Paleontological Journal, Vol. 37, No. 5, 2003, pp. 535–544. Translated from Paleontologicheskii Zhurnal, No. 5, 2003, pp. 89–96.

Leaves of *Liriodendropsis simplex* (Newb.) Newb. from the Cretaceous of Siberia

L. B. Golovneva

Botanical Institute, Russian Academy of Sciences, ul. Professor Popova 2, St. Petersburg, 197376 Russia

Received January 15, 2003

Abstract—The biternate structure of leaves of *Liriodendropsis simplex* is proved on new original material. The individual variability of the leaflets is analyzed, and the systematics of available finds is revised. During the Cenomanian the species was a characteristic member of the subtropical floras of the Euro-Sinian Paleofloristic Region of North America and Eurasia and occupied a portion of warm temperate Siberian-Canadian and tropical Equatorial regions. In the Senonian the range of this genus was restricted to Greenland and the eastern coast of the United States.

Key words: Late Cretaceous, Siberia, leaf remains.

INTRODUCTION

Elliptic and ovate leaflets of *Liriodendropsis* with an emarginated apex and a distinctive brochidodromous reticulate venation are common in the Cenomanian–Turonian of North America, Greenland, Europe, Middle Asia, and Siberia. Such leaflets were first reported from the Upper Cretaceous of Greenland by Heer (1882), who determined the finds as tulip-tree leaves and assigned them to the species *Liriodendron meekii* Heer, previously described from Cretaceous deposits of Nebraska (in Meek and Hayden, 1858). Later, Newberry found such leaflets in the Cretaceous of the Raritan Formation (New Jersey) and described them as *Liriodendron simplex* Newberry (1887), since they differed from the type material of *L. meekii.* The only common feature in the morphology of these two species was the presence of an apical sinus. Newberry also assigned to *L. simplex* the material described by Heer from Greenland. Additional analysis of the morphology and venation of the leaflets from the Raritan Formation revealed their significant distinctions from the leaves of the genus *Liriodendron* and made it possible to introduce a new genus, *Liriodendropsis* (Newberry, 1895). Newberry also divided the initial species into two groups, describing broader and shorter leaflets as *Liriodendropsis simplex* and narrower and elongate leaflets as *L. angustifolia* Newb. The leaf shape and venation of *Liriodendropsis* resemble those of some Fabaceae with an emarginate apex (e.g., *Pterocarpus, Swartzia, Sweetia*, and *Dalbergia*). This similarity forced Seward (1925) to transmit *Liriodendropsis simplex* in the form-genus *Dalbergites*. The latter was established for leaves of fossil legumes with venation similar to that of the Dalbergieae (Berry, 1916). Revising the Greenland flora, Seward (1925) studied the variations of leaflets of *Dalbergites simplex* (Newb.) Seward and assigned to this species many other specimens from Greenland, previously described by Heer in the content of other species and genera. Shaparenko (1937) continued the study of this plant on the basis of the material from the Cretaceous floras of Middle Asia and Siberia. He also transmitted *Liriodendropsis angustifolia* to the genus *Dalbergites* and proposed to assign to *Dalbergites simplex* ovate leaflets with a narrow sinus. He assigned the majority of Greenland specimens with elliptic broadly emarginate leaf blades to a new species, *Dalbergites sewardiana* Shap. Subsequently, the genus *Dalbergites* was repeatedly reported from different Cretaceous floras of Middle Asia and western Siberia. Usually, two or three species were described in each locality (Anan'ev, 1948; Vachrameev, 1952; Lebedev, 1962; Shilin, 1986). In addition to solitary leaflets, leaflets connected in threes were also occasionally found (Hollick, 1893; Bayer, 1900; Seward, 1925; Shaparenko, 1937; Lebedev, 1962). The majority of authors considered such finds as apical parts of compound odd-pinnate leaves by analogy to the Fabaceae.

New representative collections of leaflets and petioles of this plant from western Siberia allowed us to restudy variations in leaflet shape and to reconstruct the leaf organization as biternate. Since such leaf arrangement is not characteristic of the Dalbergieae, we propose to use for these leaves the first generic name *Liriodendropsis* because of its priority.

MATERIAL

The leaf remains of *Liriodendropsis* were collected from the southern part of western Siberia, in the Chulym–Yenisey Basin (Krasnoyarsk Region). The locality is an outcrop of the Kem' River, which falls into the Yenisey River slightly downstream of the town of Yeni-

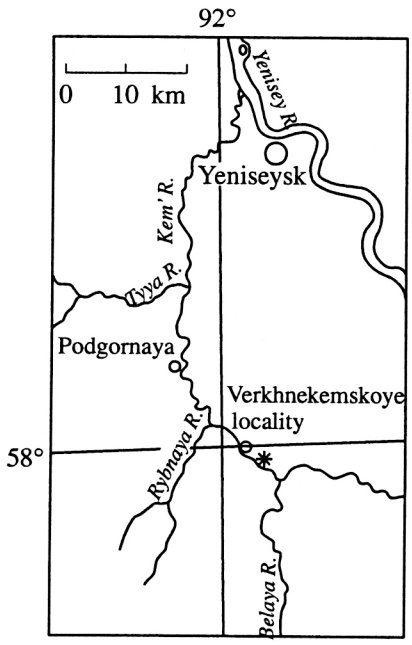


Fig. 1. Locality of *Liriodendropsis simplex* (Newberry) Newberry on the Kem' River in western Siberia.

