

Morphological Variability of Leaves in "*Platanus*" *raynoldsii* Newberry from the Maastrichtian of the Koryak Highland

M. G. Moiseeva

Geological Institute, Russian Academy of Sciences, Pyzhevskii per. 7, Moscow, 109017 Russia

e-mail: herman@geo.tv-sign.ru

Received February 21, 2002

Abstract—Leaves of "*Platanus*" *raynoldsii* Newberry were widespread in the floras of the Northern Hemisphere predominantly in the Paleocene, and were also present in the Maastrichtian and Early Eocene. As in the majority of the Platanaceae, leaves of "*P.*" *raynoldsii* are highly variable, which hampers their determination and classification. A collection of fossil leaves from the Maastrichtian deposits of the Koryak Highland is represented by a monotypic series, therefore, allowing us to define the range of morphological variability in this species. A continuous series of morphological variability is described; three basic leaf morphotypes of "*P.*" *raynoldsii* are established. The variability of characters and their relationship are traced. Earlier described members of the species are revised.

Key words: Platanaceae, fossil leaves, leaf variability, monotypic series, Maastrichtian.

INTRODUCTION

For a long time, paleobotanists have focused on the members of the family Platanaceae due to the extended geological history of this family. The prominent paleobotanists Ward (1887), Newberry (1868, 1898), Knowlton (1930), Bell (1949), Brown (1962), Vakhrameev (1952, 1976), Budantsev (1975), Krassilov (1976), Herman (1994), and others studied and described these plants for more than a century. The earliest platanaceous leaves occur in the Lower Cretaceous. Their diversity and abundance increased in the Late Cretaceous, when they were prominent in forest cenoses on vast territories of the Northern Hemisphere. Modern members of the Platanaceae are assigned to the single genus *Platanus*, which embraces approximately ten species.

"*Platanus*" *raynoldsii* Newberry is widespread predominantly in the Paleocene floras of the Northern Hemisphere. It also occurs in the Maastrichtian and Early Eocene (Budantsev, 1983). The species is known from the Amur Region, the Koryak Highland, the Kamchatka Peninsula, western Canada, the United States, and Greenland.

As in the majority of the Platanaceae, the leaves of "*P.*" *raynoldsii* are highly variable. Until recently, various morphological classifications of platanaceous leaves have been based on such characters as the general leaf outline, leaf blade dissection, the number and outline of lobes, the presence of a perfoliate base, margin morphology, and the development of the infrabasal veins. (Newberry, 1898; Vakhrameev, 1952, 1976; Budantsev, 1975; Herman and Golovneva, 1988). However, the differentiation of the Platanaceae on the basis

of these characters is dampened by their high polymorphism. The more stable microstructure of the leaves and reproductive organs has suggested it as a possible basis for the Platanaceae classification (Maslova, 1997, 2001). Regrettably, the extreme scarcity of phytolite, fruit, and flower remains forces paleobotanists to deal mostly with leaf imprints. Krassilov (1976) and Maslova and Krassilov (2002) showed that reproductive organs lacking a close similarity to those of the extant plane tree often associate with typically platanaceous leaves. Since in the collection studied, this species includes only leaf imprints, while neither reproductive organs nor phytolite remains supporting the assignment to modern *Platanus* have been found, I tentatively consider the generic name as "*Platanus*."

MATERIAL AND METHODS

The plane tree specimens of the collection studied come from several localities of the upper subformation of the Koryak Formation in the region of the Amaam Lagoon (northeast of the Koryak Highland, Fig. 1). The underlying marine deposits of the lower and middle subformations contain a rich fauna of Campanian–Early Maastrichtian mollusks (Golovneva and Herman, 1992; Herman, 1993, 1999). The upper subformation contains continental deposits, mostly sandstones and tuff-sandstones, interbedded with aleurolites, carbonaceous aleurolites, and with occasional interbeds of conglomerates and coal lenses. This subformation is overlain with insignificant erosion by the Amaam Formation. Danian–Paleocene mollusk and foraminifer remains were described from the lower part of the latter

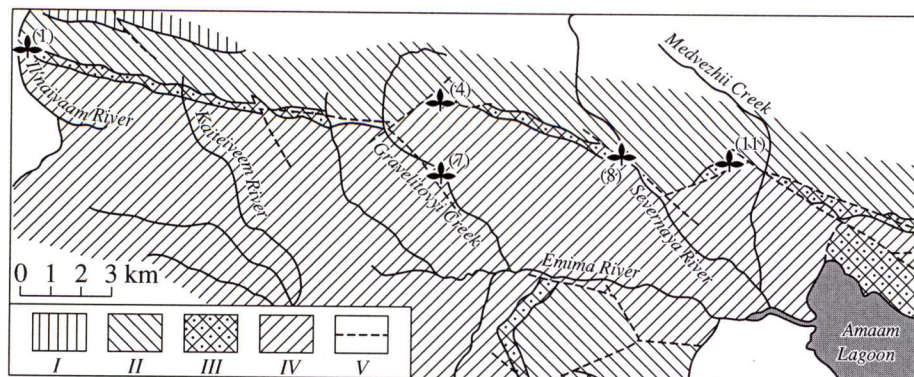


Fig. 1. Schematic geological map of the Emima–II'naivaam interflue, Amaam Lagoon region (Herman, 1999): (I) Barykovskaya Formation; (II) Lower and Middle subformations of the Koryak Formation; (III) upper subformation of the Koryak Formation; (IV) Amaam Formation; (V) ruptures; (4), (7), (8), and (11) fossil flora localities.

formation. The age of the flora-bearing deposits have been a matter of dispute for a long time. According to the latest data, it is evidently restricted to the Early (without its beginning)–Late Maastrichtian or only the Late Maastrichtian (Herman, 1999).

The collection used for the present study contains 41 specimens of the species in question and is housed at the GIN, collection no. 4843. The material includes well-preserved leaf imprints. Phytoteleims are not preserved.

The study of monotopic series, which include leaf specimens from the same layer (optimally, from the same stratification plane) and show a continuous morphological and microstructural transition, is especially important for revealing the boundaries of variability of fossil species (Meyen, 1966). In the case of monotopic series, it is possible to trace the variability of one or another character and to reveal the main unchangeable features and the most variable characters. This method is applicable for definition of “the reasonable minimal limits of the paleobotanical species” (Meyen, 1966, p. 62).

Generally, the material under consideration fits into the criteria of the monotopic series. There is a continuous transition between the marginal members of the morphological series of leaves studied, and this series lacks a remarkable accumulation of particular variants. Leaf imprints come from a narrow stratigraphic interval of a limited area. Therefore, the material enables one to show the diapason of the morphological variability of “*P.*” *raynoldsii* and revise on this basis its composition and distribution in other Asian and North American fossil floras.

