ezoensis* Tanai, *A. ishikariensis* Tanai, *Alnus* spp. (leaves and catkins), *Betula* sp., *Corylus palaeomaximovicziana* (Endo) Tanai, *Myrica vindobonensis* (Ett.) Heer, *Populus celastrophylla* (Baikovskaya) Sycheva, *P. gigantophylla* Budants, *P. grandifolia* Endo), some Ulmaceae and Rosaceae, *Archeampelos acerifolia* (Heer) McIver & Basinger, *Acer* sp., *Euonymus denticulata* Kodrul and others. Some of the species was described by Tanai (1967, 1970) from Hokkaido.

The Middle Eocene floristic layers were studied on Rechnoi peninsula (north of Vladivostok) (Fig. 4, loc. 20). The terrigenous Nadezhdinskaya Formation (predominantly silts and siltstones with rare sandstones) is subdivided into three members (Akhmetiev 1993). The Lower Member contains rare fossil plants [*Dryopteris* sp., *Metasequoia occidentalis* (Newb.)] Chaney, *Ulmus* sp., *Populus iljinskaja*a Akhmetiev, *Platanus* sp., Lauraceae gen. The Middle Member has a richer floristic assemblage. It includes *Metasequoia* and *Trochodendroides* (dominants), *Magnolia* sp., *Alnus* cf. *protohirsuta* Endo*, Ostrya* sp., Juglandaceae gen., *Ulmus* ex gr. *longifolia* Ung., *Zelkova kushiroensis* Oishi & Huzioka, *Hamamelis* sp., Leguminosae gen., *Cinnamomum* sp., *Cedrela* sp., *Plafkeria* sp. The Upper Member is the main floristic horizon. The dominant elements are M*etasequoia occidentalis* (Newb.) Chaney, *Populus iljinskajae* Akhmet., *Zelkova zelkovaefolia* (Ung.) Bůžek & Kotlaba, *Platanus aceroides* Goepp., *Laurophyllum* sp. The rarer elements are *Trochodendroides arctica* (Heer) Berry, *Nordenskioldia borealis* Heer, *Liquidambar miosinica* Hu & Chaney, *Cinnamomum* sp. and *Plafkeria* sp. The rarest elements are *Osmunda sakhalinensis* Krysht., *Ginkgo adiantoides* (Ung.) Heer, *Pinus* sp., *Taxodium dubium* (Sternb.) Heer, Zingiberaceae gen., *Magnolia* sp., *Carpinus* ex sect. *Eocarpinus, Celtis* sp., Leguminosae gen., *Hamamelis kushiroensis* Tanai, *Vitis* sp., *Tilia eojaponica* Endo, *Mallotus hokkaidoensis* Tanai, *Rhus* sp., *Fraxinus* sp. The floristic assemblage is characterized by small leaves (up to 3–5 cm long) linked to a winter wet climate.

Paleocene and Eocene floras of the Sikhote-Alin volcanic belt (Fig. 1, localities 7–10, Fig. 4, localities 19, 21)

The Sikhote-Alin volcanic belt is limited to the east by the Tatarian strait and the coast of Japan. The belt experienced two stages of volcanic activity: Senonian-Paleocene and late Middle Eocene-Early Miocene. These volcanic sequences are separated by gaps. In the southern part of the volcanic belt sedimentary lenses with floras accumulated in intermontane valleys and small lake depressions above the sea-level (Takhobe and Zerkalnaya localities, Fig. 1, locs 9, 10). In the northern part (Malo-Mikhailovka locality, Fig. 1, locs 7, 8) fossiliferous layers accumulated in swampy depressions near volcanoes. Their Danian or Selandian age is based on radiometric data and comparisons of these floras with the Tsagayan floras in the Zeya-Bureya depression. Most typical common elements are *Ginkgo*, *Taxodium*, *Cupressinocladus*, *Trochodendroides*, *Nyssidium*, *Nyssa*, *Tiliaephyllum*, platanoids *etc*. Elements which differ from the typical Tsagayan flora are diverse conifers, various Amentiferae *e.g.*, *Alnus* and *Betula* (fruits and leaves) (Takhobe and Zerkalnaya localities), *Corylites* and *Palaeocarpinus* (Malo-Mikhailovka locality), Juglandaceae and *Fagopsis* (Takhobe). *Ulmus furcinervis* is a common component of the Kivda flora (Bureya River Area, Fig. 1, loc. 5 same locality as Tsagayan flora) and the main dominant in the Takhobe and Zerlalnaya floras. *Sorbus* and *Davidia* also occur there. These Paleocene assemblages typically have leaves and fruits of large size. Lignites and coaly clays at the Malo-Mikhailovka locality accumulated in swampy depressions and small river systems and yielded *Muscites*, *Equisetum*, *Onoclea*, *Dennstaedtia*, *Asplenium*, *Ginkgo*, *Fokieniopsis*, *Cryptomerites*, *Amurocyparis*, *Palaeocarpinus*, *Corylites*, *Trochodendroides*, *Trochodendrocarpus*.