seysk (Fig. 1). Numerous leaves of *Liriodendropsis* were found in the clay lens in the alluvial deposits of the Simonovo Formation, about 5 km upstream of the village of Verkhnekemskoe. The Simonovo Formation is dated as the Cenomanian–Turonian and is widespread in the Chulym–Yenisey Basin (Lebedev, 1958, 1962). The deposits of the formation represent loosely cemented bright gray kaolinized sandstones and clays. Most of the leaflets of *Liriodendropsis* are light brown impressions with partially preserved compressions. These remains fill the rock to form an almost monodominant locality. In addition to the leaflets, the bedding surfaces contain many compound leaf petioles and petiolules with widened articulate surfaces. Some of them are connected with each other and leaflets of *Liriodendropsis*. This allows us to consider these petioles as parts of compound leaves of *Liriodendropsis* and to reconstruct the leaf organization. The specimens were collected by L.B. Golovneva and A.B. Hvali and housed at the Botanical Institute of the Russian Academy of Sciences (BIN), collection no. 1198. Remains of *Liriodendropsis* from the Kem' River were previously described by Anan'ev (1948) and Lebedev (1962) as *Dalbergites*. Such fossils were also found on the Chulym River, near the village of Simonovo, in deposits of the Simonovo Formation (Shaparenko, 1937; Anan'ev and Lebedev, 1955). The material studied by Shaparenko was collected by A.L. Yachevskii and housed at BIN, collection no. 53. Heer (1878) was the first to describe the flora of the Simonovo Formation on the basis of collections amassed by Lopatin. The most representative collections from these deposits were accomplished by Anan'ev and Lebedev (Anan'ev, 1948; Ana'ev and Lebedev, 1955; Lebedev, 1962). Several species of plane-trees, leaves of *Trochodendroides, Celtidophyllum, Sapindopsis, Nelumbites, Magnoliaephyllum, Cissites, Araliaephyllum, Menispermites*, and several problematic taxa were also described from the Simonovo Formation.

In addition to the material from the Chulym–Yenisey Basin, we have studied remains of *Liriodendropsis* from other Siberian localities. The leaf remains of *Liriodendropsis* from the Lena–Vilyui depression were collected by G.D. Lavrov (All-Union Oil Institute) in the middle reaches of the Tyung River, which falls into the Vilyui River near the town of Vilyuisk, approximately 180 km upstream from the mouth of the Tyung River, in the lower part of the Agrafena Formation, which is dated as the Cenomanian (Zabaluev *et al.*, 1976). This collection is presently housed at BIN, nos. 1181, 1531. The material collected by V.A. Vachrameev from the Geological Institute of the Russian Academy of Sciences (GIN) comes from approximately the same beds (collection no. 3373). We also restudy the leaf remains from Greenland, which initially were studied by Heer, in the Geological Museum of Copenhagen and the Swedish Museum of Natural History (Stockholm, SMNH). European finds from the Peruč Formation (Cenomanian) were studied in the National Museum of Prague (NMP).

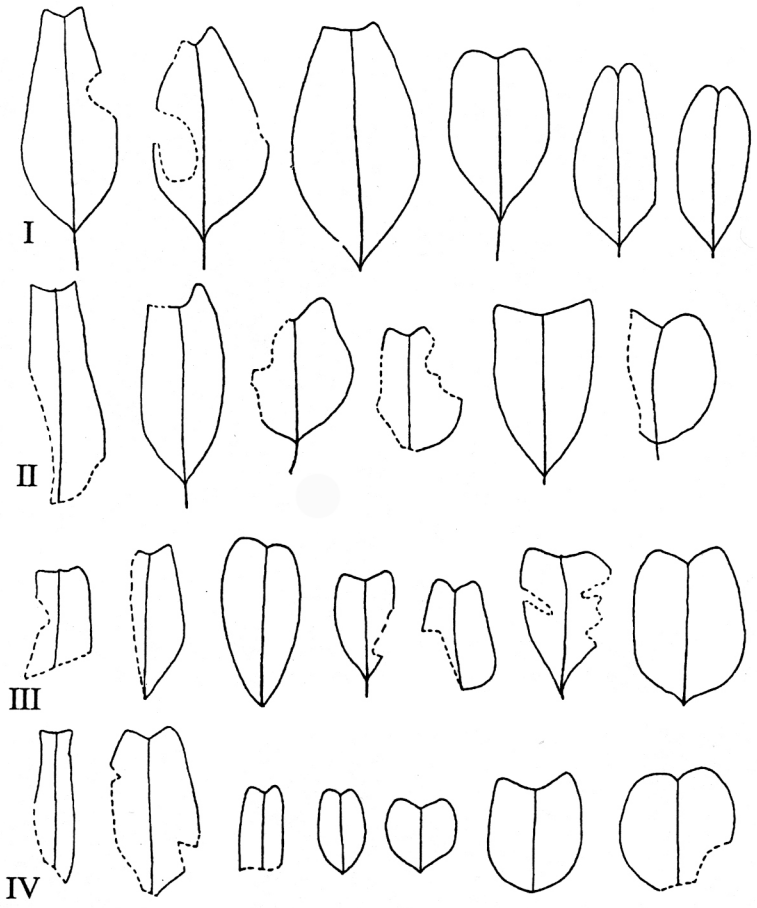
SYSTEMATIC PALEOBOTANY

Genus *Liriodendropsis* Newberry 1895, emend.

Type species. *Liriodendropsis simplex* (Newb.) Newb. 1895, Cenomanian–Turonian of the northern hemisphere.

Diagnosis emended. Leaves compound, probably biternate, with nine leaflets. Leaflets symmetrical, ovate, lanceolate or elongate, with long petiolules, 30–70 mm long and 24–40 mm wide, base cuneate or rounded, apex broadly emarginate with wedge-shaped sinus, margins entire. Primary vein strong, terminating abruptly in the bottom of the apical sinus. Secondary venation pinnate, brochidodromous. Secondary veins 8–11 pairs, leaving midrib at an angle of 40°–60°, irregularly spaced, arched apically, and uniting in festoons near margins. Intersecondary veins common. Tertiary venation thin, reticulate, filling space between the secondaries with relatively fine network; meshes elongated near the midrib, oriented in parallel to the secondaries, and rounded or polygonal near margins. Rachis 40–60 mm long, 3–4 mm in diameter, bearing 3 petiolules of the first order 30–55 mm long and 1.2–2 mm in diameter. Rachis and petiolules of the first order expanded basally and apically, with well-developed articulate surfaces. Each petiolule of the first order bearing 3 petiolules of the second order 20–40 mm long and 0.6–1 mm in diameter that bear the leaflets.

Species composition. Type species.