Leaves of “*P.*” *raynoldsii* were photographed at a low angle incident light using a Contax 167 camera

with a S-Planar 2.8/60 macro lens. Ink drawings were made directly on printed photographs; then, the photographic images were removed with a water solution of potassium iodide and iodine. The drawings were scanned and processed with the aid of a PC using ADOBE PHOTOSHOP 6.0 and STREAMLINE.

SYSTEMATIC PALEOBOTANY
DIVISION MAGNOLIOPHYTA
CLASS MAGNOLIOPSIDA
Order Hamamelidales

Family Platanaceae Dumortier, 1929

Genus *Platanus* Linnaeus, 1753

“*Platanus*” *raynoldsii* Newberry, 1868

Plate 7, figs. 1–6; Plate 8, figs. 1–5.

Platanus raynoldsii: Newberry, 1868, p. 69; 1898, p. 109, pl. XXXV; Bell, 1949, p. 59, pl. XXXVII, fig. 2; pl. XXXVIII; pl. XXXIX; pl. XL; pl. XLI; pl. XLIV, fig. 3; Brown, 1962, p. 64, pl. XXX, figs. 1, 2, and 4; pl. XXXI, figs. 1–3, 6; pl. LXVI, fig. 8; Krassilov, 1976, p. 63, pl. XXVIII, fig. 1; pl. XXIX, figs. 3 and 5; Golovneva, 1994, p. 77, pl. XXVI, figs. 1, 3, and 4; pl. XXVII, figs. 1–3; pl. XXVIII, figs. 4–6; pl. LXV, fig. 16; pl. LXVI, figs. 10, 11, and 13.

Platanus haydenii: Newberry, 1898, p. 103, pl. XXXVI; pl. LVI, fig. 3.

Celastrus taurinensis: Ward, 1887, p. 79, pl. XXXIV, fig. 5.

Grewiopsis populifolia: Ward, 1887, p. 90, pl. XL, fig. 4.

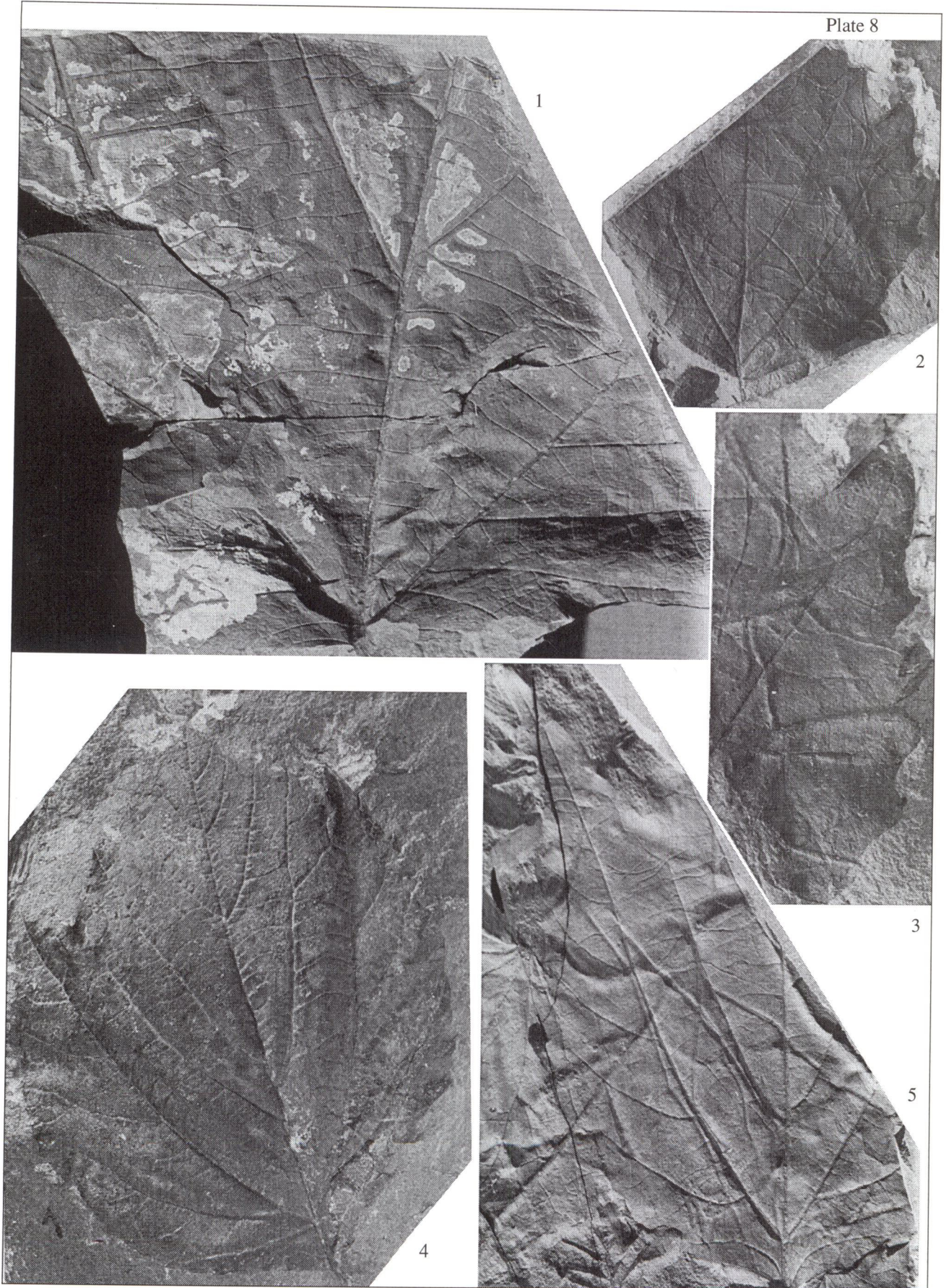
Description (Figs. 2, 3, 5, 6). The dimensions of the leaf blade broadly vary from 2.7 to 20 cm, and more, in length and 1.7–18 cm in width; leaves are small to large, large leaves dominate. Leaves are simple, trilobate, or indistinctly lobed. The lobes are variously expressed: from hardly distinct (virtually absent) lobes to distinctly defined large lobes. There are also

Explanation of Plate 7

Figs. 1–6. “*Platanus*” *raynoldsii* Newberry: (1) GIN, no. 4843/2a, leaf, morphotype 1, view, $\times 1$; (2) GIN, no. 4843/2a, leaf margin and venation in detail, $\times 3$; (3) GIN, no. 4843/87, simple leaf, morphotype 1, $\times 1$; (4) GIN, no. 4843/50/2, simple leaf, morphotype 1, $\times 1$; (5) GIN, no. 4843/419, lower part of a leaf with distinct double serration, $\times 1$; and (6) GIN, no. 4843/453b, leaf with large lateral lobes, morphotype 3, $\times 1$.