The oldest Eocene floras of the Eastern Sikhote-Alin basaltic belt are found on the north coast at Sonye Bay (Fig. 4, loc. 19), 200 km south of Sovietskaya Gavan town. Thin ash lenses between basaltic flows (Kizi Group) contain different gymnosperms (more than 50% of specimens) [*Ginkgo, Pinus, Picea, Metasequoia, Taxodium, Glyptostrobus, Cryptomeria, Metasequoia, Taxodium, Cunninghamia, Torreya,* (?)Cupressaceae, (?)*Podocarpus* and others]. Angiosperms are represented by *Quercus* ex gr. *Dentatae, Fagus* sp., *Acer ezoanum* Oishi & Huzioka and

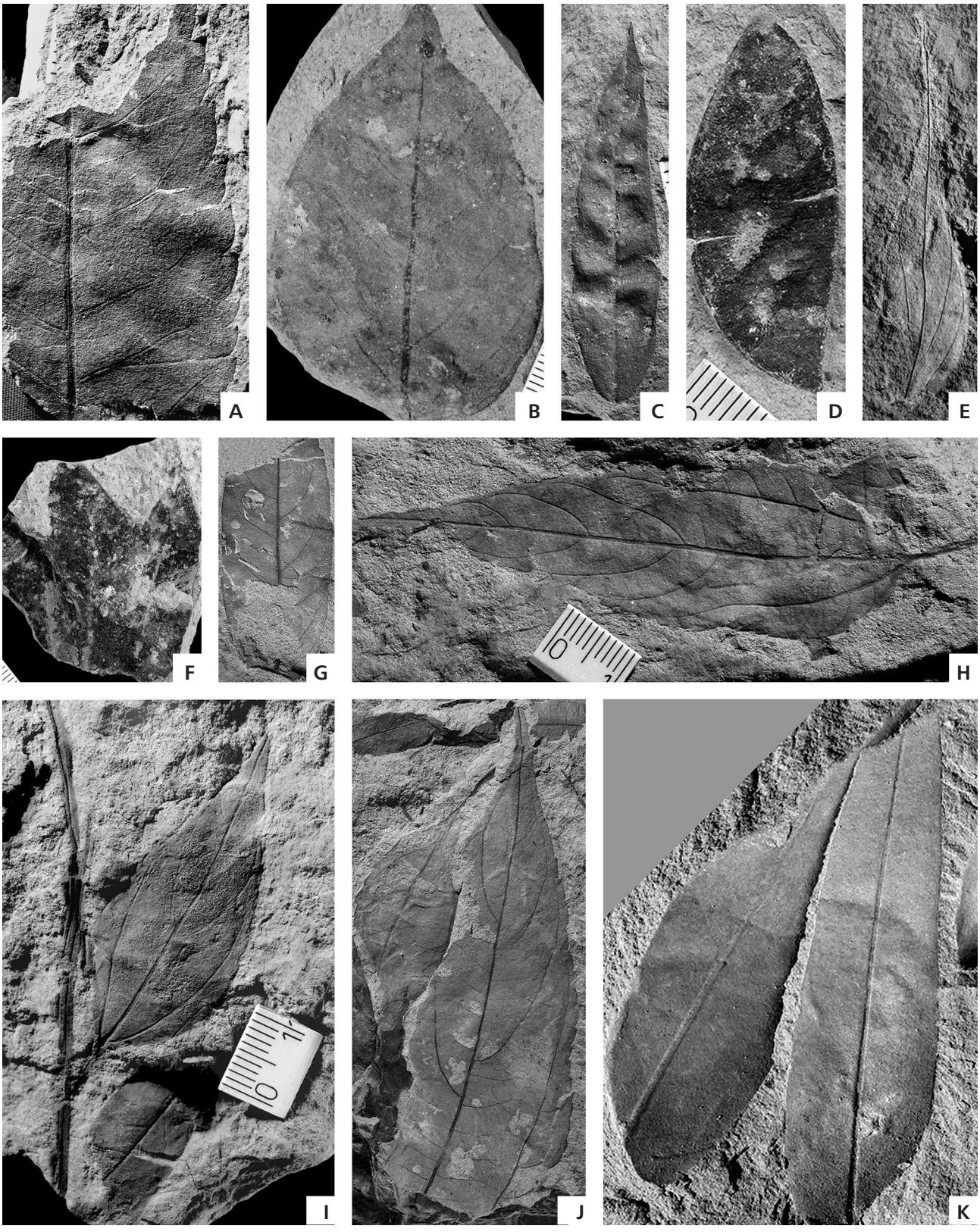

Figure 7. A – *Rhus* sp., No. 3816/70 (× 2). • B – *Ficus schimperi* Lesq., No. 3816/417 (× 1). • C – *Delavaya fraxinifolia* Fedotov, No. 3816/287 (× 2). • D – *Leguminocarpon* sp. (associated with leaves of *Stenolobium*), No. 3816/389 (× 3). • E, H, I, J – *Celtis* sp. E – No. 3816/139 (× 1), H – No. 3816/140 (× 1), I – No. 3816/178 (× 1), J – No. 3816/144 (× 1). • F – *Lindera raiczichensis* Fedotov, No. 3816/372 (× 1). • G – *Stenolobium* sp., No. 3816/6 (× 1). • K – *Leguminosites raiczichensis* Fedotov, No. 3816/251a (× 3).

others. The abundance of conifers is connected with an upland habitat of the assemblage (Akhmetiev 1993).

A very similar flora was described by Akhmetiev (1993) from near the Svetlovodnaya River valley (Fig. 4, loc. 21). This flora contains *Ginkgo*, *Metasequoia*, *Trochodendroides*, *Fagopsis*, Ulmaceae gen., *Craigia*, *Plafkeria*, *Vitis*, *Acer* and others.

Conclusions

The Paleogene floristic evolution of Russia provides a reliable proxy for coeval climatic trends and stages. The floras were mainly determined by the paleogeographic configuration and current dynamics of the N-S and W-E trending systems of epicontinental seas and straits that connected the Arctic, Tethys and Atlantic Oceans. The global regression at the Maastrichtian-Danian transition resulted in the dewatering