Figs. 2. Leaflet variations in *Liriodendropsis simplex* (Newberry) Newberry: (I) North America, Raritan Formation, Cenomanian–Turonian (Newberry, 1895); (II) Siberia, Simonovo and Agrafena formations, Cenomanian; (III) Greenland, Atane Formation, Cenomanian–Turonian (Heer, 1882); (IV) Kazakhstan, Altykuduk and Kyrykkuduk formations, Late Albian–Turonian (Vachrameev, 1952; Shilin, 1986).

Comparison. Leaflets of *Densinervum kaulii* Upchurch et Dilcher from the Cenomanian Dakota Formation (Upchurch and Dilcher, 1990) closely resemble those of *Liriodendropsis* in shape and venation. It is quite possible that these leaflets should be assigned to the genus *Liriodendropsis* and the genus *Densinervum* is a younger synonym of *Liriodendropsis*. Dilcher (Kvaček and Dilcher, 2000) compared the leaflets of *Densinervum* with the leaflets of *Liriodendropsis* from Europe described as *Bignonia pulcherrima* Bayer (Bayer, 1900). In the same paper he refers to the emarginate apex of *Densinervum*, although the diagnosis lacks this character and the figured type material of *Densinervium* have damaged apices.

The genus *Liriodendropsis* differs from the genus *Dalbergites* in the biternate organization of leaves.

***Liriodendropsis simplex* (Newb.) Newb.**

Plate 1, figs. 1–11, Plate 2, figs. 2, 4, and 6

Liriodendron meekii auct. non Heer in Meek and Hayden, 1858: Heer, 1882, p. 87, pl. 22, figs. 2–11, pl. 23, fig. 3, pl. 25, fig. 5a, pl. 45, figs. 13a and 13b.

Liriodendron simplex Newberry, 1887: Newberry, 1887, p. 6, pl. 62, figs. 2–4; Hollick, 1893, p. 135, pl. 5, figs. 1–5, pl. 7, figs. 2 and 3.

Bignonia pulcherrima Bayer, 1900: Bayer, 1900, p. 33, pl. 1, figs. 9–14, pl. 2, figs. 4–10, text-figs. 11 and 12; Kvaček and Dilcher, 2000, p. 24, pl. 1, fig. 4.

Liriodendropsis simplex (Newb.) Newberry, 1895: Newberry 1895, p. 83, pl. 19, figs. 2, 3, pl. 53, figs. 1–4, 7; Hollick, 1906, p. 72, pl. 23, figs. 1–7, pl. 24, figs. 1–9, pl. 25, figs. 1, 4, 5, 7, 10–12, pl. 26, figs. 1b–1d; Hollick, 1930, pl. 28, fig. 4b.

Liriodendropsis angustifolia Newberry, 1895: Newberry, 1895, p. 84, pl. 53, fig. 8.

Dalbergites simplex (Newb.) Seward, 1925: Seward, 1925, p. 252, pl. B, fig. 17, pl. C, fig. 18; Shaparenko, 1937, p. 120, pl. 2, fig. 2; Anan'ev, 1948, p. 47, pl. 4, fig. 4; Vachrameev, 1952, p. 234, pl. 35, figs. 1–5; Shilin, 1986, pl. 32, figs. 1, 10, pl. 33, figs. 1A, 2, 9.

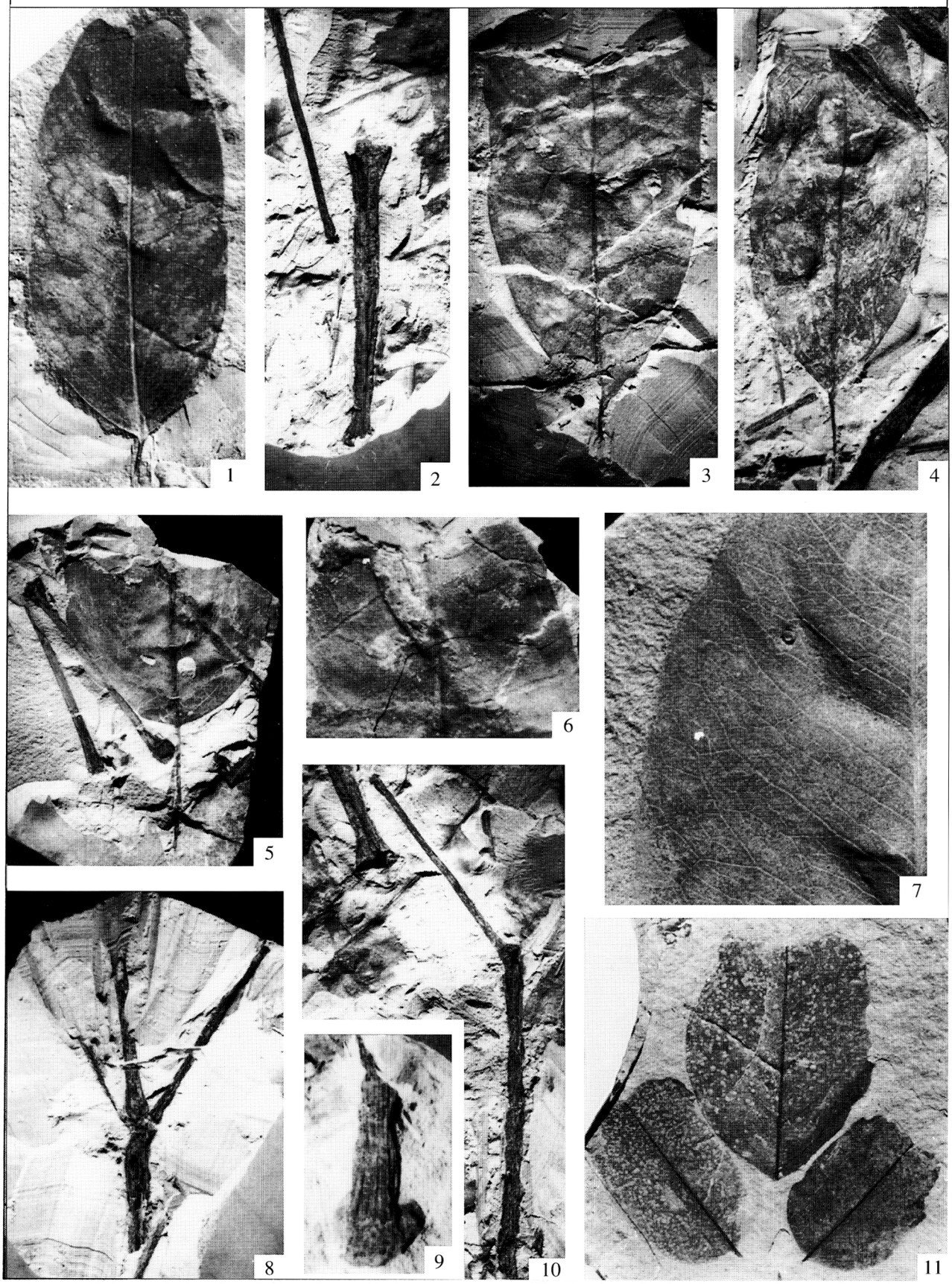
D. pulcherrima (Bayer) Seward, 1925: Seward, 1925, p. 249.