Plate 7





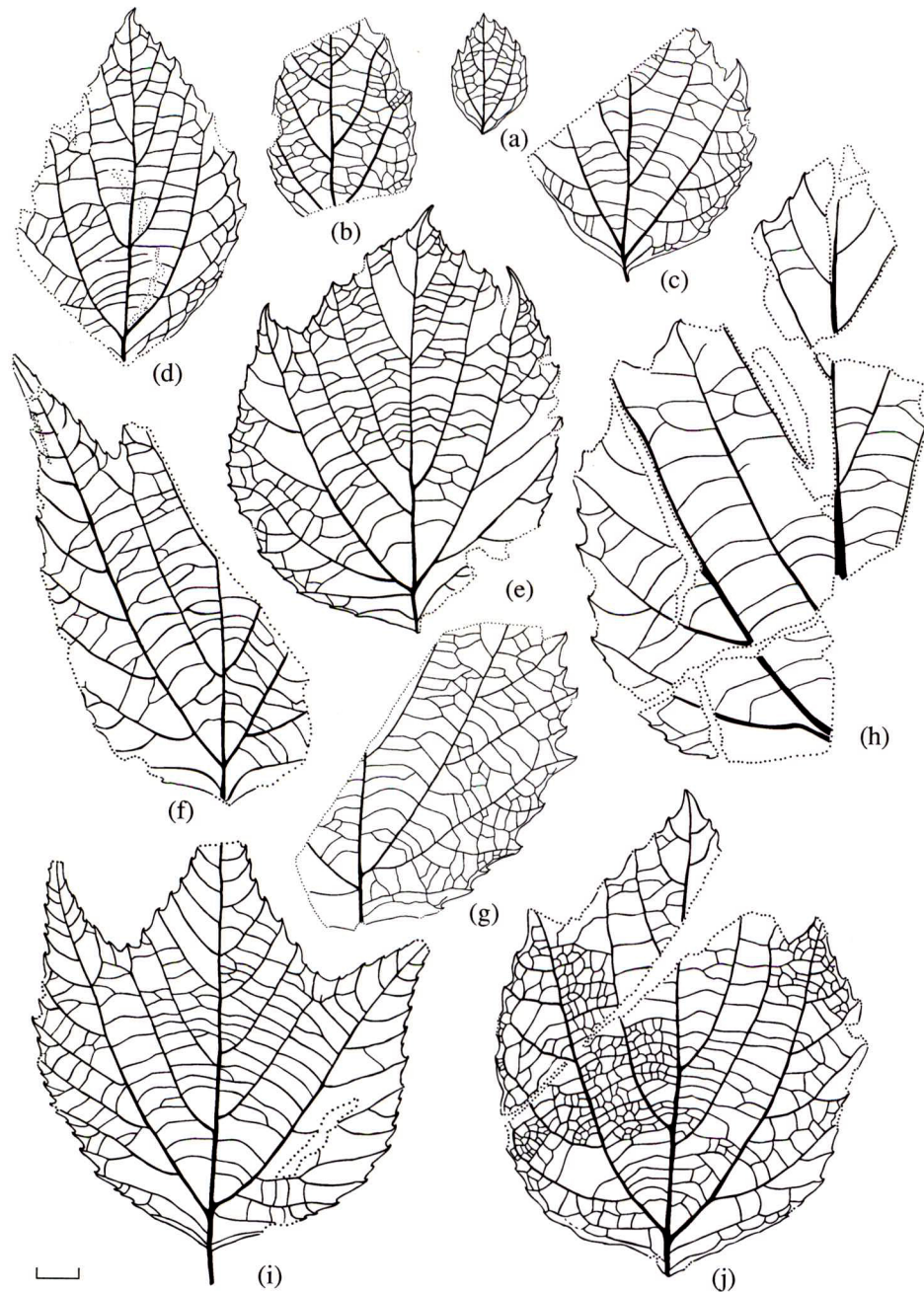


Fig. 2. Leaf morphological variability of "*Platanus*" *raynoldsii* Newberry: (a) GIN, no. 4843/50/2; (b) GIN, no. 4843/87; (c) GIN, no. 4843/86; (d) GIN, no. 4843/93; (e) GIN, no. 4843/1a; (f) GIN, no. 4843/451/3; (g) GIN, no. 4843/419; (h) GIN, no. 4843/90; (i) GIN, no. 4843/453b; and (j) GIN, no. 4843/2a. Scale bar, 1 cm.

several transitions. The middle lobe is usually larger than the lateral lobes. The lateral lobes are narrower, upward and slightly sideways directed. Leaves are symmetrical or slightly asymmetrical. The leaf outline is

variable: oval, oval-ovate, broadly ovate to obovate. The leaf base tends to be broadly cuneiform, decurrent; more rarely, it is narrowed, narrowly cuneiform, or truncate. The leaf apex is acute or slightly attenuate.

Explanation of Plate 8

Figs. 1–5. "*Platanus*" *raynoldsii* Newberry: (1) GIN, no. 4843/396, lower part of a large leaf, $\times 1$; (2) GIN, no. 4843/86, small leaf with a rudimentary lateral lobe, morphotype 1, $\times 1$; (3) GIN, no. 4843/86, margin of lobate leaf in detail, $\times 3$; (4) GIN, no. 4843/1a, leaf, morphotype 2, general view, $\times 1$; and (5) GIN, no. 4843/451/3, leaf fragment with a long lobe, morphotype 3, $\times 1$.