of Northern Central Eurasian seas and straits and was accompanied by migration of deciduous mesophilic warm temperate Tsagayan ecotype flora from Eastern Asia to East and North Kazakhstan and Siberia. During the Late Paleocene and Early Eocene North Central Eurasia was included in the paratropical humid climate zone. The main fossil plant localities (Kamyshin, Romankol *etc*.) correspond to a typical paratropical Gelinden-type flora. At the PETM episode and Early-Middle Ypresian some evergreen plants migrated and reached the Arctic Siberian Coast. Thermophilic plants migrated to the north. *Sabal*, Myrtaceae and Lauraceae reached Koryakia, North Western Kamchatka. Some subtropical plants were found near the recent Polar circle. The subtropical Raichikha-type Flora lost temperate elements and, by ecological and climatic types, it is more similar to the Recent flora of South-West and South China.

In the Late Ypresian and Lutetian the latitudinal straits connecting the West Siberian Sea and the Turgai strait with the Atlantic were reduced. As a result the subtropical monsoon climate spread over North Central Eurasia. A subtropical flora, with dominant Fagaceae (especially *Castanopsis*) and Lauraceae, was developed. In the Bartonian the West Siberia sea was isolated from the Polar Basin, but a connection with Tethys still existed. The paleogeographic evolution was accompanied by a climatic change from summer-wet conditions to a winter-wet climate, which is similar to the recent Mediterranean subtropical climate characterized by dry and hot summers. *Palibinia*, *Leucothoë*, small sclerophyllous Fagaceae and other xeromorphic angiosperms together with *Quasisequoia* were the main components of this North-Central Eurasia flora. Paleocene and Eocene warm-temperate mesophilic deciduous floras were distributed at the West Pacific periphery.

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