D. angustifolia (Newb.) Shaparenko, 1937: Shaparenko, 1937, p. 121; Lebedev, 1962, p. 271, pl. 46, fig. 1.

D. sewardiana Shaparenko, 1937: Shaparenko, 1937, p. 121, pl. 2, figs. 3–5; Vachrameev, 1952, p. 234, pl. 35, figs. 6–9, pl. 42, fig. 3; Anan'ev and Lebedev, 1955, p. 195, pl. 26, fig. 3; Shilin, 1986, pl. 32, figs. 4, 6, 8, 9, pl. 33, figs. 4–6.

Dalbergites sp.: Lebedev, 1962, p. 271, pl. 58, figs. 3, 4; Shilin, 1986, pl. 31, fig. 6, pl. 32, figs. 3, 11, pl. 33, fig. 1B.

Plate 5



Explanation of Plate 5

Leaf morphology of *Liriodendropsis simplex* (Newberry) Newberry: (1–10) western Siberia, Kem' locality; (11) Greenland; (1) narrow elliptic leaflet with a narrow apex, GIN, no. 3373, ×1; (2) petiole with a widened articulate surface in its upper part and thinner petiolule of the first order, BIN, no. 1198/63; (3) elliptic leaflet with a widened apex and wide triangular sinus, BIN, no. 1198/20; (4) narrow elliptic leaflet, BIN, no. 1198/11; (5) lower portion of a leaf with a petiolule of the second order and two petiolules of the first order having widened articulate surfaces, BIN, no. 1198/18; (6) leaf let apex with a prominent midvein, BIN, no. 1198/15, ×2; (7) enlargement of (1) showing details of venation, ×2; (8) leaf petiole with three petiolules of the first order in attachment, BIN, no. 1198/12; (9) lower part of a leaf petiole with bractlike structures in its base, BIN, no. 1198/14, ×1.5; (10) leaf petiole with an attached petiolule of the first order, BIN, no. 1198/62; (11) three apical leaflets, SMNH (all specimens are natural size, except specified).

Lectotype. The specimen described as *Liriodendron simplex* Newberry (Newberry, 1887, pl. 62, fig. 2) and subsequently as *Liriodendron simplex* (Newb.) (Newberry, 1895, pl. 19, fig. 2), Woodbridge locality, Raritan Formation, Cenomanian. (Fig. 3a, third from the left).

Diagnosis. As for the genus.

Description (Figs. 2–4). Leaves are compound, biternate. Articulate petioles and petiolules widen at the edges (Pl. 1, figs. 2, 8, 10). At the base of a petiole there is a bractlike widening of an oval-ovate shape which is about 5 mm long (Pl. 1, fig. 9). Main