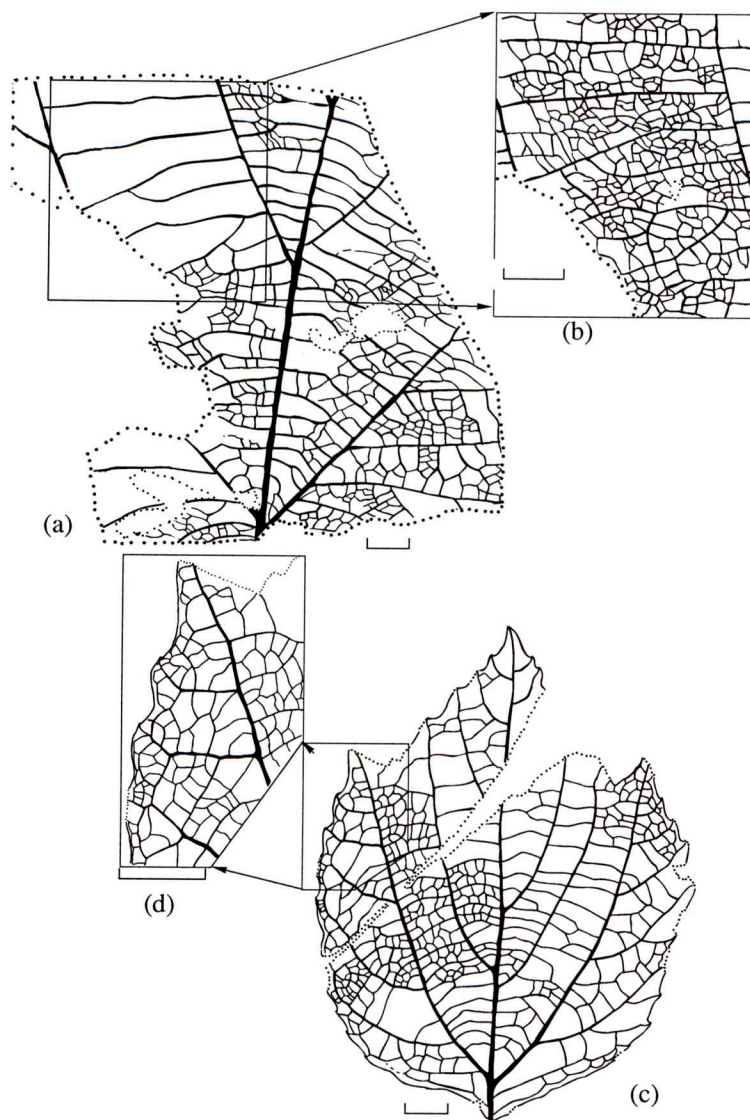


Fig. 3. The third and fourth order venation in leaves of "*Platanus*" *raynoldsii* Newberry: (a) GIN, no. 4843/396, leaf, general view; (b) GIN, no. 4843/396, venation; (c) GIN, no. 4843/2a, leaf, general view; and (d) GIN, no. 4843/2a, leaf margin venation. Scale bar, 1 cm.

The leaf margin varies from weakly undulate to serrate or crenate. Usually, the lower margin of the leaf is whole or with fine bristled teeth. Towards the upper margin, the teeth become larger and directed to the apex. Leaves with variously developed double serration are occasionally present. A quite regular alternation of larger and smaller teeth is seen in some specimens (Fig. 2g). The teeth are glandular, 1.5–4 mm high, and mostly have a broad base 4–10 mm wide. The teeth are broadly triangular and asymmetrical. The tooth apex is mostly acuminate, with a gland; more rarely it is rounded. As a rule, the apical side of a tooth is concave; the basal side is convex. The main vein ends in the tooth apex, additional veins are not preserved. Sinuses between the teeth are rounded and mostly superficial. The petiole is rarely preserved. It is up to 3.5 cm long and up to 1.8 mm wide.

The venation is palmate–peltate or palmate, craspedodromous, or semicraspedodromous. There are 5–12 pairs of lateral veins. They are alternate, occasionally, nearly opposite; among them one pair of basal veins is sharply distinct. The basal veins deviate at a distance of 0.2–1.5 cm from the leaf base at an angle of 40°–50°. They have 1 to 3 acroscopic and 5 to 9 basis-copic branches (at an angle of 25°–30°), looping in the case of an undulate margin (Fig. 2j) or ending in teeth (Figs. 2e, 2i). Some veins branch near the margin, one branch ends in a tooth, the other connects with the upper vein (Figs. 2b–2d). There are one or two pairs of infrabasal veins. They are thin, often S-shaped, usually deviating from the middle vein close to the leaf margin at an angle of 45°–50°. They tend to connect with the branches of basal veins and between themselves, forming a series of loops (Figs. 2c, 2d, 2j) or, more rarely,

ending in a tooth (Fig. 2e). There are 3–8 pairs of supra-basal veins, mostly nonbranched or with one or two basicopic distal deviations. The tertiary venation is scalariform or branching scalariform and looks like sinuous, rather loose, occasionally branching scalariform anastomoses (Fig. 3a). They deviate from the secondary veins at an angle of about 90°. The fourth order venation is orthogonal-reticulate (Fig. 3b), i.e., veins deviate at a nearly right angle. The areolas are closed, well-developed, and polygonal. Thin veins form loops near the margin (Figs. 3c, 3d).

Variability. On the basis of numerous leaf imprints of "*Platanus*" *raynoldsii*, the most constant features of this species are shown to be the outline of the base and apex, the tooth peculiarities (tooth outline and the presence of glands), venation (excluding the morphology of branches of basal veins situated near the leaf margin), and the shape and angle of the deviation of basal veins.

Certain morphological features of the species follow a regular pattern of variation, depending on each other. These are the leaf outline and dimensions, the lobe development, leaf margin morphology, and the venation pattern near the leaf margin. As was noted above, the leaf outline and dimensions broadly vary. The most characteristic outlines of the leaf blades are oval to broadly oval (or rounded), ovate or broadly ovate, and rounded obovate. The leaf is 2.7–20 cm long and 1.7–18 cm wide. The following leaf types are distinguished by the size of the lobes: almost entire leaves or leaves with slightly developed lateral lobes; leaves with small lateral lobes and a large middle lobe; and leaves with large lateral lobes, which are only slightly smaller than the middle lobe. It is important that the above three characters are clearly correlated with each other. Small leaves tend to have underdeveloped lobes and ovoid or rounded outlines (Figs. 2a, 2b). Medium-sized or large leaves with small lobes are usually ovoid or rounded oval (Figs. 2e, 2j). Leaves with well-developed lobes are always large. Due to their large lobes, the maximal width is found in the upper part of such a leaf, resulting in an obovate leaf outline (Fig. 2i).

Another correlation is observed between the leaf margin morphology and the peculiarities of the lateral veins near the leaf margin. Using these features, one can differentiate: (1) leaves with a serrate margin, well-developed large teeth, and secondary veins and their branches ending in teeth (craspedodromous venation); (2) leaves with a serrate margin, some of the secondary veins and their branches ending in teeth, others branch near the leaf margin into one branchlet ending in the tooth and another connecting with the upper vein (semicraspedodromous venation); and (3) leaves with undulate or a nearly entire margin, looping branches of secondary veins that become thinner towards the margin forming a series of loops (brochidodromous venation).

Considering the combinations of these features, one can reveal the three main leaf morphological types of "*Platanus*" *raynoldsii* (with intermediate forms).

Morphotype 1. Leaves are small or medium-sized, 2.7–8 cm long, 1.7–5.5 cm wide, slightly asymmetrical, and have entire margins or underdeveloped lateral lobes (Figs. 2a–2d). The leaf outline varies from oval or oval-ovate to broadly oval. The leaf margin is serrate. The teeth are distinct, large, glandular, and become smaller in the lower part of the leaf. The venation is palmate-pinnate, craspedodromous, or semicraspedodromous. The basal veins are well developed, with 6 or 7 basicopic branches.