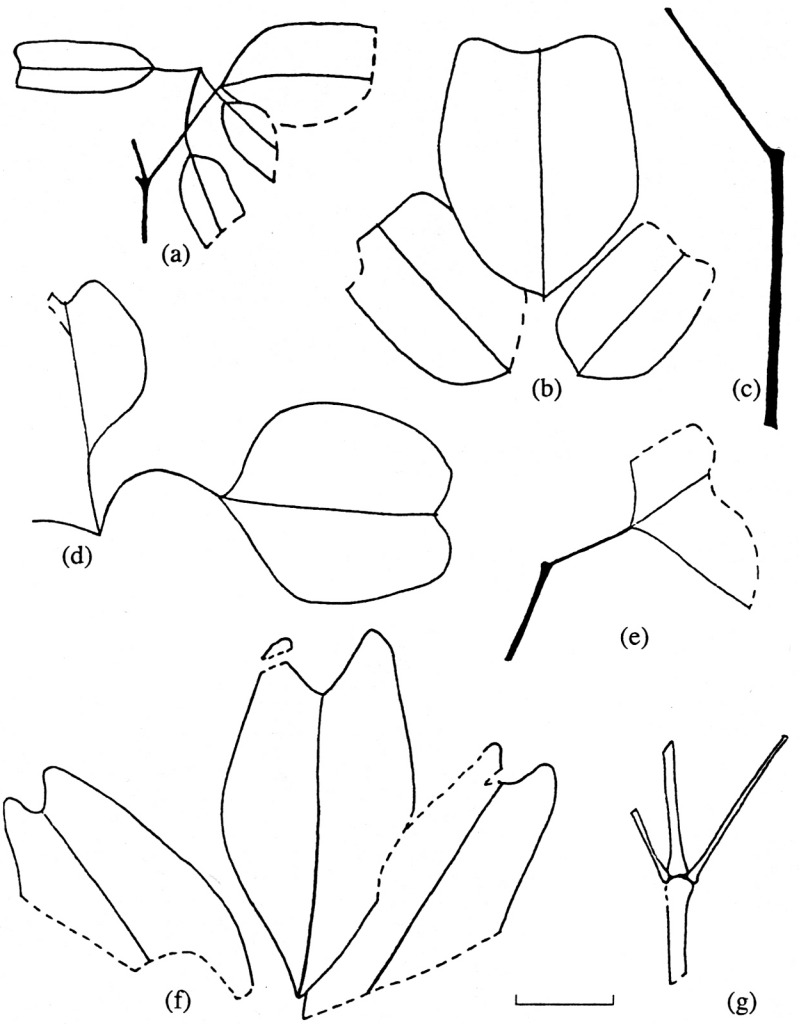
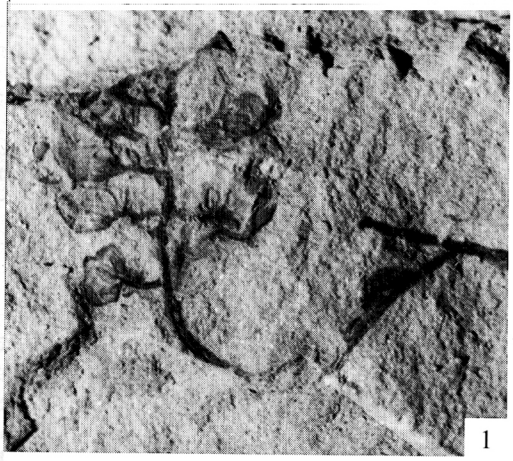
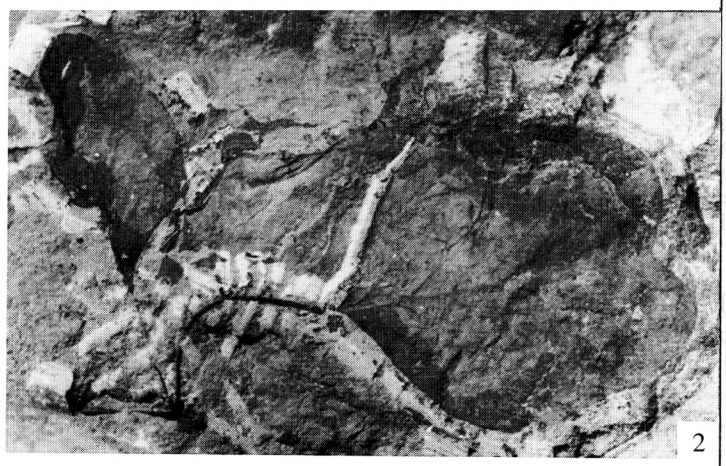
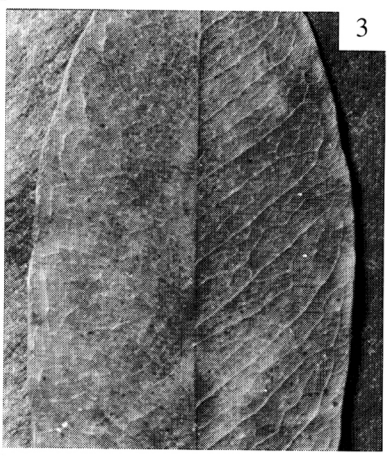


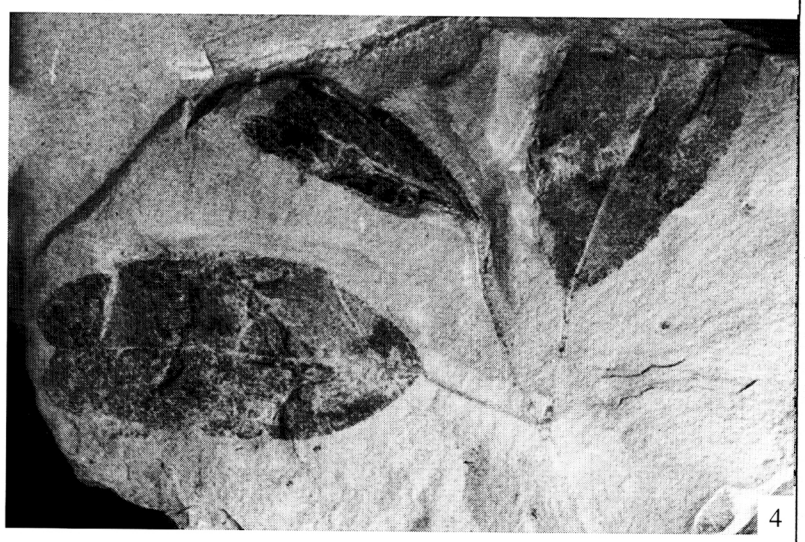
Fig. 3. Morphology of the compound leaf of *Liriodendropsis simplex* (Newberry) Newberry: (a) united apical leaflets, western Siberia, Kem' River (Lebedev, 1962); (b) three apical leaflets, Greenland (Seward, 1925); (c) a leaf petiole with a petiolule of the first order in attachment, western Siberia, Kem' River, BIN, no. 1198/62; (d) united apical leaflets, western Siberia, Simonovo locality, BIN, no. 53/30 (Shaparenko, 1937); (e) a leaflet with petiolules of the first and second orders, western Siberia, Kem' River, BIN, no. 1198/23; (f) three apical leaflets (Hollick, 1893); (g) leaf petiole and three petiolules of the first order in attachment, western Siberia, Kem' River, BIN, no. 1198/12. Scale bar is 1 cm.

Plate 6

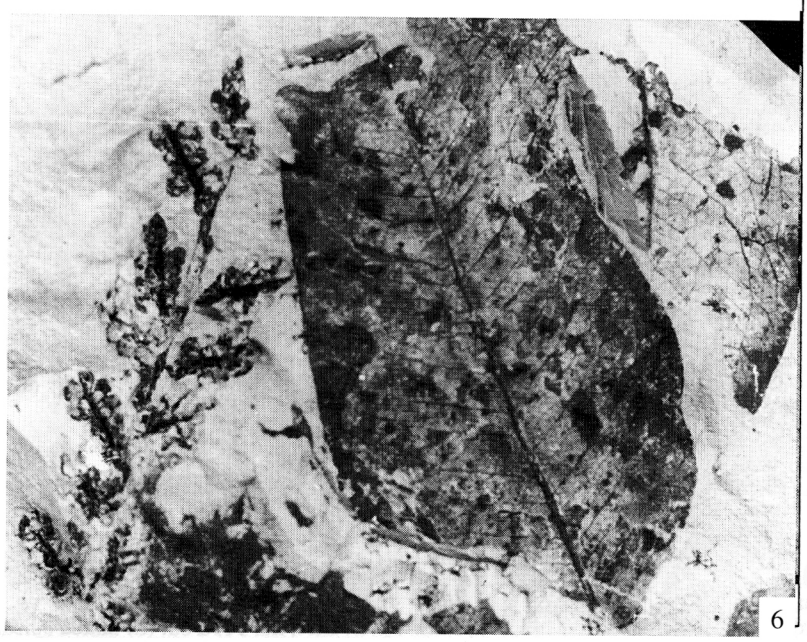

1


2


3


4


5


6

Explanation of Plate 6

Leaves of *Liriodendropsis simplex* (Newberry) Newberry and associate generative structures: (1) staminate inflorescences of *Freyantha sibirica*, western Siberia, Kem' locality, BIN, no. 1198/42, ×4; (2) united leaflets of *Liriodendropsis simplex*, western Siberia, Simonovo locality, BIN, no. 53/30; (3) leaflet venation in *Dalbergia* sp., ×1.5; (4) united leaflets of *Liriodendropsis simplex*, Czech Republic, Mala Chuchla, Peruč Formation, NMP; (5) infructescence associate with the foliage of *Liriodendropsis*, BIN, no. 1198/105, ×2; (6) leaflet of *Liriodendropsis* and an associate infructescence, BIN, no. 1531/6, ×1.3 (all specimens are natural size except specified).

petioles of the leaf reach 40–60 mm in length and 3–4 mm in diameter. Petiolules of the first order are 30–55 mm long and 1.2–2 mm in diameter. Petiolules of the second order (petiolules of leaflets) are about 20–40 mm long and 0.6–0.9 mm in diameter. The leaflets are oval, ovate or obovate, entire-margined, with a rounded or cuneate base and an emarginate apex (Pl. 1, figs. 1, 3, 4; Fig. 3). The leaflets are usually 30–70 mm long and 25–40 mm wide, maximally reaching 90 mm length and 60 mm width. The apical sinus is usually wide, triangular, with an acute apex and straight sides, which make an angle of 100°–160°. Apical lobes are 3–9 mm high, triangular or rounded triangular, with obtuse apices. More rarely, the lobes are rounded and separated by a narrow sinus. The leaflet venation is pinnate and brochidodromous. The midvein ends in the sinus base and can exceed the leaf margin in 1–1.5 mm (Pl. 1, fig. 6). There are 8–11 pairs of secondary veins, which leave the midvein at an angle of 40–60°, uniting in festoons. Tertiary venation is reticulate. The meshes are polygonal. Centrally, they are elongated along secondary veins, being more or less equilateral or rounded in the marginal regions (Pl. 1, fig. 7; Fig. 2).

Comparison. Leaflets of *Liriodendropsis* are highly variable. Among the leaflets from the Agrafena and Simonovo formations, there are both narrow long leaflets with a wide or narrow sinus and shorter, elliptic, ovate, or obovate with wide or narrow sinus and triangular or rounded lobes. No correlation between the shapes of leaflets and apices has been found. We consider these variations as individual variability of *Liriodendropsis* leaflets. Similar variability is observed in nearly all localities of *Liriodendropsis* showing a representative number of specimens (North America, Greenland, and Middle Asia; Fig. 2). Therefore, we consider the present division of the genus *Liriodendropsis* into species on the basis of leaf shape to be artificial and establish only one species *L. simplex*, which includes all observed variants of the leaflets. Hollick (1906) and Seward (1925) also shared this opinion. Our point of view is additionally confirmed by the fact that all authors who separated *Liriodendropsis* into several species differently treated their morphological diagnoses. As a result the same morphotypes were considered by different authors as different species. More evidence is the occurrence of an identical assemblage of morphotypes in nearly all localities. The genus *Liriodendropsis* has a wide geographic and stratigraphic range. It was quite common in the Cenomanian–Turonian subtropical and warm temperate floras of Eurasia and North America, but it also occurred in younger Senonian floras of Greenland and the eastern United States (Heer, 1883; Hollick, 1906). The wide distribution of the genus implies the existence of more than one species. However, we have failed to distinguish species on the basis of leaflet morphology since they are nearly indistinguishable morphologically and greatly vary with location.

Remarks. In addition to the leaflets, our collections contain numerous detached and partially united petioles and petiolules (Fig. 3). At their ends they widen and have well-defined articulate surfaces. Due to these articulations the compound leaf of *Liriodendropsis* could easily disintegrate and, thus, is usually found in the form of separated leaflets and petiolules. The largest petiole reaches 6 cm length and 3–4 mm in thickness. Some of them have a small bract in their bases that allows one to consider them as main leaf petioles. Three petiolules of the first order (Pl. 1, fig. 8) reaching 1.5–2.5 mm in diameter were attached to the petiole. The middle petiolule was more prominent than the two lateral petiolules. The relative thickness of the petiolules and articulate surfaces at their upper parts support that they were not petiolules of leaflets (1 mm in diameter) but represented intermediate axes (Pl. 1, fig. 5). Distal parts of compound leaves are occasionally preserved as three united leaflets. Such finds are known from Greenland, America, Europe, and western Siberia (Pl. 2, figs. 2, 4; Figs. 3a, 3d). All these remains suggest that

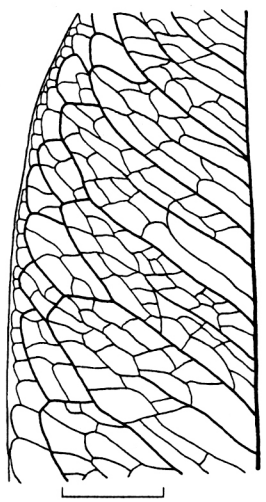


Fig. 4. Leaflet venation in *Liriodendropsis simplex* (Newberry) Newberry, GIN, no. 3373. Scale bar 1 cm.

the organization of the compound *Liriodendropsis* leaves was most likely biternate.