Morphotype 2. Leaves are medium-sized or large, 8–19 cm long and 6–15 cm wide. The lateral lobes are distinct, small, narrow, and directed upward. The middle lobe is larger than the lateral lobes. As a rule, leaves are oval-ovate, broadly ovate to subrhomboidal, the maximal width is in the lower part of the leaf blade. The leaf margin is serrate or undulate (Figs. 2e, 2h, 2j). The venation is palmate-pinnate, craspedodromous, or semicraspedodromous. The basal veins have 7 or 8 basicopic branches and 1 or 2 acroscopic branches. The branches of basal veins end in marginal teeth or form a looplike structure in the case of an undulate margin.

Morphotype 3. Leaves are usually large, 10–13 cm long and 9–10 cm wide. The lateral lobes are large, nearly as pronounced as the middle lobe; they are narrower and upward and slightly sideways directed. The leaf outline is rounded obovate. The leaf margin is serrate, the teeth are large, well developed, and become slightly smaller toward the base (Figs. 2f, 2i). The venation is palmate-pinnate and craspedodromous. The basal veins have up to ten basicopic branches and up to six acroscopic branches.

Such a morphological variability of leaves within the same species is often present in Late Cretaceous broad-leaved angiosperms and could have different reasons (Herman, 1994). It could be related to a different position of the leaves within the tree crown or it could be explained by the seasonal development of annual shoots. A similar morphological variability of leaves is observed within a shoot of extant *P. acerifolia* Willd. (Fig. 4). Taking an annual shoot of the London plane as a model for the reconstruction of the annual shoot of "*P.*" *raynoldsii* (Fig. 5), one can suppose that early spring leaves were small, whole or with underdeveloped lateral lobes, slightly asymmetrical, oval or oval-ovate; early summer leaves were larger and had small lateral lobes and a larger middle lobe; and late summer leaves were large with maximally developed lobes.

Comparison. This species differs from *P. latifolia* described by Krishtofovich (1958) from the Paleocene of Lake Tastakh by having more sinuous basal veins and less numerous acroscopic branches of the basal veins (1–2 and 4–5 respectively). In addition, the secondary veins of "*P.*" *raynoldsii* are usually alternate, whereas those of *P. latifolia* are nearly opposite.

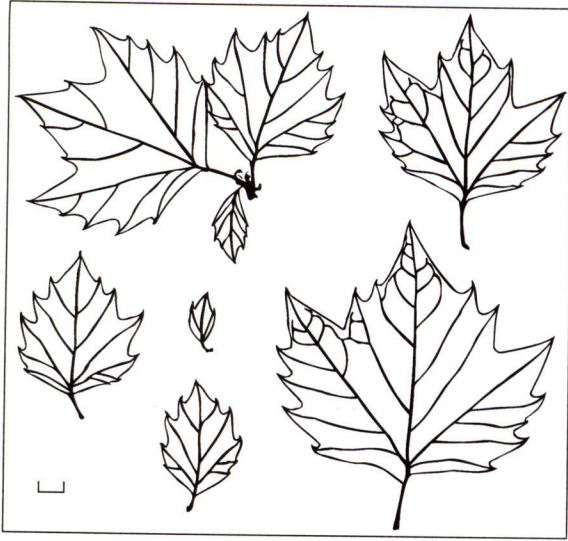


Fig. 4. Leaf morphological variability within a shoot of extant *Platanus acerifolia* Willd. Scale bar, 1 cm.

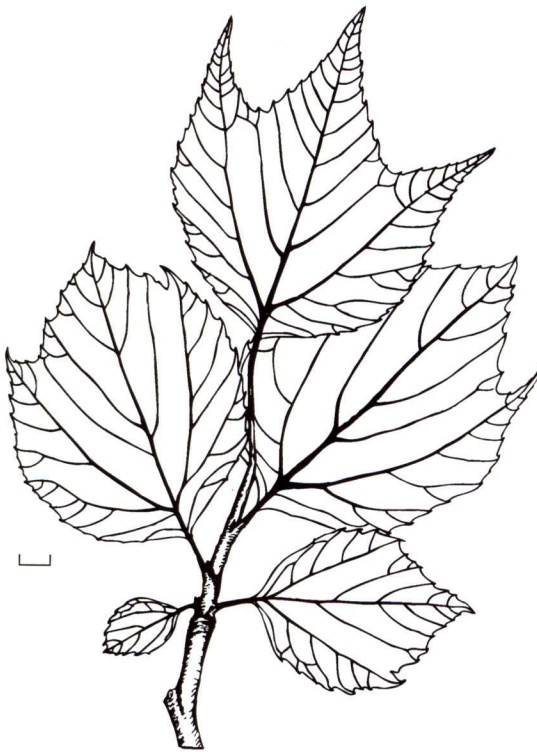


Fig. 5. Reconstructed annual shoot of "*Platanus*" *raynoldsii* Newberry. Scale bar, 1 cm.

The similarity of these species consists in their tertiary and fourth order venation, general leaf morphology, and the degree of lateral lobe development.

Leaves of "*P.*" *raynoldsii* are similar to those of *P. newberryana* described by Krassilov (1976) from the Tsaayan Flora and differ from the latter by the greater

angles of deviation of the secondary veins, their sinuous shape, not exactly opposite basal veins, and the better developed infrabasal veins.

The species studied differs from *P. cuneifolia* from the Upper Albian of Kazakhstan (Vakhrameev, 1952) by the leaf outline (from oval–ovate to subrhomboidal), an acute or slightly attenuate apex, sinuous inward basal veins, upward directed lobes, and weakly developed acroscopic branches of the basal veins. *P. cuneifolia* is characterized by a cuneiform or hexagonal leaf outline, an obtuse and weakly detached apex, straight, widely diverging basal veins with well-developed acroscopic branches. The common character of these species is relatively weakly developed lobes, although in "*P.*" *raynoldsii*, lobed leaves often occur.

The species studied differs from *P. embicola* from the Cenomanian of western Kazakhstan (Vakhrameev, 1952) by the leaf outline: the maximal width of the leaf is in the middle of the leaf blade or slightly lower, whereas in *P. embicola*, the width of the lower leaf part is 1.5 times as great as the leaf length. In addition, "*P.*" *raynoldsii* differs by concave basal veins with weakly developed or absent acroscopic branches and by the absence of branchlets deviating from the secondary veins above the basal veins. In contrast, in *P. embicola*, a pair of secondary veins immediately above the basal veins is well developed and has several basispic and acroscopic branches.