The leaflet shape and venation of *Liriodendropsis* resemble those of some Fabaceae from the genera *Pterocarpus, Sweetia, Swartzia*, and *Dalbergia* (Pl. 1, fig. 7, Pl. 2, fig. 3). The leaflets of *Liriodendropsis* and those of these genera were compared in detail in Seward (1925) and Shaparenko (1937), who assigned *Liriodendropsis* to the Fabaceae. The venation of *Liriodendropsis* differs from the venation of Fabaceae in the lower regularity (Fig. 4) and the deeper apical sinus. In the Fabaceae, leaflet petiolules are very short, not exceeding one-fifth of the leaf blade length. In *Liriodendropsis*, the petiolules are approximately as long as the leaf blades. The biternate leaf organization is not characteristic of Fabaceae. In addition, the venation of *Liriodendropsis* was compared with that of leaves in the extant families Bignoniaceae (Bayer, 1900) and Canellaceae (Upchurch and Dilcher, 1990). A similar venation with numerous irregular brochidodromous secondaries, numerous intercalate veins and a reticulum between them with horizontally elongate meshes is observed in several taxa of the Albian–Cenomanian floras, e.g., *Crassidenticulum* (Upchurch and Dilcher, 1990), *Ficophyllum* (Fontaine, 1889), and *Sapindopsis* (Crane *et al.*, 1993). Such a venation possibly indicates a certain level of leaf morphological evolution and cannot serve as a systematic character of the mid-Cretaceous leaves.

In extant plants, biternate leaves are common in the Ranunculales. Among fossil plants, biternate leaves are described for *Leguminosites karatscheensis* Vachr. from the Albian deposits of the Kyzylshen Formation of western Kazakhstan (Vachrameev, 1952; Krassilov *et al.*, 1983). This species also has entire-margined leaflets with brochidodromous venation, but they are smaller (15–60 mm) and have a different blade shape with a rounded apex and cuneate decurrent base. Since secondary venation in this plant is very fine and venation of subsequent orders was not preserved, a more detailed comparison between this plant and *Liriodendropsis* is impossible. The leaf organization and association with the fruits of *Hyrcantha* make it possible to relate leaves of *Leguminosites karatscheensis* to the Paeoniaceae (Krassilov *et al.*, 1983).

Material. BIN, nos. 1198/11–26, 28–32, 36, 57, 62, 63, 1181/568, 53/30.

GENERATIVE STRUCTURES

In the most studied localities leaflets of *Liriodendropsis* form nearly monodominant taphocenoses. The taphocenoses mostly come from clay lacustrine facies. Localities of *Liriodendropsis* from sandy or coal deposits have not been found yet. It is possible that these plants could form monospecific communities along lakes or oxbows where they were subsequently burried. The leaflets of *Liriodendropsis* rather often cooccur with undescribed paniculate infructescences (Pl. 2, figs. 3, 6) and inflorescences of *Freyantha* (Golovneva *et al.*, 2000; Krassilov and Golovneva, 2001).

The infructescences are composed of axes of two orders and numerous fruits. Lateral axes are opposite or decussate and flattened. At the upper surface, each of them bears 8–12 sessile nutletlike fruits about 2–3 mm long. Remains of the stigma are bilobed. Fruits are either unicarpellate or bicarpellate, with one seed. Each fruit is surrounded by a cuplike structure, which is possibly a remnant of fused perianth or bracts. These infructescences are found in association with leaflets of *Liriodendropsis* in two localities of the Lena-Vilyu' Basin, Kem' River locality (Chulym-Yenisey Basin), Kachar locality (Fore-Urals), and in the Mala Chuchla locality of the Peruč Formation (Czech Republic). The association of numerous infructescences and leaflets in several nearly monodominant localities suggests that they could belong to the same plant. In addition to these fossils, numerous staminate flowers and one complete inflorescence of *Freyantha* were found in the Kem' River locality (Krassilov and Golovneva, 2001). The inflorescence is paniculate, with a limber long pedicel (Pl. 2, fig. 1). The staminate flowers are arranged on the axis of inflorescence laterally, in two opposite rows. The flowers are pedicellate, slightly zygomorphous, with one large curved bract protecting the flower on the bottom and outside. There are five stamens, three proximal stamens are basally fused, and two others are arranged on the receptacle more distally. The stamens consist of a short filament and massive anthers with a slightly protruding extension of the connective. The pollen grains are tricolpate, with reticulate exine. The suggestion *Freyantha* inflorescences and paniculate infructescences belong to one plant is confirmed by the cooccurrence, similar morphology of unisexual inflorescences, and the presence of *Freyantha* pollen on the surfaces of juvenile fruits. The systematic position of this plant is still uncertain.

GEOGRAPHIC DISTRIBUTION

The genus *Liriodendropsis* was widely distributed in Eurasia and North America in the Cenomanian–Turonian and more rarely in Senonian deposits. In Europe, remains of *Liriodendropsis* occur in the Cenomanian deposits of the Peruč Formation (Czech Republic). There they were described from the localities of Otrub and Mala Chuchla as *Bignonia pulcherrima* Bayer (Bayer, 1900). Apart from solitary leaflets, leaflets united in threes were also described (Pl. 2, fig. 4). Numerous *Cathiaria* infructescences have been found together with *Liriodendropsis* leaflets in the collections of the National Museum of Prague. *Liriodendropsis* leaflets were reported from the Cenomanian deposits of Jordan and described as *Ficophyllum jordanicum* Bender et Mädler (Bender and Mädler, 1969).