Remarks. Broadly varying from small forms without lobes to large ones with well-developed lobes, leaves of "*Platanus*" *raynoldsii* suggest that they may be members of a compound leaf, as is known in some species of *Platanites* Forbes. In particular, compound leaves are characteristics of *P. hebridicus* Forbes (Crane *et al.*, 1988; Boulter and Kvaček, 1989) and *P. canadensis* McIver et Basinger (McIver and Basinger, 1993) from the Paleocene floras of Mull Island (Scotland) and the Ravenscrag Formation (Canada) and *P. marginata* (Lesquereux) Johnson from the Maastrichtian of the Hell Creek Formation (Dakota and Montana) (Johnson, 1996). A comparison between our specimens of the second and third morphotypes and terminal leaflets of *Platanites* reveals a certain similarity, i.e., relatively large trilobate leaves with well developed lateral lobes and a toothed leaf margin. The first morphotype of "*Platanus*" *raynoldsii* (leaves lacking lobes or with rudimentary lateral lobes, occasionally, asymmetrical) could be compared to small lateral leaflets of *Platanites*, which occurred on either side of the petiole at a certain distance below the terminal leaflet base. The dimensions and outlines of these leaves are comparable, but the venation of the first and second orders is often different. Even the smallest specimens of the collection studied show palmate–peltate venation. The basal veins are sharply distinct and often end in a larger tooth. These like veins are longer and more sinuous, and have basispic branchlets, those of in specimens with well-developed lobes. As a rule, the basal veins of

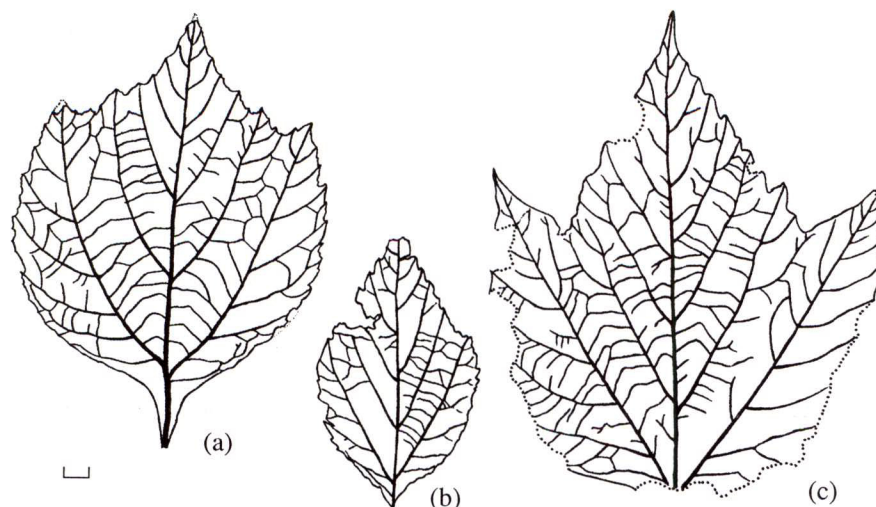


Fig. 6. Extinct members of the genus *Platanus* L.: (a) "*Platanus*" *raynoldsii* Newberry, lectotype (after Newberry, 1898, pl. XXXV); (b) *P. haydenii* Newberry (after Newberry, 1898, pl. LVI); and (c) *P. haydenii* Newberry (after Newberry, 1898, pl. XXXVI). Scale bar, 1 cm.

the lateral leaflets of *Platanites* are identical to other veins in thickness, length, and branching. It could not be completely excluded that the specimens under description were leaflets of a compound leaf. However, this assumption could be substantiated only by finding elements of a compound leaf under natural conditions.

Occurrence. Maastrichtian–Danian deposits of the Koryak Highland and Rarytkin Ridge, Danian Tsaganay Flora from the lower course of the Amur River, Maastrichtian–Paleocene deposits of North America (Fort Union, Lance, Paskapoo, Denver, and Dawson formations), and Danian deposits of Greenland.

Material. Amaam Lagoon region, upper subformation of the Koryak Formation. Point no. 1, Il'naivaam River: GIN, nos. 1/1a, 1b, 2a, 2b, 3, 50/2, 57, 71a, 71b, 76, 80, 86, 87, 88, 90, and 93/1; Point no. 4, Gravelitovy Creek, GIN, nos. 508a, 508b, 531, and 532; Point no. 7, Skalystyi Creek, GIN, nos. 117/3, 163/1, 170/2, 181a, 181b, 316, 332, 616/4b, and 616/4c; Point no. 8, Severnaya River, GIN, nos. 595, 608, and 614; and Point no. 11, Medvezhii Creek, GIN, nos. 388, 391/1, 393/1, 396, 407, 411, 416, 419, 422a, 422b, 451/3, 452, 453a, 453b, 454, 457, and 458.

COMPOSITION AND DISTRIBUTION OF "*PLATANUS*" *RAYNOLDSII* IN ASIA AND NORTH AMERICA

To reveal the variation range of the species "*Platanus*" *raynoldsii*, one should consider the ideas of different scientists concerning the volume of this species, compare the earlier described material and the collection being studied, and performed a detailed analysis of the synonymy. The variability of the monotypic series described above is used as a basis of the taxonomic revision.

Primarily, leaves of "*P.*" *raynoldsii* were defined as large, rounded or triangular leaves, more or less rounded in the lower part and trilobate in the upper part (Newberry, 1898). Lobes are small and wide and developed to a lesser extent than in the majority of other species of the genus. The leaf base is usually decurrent. Newberry paid special attention to the leaf margin morphology. As a characteristic feature of "*Platanus*" *raynoldsii*, the researcher considered the double serration with large and obtuse teeth in the upper part of the leaf and the entire margin of the leaf base. Newberry considered the venation of "*P.*" *raynoldsii* to be identical to that of extinct *P. aceroides* Goepp. and extant *P. occidentalis* L.

The specimens examined in the present study from the middle of the morphological series (morphotype 2), with medium-sized lobes (Figs. 2e, 2j) evidently resemble the lectotype of "*P.*" *raynoldsii* (Newberry, 1898, pl. XXXV) in the general shape of the leaf base, and apex; venation; and shape and dimensions of lobes (Fig. 6a).

Leaf imprints with well-developed lobes (morphotype 3) are reminiscent of the leaves described by Newberry (1898) as *Platanus haydenii* (pls. XXXVI, LVI, fig. 3). The teeth of the specimens being described are identical to those of *Platanus haydenii* in outline and dimensions, but differ by the frequent presence of small apical glands. The specimen depicted by Newberry (1898, pl. XXXVI; Fig. 6c of the present paper) has rounded teeth. However, small glands were possibly not preserved. Moreover, the other leaf of *P. haydenii* depicted by Newberry (1898, pl. LVI) exhibits teeth identical to those of the leaves under description (Fig. 6b). Other scientists (Knowlton, 1930; Bell, 1949; Brown, 1962) also questioned the validity of the species *P. haydenii*. Knowlton noticed that *P. haydenii* dif-

ferred from "*P.*" *raynoldsii* mostly by the more developed lobes. This researcher also demonstrated not double, but simple (like in *P. haydenii*) teeth in the type specimen of "*P.*" *raynoldsii*.

Ward (1887) also described "*P.*" *raynoldsii*, which was based, however, on relatively limited and poorly preserved material. The illustrations show two incomplete leaves (pl. XX). One (Ward, 1887, pl. XX, fig. 2) only vaguely resembles "*P.*" *raynoldsii*, differing from the specimens under study by the morphology of the basal and infrabasal veins and the outline and dimensions of the leaf region separated by the lowest pair of the basal veins. The second specimen (Ward 1887, pl. XX, fig. 3) possibly belongs to "*P.*" *raynoldsii*; however, it is too fragmentary to be identified with certainty. I include two specimens described by Ward as *Celastrus taurinensis* (pl. XXXIV, fig. 5) and *Grewiopsis populifolia* (pl. XL, fig. 4) in the synonymy of the species. These specimens demonstrate the same set of features as the nonlobate forms described above and fit into the variability revealed in the present study, although both specimens are incompletely preserved. I did not find in Ward's illustrations any clearly typical leaf of "*Platanus*" *raynoldsii*.

Leaves shown by Bell (1949, pls. XXXVII–XLI), having weakly developed lobes, are greatly reminiscent of morphotypes 1 and 2 of the collection under study. Like in the specimens under study, the leaves shown by Bell are usually oval or oval-ovate and without lobes, with weakly developed lobes, or with a large middle and two small lateral lobes. The only distinction of the material from western Alberta is the absence of leaves with well-developed lobes.

Brown (1962) treats the species "*P.*" *raynoldsii* in a broad sense. This author gave a comprehensive synonymy (Newberry, 1898; Lesquereux, 1978, 1883; Knowlton, 1917, 1930; Ward, 1887; Bell, 1949; etc.), which includes various species and generic names and is reflected by the great variability of plane tree leaves. This paper also contains illustrations of well preserved plane tree leaves greatly resembling the specimens under study. There are nonlobate leaves similar to those under study, leaves with weakly developed lobes (identical to morphotype 2), and even leaves with more developed lobes, which are, however, smaller than those of morphotype 3.

Only three specimens among those shown by Brown (1962) should not be included in the synonymy of "*P.*" *raynoldsii*. The leaf imprint shown by Brown (1962, pl. XXX, fig. 3) differs from the specimens under study by the absence of lobes in large leaves and in the relatively numerous and densely spaced suprabasal veins. The assignment of the specimen from pl. XXXI, fig. 4 to "*P.*" *raynoldsii* is also doubtful because of its pentagonal outline and different morphology of the leaf region delineated by the lowest pair of basal veins. The specimen shown in pl. XXXI, fig. 5 differs by the close positions of the basal veins to the truncate base.

Krassilov (1979) and Vakhrameev (1981) discussed the species variability of "*P.*" *raynoldsii* in connections with the angiosperm diversity in the Late Cretaceous. Vakhrameev believed that the extended approach to this species used by Krassilov, namely, the fusion of morphologically different leaves within one and the same species led to underestimation of angiosperm diversity. Considering the problems of classification of extinct plane trees, Vakhrameev (1952) notices that the leaf polymorphism of extant plane trees suggests that some extinct species are only leaf morphotypes rather than species in the sense accepted in modern botany. Nevertheless, he believed that methodologically it is expedient to establish extinct plane tree species on the basis of the leaf shape than to combine various forms from different distant regions of the earth in the same species, based only on the presence of transition forms between rather different fossil material (Vakhrameev, 1952, p. 204).

Describing "*P.*" *raynoldsii* from the Tsagayan Flora of the Amur Region, Krassilov (1976) emphasizes that fossil leaves of plane trees can be classified only tentatively because of a wide range of their variations. He states, however, that the mode of variation can be taken as the basis of species diagnostics (Krassilov, 1976, p. 64). The material described by Krassilov significantly differs from the material being described under description in its mode of variation and, especially, in the extreme members of the series. Leaves, shown in pls. XXVI, XXVII, XXVIII, fig. 2; and XXXI, figs. 1–3 (Krassilov, 1976) exhibit a range of features, lacking in the specimens under study. For instance, although the leaves are relatively large, lobes are absent; the leaf base is cordate or peltate, with the basal veins located close to the leaf base; the outline of the leaf region delineated by the lowest pair of the basal veins is substantially different; and the suprabasal veins repeatedly branch basiscopically. Small leaves from the Tsagayan Flora show certain similarities to morphotype 1 but differ in the following features: the basal veins diverge close to the leaf base, they are shorter than the next (upper) pair of the suprabasal veins; leaf regions delineated by the lowest pair of the basal veins are narrower and shorter; the infrabasal veins are often absent or a single vein is present, the suprabasal veins are positioned more densely and they are more numerous, often opposite and basiscopically branching; and the leaf margin is usually finely and densely toothed.

Among all the leaves described by Krassilov (1976), the leaf shown in pl. XXVIII, fig. 1 is the single leaf evidently similar to the specimens under study, although its basal veins diverge from the leaf base and slightly turn outwards. I believe that the leaves shown in pl. XXIX, figs. 3 and 5 (Krassilov, 1976) supposedly belong to "*Platanus*" *raynoldsii* and are included here in the synonymy of this species.

The material from the Maastrichtian–Danian floras of the Koryak Highland (Golovneva, 1994) is one of the closest to the present material in geological age and

geographical position. Plane trees assigned here to morphotypes 2 and 3 (medium-sized and large leaves with well-developed lobes) are especially frequent in Golovneva's collection. Unlike the present material, the collection described by Golovneva lacks morphotype 1, i.e., small or medium-sized, oval, and nonlobate leaves (Figs. 2a, 2b).

CONCLUSIONS

The analysis of published descriptions of "*Platanus*" *raynoldsii* allows one to conclude that, in spite of the wide distribution of this species and the fact that it has been studied for over a century the range of its morphological variability remains incompletely revealed. Different authors treated this species differently, using different characters of plane tree leaves as the basis of classification. Initially, the extreme forms of this species were assigned to different taxa.

I described a continuous series of variation, which includes specimens from a narrow stratigraphic interval and a limited territory. The material represents a monotypic series and, therefore, is optimal to the most complete study of the morphological variability of "*P.*" *raynoldsii*.

Particular characters of the plane tree and their variability and relationships were traced. Three main leaf morphotypes of "*Platanus*" *raynoldsii* were recognized. The composition of the characteristic features of these morphotypes was analyzed.

The comparison between the material studied and that earlier described collections allowed us to revise the composition and distribution of "*P.*" *raynoldsii* in other fossil floras of Asia and North America.

ACKNOWLEDGMENTS

I am grateful to A.B. Herman (GIN) for lending material, discussion of the manuscript, and assistance in making photographs; to M.A. Akhmetiev (GIN) and N.P. Maslova (Paleontological Institute of the Russian Academy of Sciences) for valuable discussion; and to A.I. Nazarov (GIN) for making photographs.

REFERENCES

- Bell, W.A., Uppermost Cretaceous and Paleocene Floras of Western Alberta, *Can. Geol. Surv. Bull.*, 1949, no. 13, pp. 1–231.
- Boulter, M.C. and Kvaček, Z., *The Palaeocene Flora of Isle of Mull*, London: Palaeontol. Ass., 1989.
- Brown, R.W., Paleocene Flora of the Rocky Mountains and Great Plains, *Geol. Surv. Prof. Pap.*, 1962, no. 375, pp. 1–119.
- Budantsev, L.Yu., Comparative Morphology of Leaves and the Taxonomy of the Genera *Protophyllum* Lesq. and *Pseudoprotophyllum* Hollick, in *Voprosy sravnitel'noi morfologii semennykh rastenii* (Questions of Comparative Morphology of Seed Plants), Budantsev, L.Yu., Ed., Leningrad: Nauka, 1975, pp. 90–107.
- Budantsev, L.Yu., *Istoriya arkticheskoi flory epokhi rannego kainofita* (The History of the Arctic Flora from the Early Cenophytic), Leningrad: Nauka, 1983.
- Crane, P.R., Manchester, S.R., and Dilcher, D.L., Morphology and Phylogenetic Significance of the Angiosperm *Platanites hebridicus* from the Palaeocene of Scotland, *Palaeontology*, 1988, vol. 31, part 2, pp. 503–517.
- Golovneva, L.B., *Maastrikht–datskie flory Koryakskogo nagor'ya* (The Maastrichtian–Danian Floras from the Koryak Plateau), Petersburg: Botan. Inst. Ross. Akad. Nauk, 1994.
- Golovneva, L.B. and Herman, A.B., New Data on the Composition and Age of the Flora from the Koryak Formation (Koryak Highland), *Botan. Zh.*, 1992, vol. 77, no. 7, pp. 60–71.
- Herman, A.B., The Late Maastrichtian Flora from the Emima–Il'naivam Interfluvium (Northeastern Koryak Highland) and Its Stratigraphic Significance, *Stratigr. Geol. Korrelyatsiya*, 1993, vol. 1, no. 4, pp. 64–72.
- Herman, A.B., The Diversity of the Cretaceous Platanaceae from the Anadyr–Koryak Subregion with Special Reference to Climatic Changes, *Stratigr. Geol. Korrelyatsiya*, 1994, vol. 2, no. 4, pp. 62–77.
- Herman, A.B., The Cretaceous Flora from the Anadyr–Koryak Subregion (Northeastern Russia), *Tr. Geol. Inst. Ross. Akad. Nauk* (Moscow), 1999, vol. 529, pp. 1–122.
- Herman, A.B. and Golovneva, L.B., A New Genus of the Late Cretaceous Platanaceae from the Northeast of the USSR, *Botan. Zh.*, 1988, vol. 73, no. 10, pp. 1456–1468.
- Johnson, K.R., Description of Seven Common Fossil Leaf Species from the Hell Creek Formation (Upper Cretaceous: Upper Maastrichtian), North Dakota, South Dakota, and Montana, *Denver Mus. Nat. Hist. Ser.* 3, 1996, no. 12, pp. 1–47.
- Knowlton, F.H., Fossil Floras of the Vermejo and Raton Formations of Colorado and New Mexico, *US Geol. Surv.*, 1917, pap. 101, pp. 223–435.
- Knowlton, F.H., The Flora of the Denver and Associated Formations of Colorado, *US Geol. Surv.*, 1930, pap. 155, pp. 1–142.
- Krassilov, V.A., *Tsagayanskaya flora Amurskoi oblasti* (Tsagayan Flora of the Amur Region), Moscow: Nauka, 1976.
- Krassilov, V.A., *Melovaya flora Sakhalina* (Cretaceous Flora of Sakhalin), Moscow: Nauka, 1979.
- Krishtofovich, A.N., Fossil Flora from the Penzhinskaya Inlet, Lake Tas-Takh, and the Rarytkin Mountain Range, *Tr. Botan. Inst., Ser. 8, Paleobotan.*, 1958, vol. 3, pp. 74–120.
- Lesquereux, L., Contributions to the Fossil Floras of the Western Territories: Part 2. The Tertiary Flora, *US Geol. Surv. Terr. Rept.*, 1878, vol. 7, pp. 1–366.
- Lesquereux, L., Contributions to the Fossil Floras of the Western Territories: Part 3. The Cretaceous and Tertiary Floras, *US Geol. Surv. Terr. Rept.*, 1883, vol. 8, pp. 1–283.
- Maslova, N.P., The Genus *Platanus* L. (Platanaceae Dumortier) in the Paleocene of the Kamchatka Peninsula, *Paleontol. Zh.*, 1997, no. 2, pp. 88–93.
- Maslova, N.P., Cretaceous–Paleogene Platanaceae and Hamamelidaceae from the Far East and Siberia: Morphology, Systematics, and Phylogeny, *Cand. Sci. (Biol.) Dissertation*, Moscow: Paleontol. Inst. Ross. Akad. Nauk, 2001.
- Maslova, N.P. and Krassilov, V.A., A New Genus of the Platanaceae from the Paleocene of the Amur Region, *Paleontol. Zh.*, 2002, no. 1, pp. 106–110.

- McIver, E.E. and Basinger, J.F., Flora of the Ravenscrag Formation (Paleocene), Southwestern Saskatchewan, Canada, *Palaeontogr. Can.*, 1993, vol. 10, pp. 1–167.
- Meyen, S.V., Cordaitales from the Upper Paleozoic of Northern Eurasia (Morphology, Epidermal Structure, Systematics, and Stratigraphic Significance), *Tr. Geol. Inst. Akad. Nauk SSSR*, 1966, no. 150, pp. 1–184.
- Newberry, J.S., Notes on the Later Extinct Floras of North America, with Descriptions of Some New Species of Fossil Plants from the Cretaceous and Tertiary Strata, *New York Lyceum Nat. Hist. Ann.*, 1868, vol. 9, pp. 1–76.
- Newberry, J.S., Later Extinct Floras of North America, *US Geol. Surv.*, 1898, vol. 35, pp. 1–295.
- Vakhrameev, V.A., Stratigraphy and Fossil Flora from the Cretaceous Strata of Western Kazakhstan, *Regional'naya stratigrafiya SSSR* (Regional Stratigraphy of the USSR), Moscow: Akad. Nauk SSSR, 1952, vol. 1.
- Vakhrameev, V.A., The Platanaceae from the Late Cretaceous, in *Ocherki geologii i paleontologii Dal'nego Vostoka* (Essay on the Geology and Paleontology of the Far East), Vladivostok: Dal'nevost. Nauch. Tsentr Akad. Nauk SSSR, 1976, pp. 66–78.
- Vakhrameev, V.A., Development of Floras in the Middle Part of the Cretaceous and Early Angiosperms, *Paleontol. Zh.*, 1981, no. 2, pp. 3–14.
- Ward, L.F., Types of the Laramie Flora, *US Geol. Surv.*, 1887, no. 37, pp. 1–354.