In western Siberia, localities of *Liriodendropsis* mainly come from deposits of the Simonovo Formation

(Cenomanian–Turonian) on the Kem' and Chulym rivers. Remains of *Liriodendropsis* were also found in deposits of the Keya Formation (upper Albian) near the Keya River. In eastern Siberia, these leaves were found in the lower part of the Agrafena Formation (Cenomanian) on the Tyung and Lepisk rivers of the Lena–Vilyui depression. Remains of *Liriodendropsis* do not occur in Cretaceous floras of more northern localities in the Khatanga depression, Novosibirsk Islands, and northeastern Russia. Numerous localities of *Liriodendropsis* are known in Kazakhstan and Middle Asia (Vachrameev, 1952; Shilin, 1986). There, *Liriodendropsis* is restricted to Upper Albian–Cenomanian and Cenomanian–Turonian deposits of the Mysovskaya, Kyrykkuduk, and Altykuduk formations (Fig. 5).

In North America, leaflets of *Liriodendropsis* were described from the Cenomanian deposits of the Raritan Formation, Senonian deposits of the Magothy Formation on the eastern coast of the United States (Newberry, 1895; Hollick, 1906), and from the Tuscaloosa Formation in Alabama (Berry, 1919). In Greenland, this genus was first reported by Heer (1882) from the Atane Formation of the Cenomanian age. Because of high morphological variability of *Liriodendropsis* leaflets, Heer described several genera and species on the basis of this material. Later these taxa were revised by Seward (1925). Remains of *Liriodendropsis* were also found in Patut locality (Heer, 1883) dated to the Campanian (Budantsev, 1983). In the northern part of North America, single remains of *Liriodendropsis* were reported from the Cenomanian deposits of the Yukon River (Hollick, 1930), but they are lacking in the more southern Dunvegan flora of Canada (Bell, 1963).

During the Cenomanian epoch, the floras of Greenland, the eastern coast of the modern United States, Europe, Middle Asia, Kazakhstan, and southern Siberia (Chulym-Yenisey Basin) belonged to the Euro-Sinian phytogeographical region (Vachrameev, 1988; Shilin, 1986), which was characterized by a subtropical climate. Most *Liriodendropsis* localities come from this region. In the more northern Siberian-Canadian region with a warm temperate humid climate, *Liriodendropsis* was found only in two localities: one in the Lena–Vilyui Basin and another on the Yukon River. Therefore, east Siberian localities indicate the northern and eastern limits of this genus in Eurasia. In the Far East, Japan, and China, finds of Upper Cretaceous floras are very uncommon and *Liriodendropsis* remains from these regions have not been reported. The most southern locality (Jordan, in the latitude of 30° N.) is situated near the boundary between the Euro-Sinian and Equatorial regions. *Liriodendropsis* associated there with entire-margined leaves of Magnoliaceae and Lauraceae.

Therefore, the genus *Liriodendropsis* was a characteristic element of the Cenomanian subtropical floras of the Euro-Sinian paleofloristic region and could occupy some portion of the warm temperate Siberian-Canadian and tropical Equatorial regions. In the Senonian, the geographical range of the genus was significantly restricted and its remains are known only from Greenland and the eastern coast of the United States.

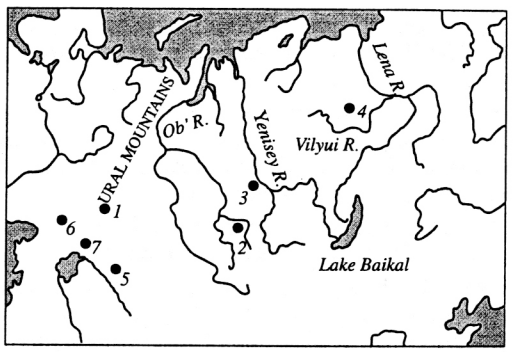


Fig. 5. Occurrence of the genus *Liriodendropsis* in Kazakhstan and Siberia: (*1*) Ayat locality, Mysovskaya Formation, Cenomanian; (*2*) Simonovo locality, Simonovo Formation, Cenomanian; (*3*) Kem' locality, Simonovo Formation, Cenomanian; (*4*) Tyung locality, Agrafena Formation, Cenomanian; (*5*) Taldyespesai locality, Kyrykkuduk Formation, Cenomanian–Turonian; (*6*) Kul'denentemir and Terektysai localities, Altykuduk Formation, Late Albian–Cenomanian; (*7*) Tasaran locality, Altykuduk Formation, Cenomanian (the ages of the Kazakhstan localities after Shilin, 1986).

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research, project no. 01-04-49-489.

REFERENCES

Anan'ev, A.R., Remains of Upper Cretaceous and Tertiary Floras from the Kem River, a Left-Bank Tributary of the Yenisey River, *Tr. Tomsk. Gos. Univ. Ser. Geol.*, 1948, no. 99, pp. 29–74.

Anan'ev, A.R. and Lebedev, I.V., Cretaceous Flora: Chulym Assemblage, in *Atlas rukovodyashchikh form iskopaemykh fauny i flory Zapadnoi Sibiri* (Atlas of Index Forms of the Fossil Fauna and Flora of Western Siberia), Moscow: Gosgeoltekhizdat, 1955, pp. 191–195.

Bayer, E., Einige neue Pflanzen der Perucer Kreideschichten in Böhmen, *Sitzungsber. Königl. Böhm. Gesell. Wiss.*, 1900, vol. 30, pp. 1–51.

Bell, W.F., Upper Cretaceous Floras of the Dunvegan, Bad Heart and Milk River Formations of Western Canada, *Geol. Surv. Can. Bull.*, 1963, vol. 94, pp. 1–76.

Bender, F. and Mädler, K., Die sandige Schichtenfolge der Kreide mit einer Angiospermen-Flora in Sudjordanien, *Beihefte, Geol. Jahrb.*, 1969, vol. 81, pp. 35–92.

Berry, E.W., Upper Cretaceous, *Maryland Geol. Surv.*, 1916, pp. 1–1022.

Berry, E.W., Upper Cretaceous Floras of the Eastern Gulf Region in Tennessee, Mississippi, Alabama, and Georgia, *US Geol. Surv. Prof. Pap.*, 1919, vol. 112, pp. 1–143.

Budantsev, L.Yu., *Istoriya arkticheskoi flory epokhi rannego kainofita* (The History of the Early Cenophytic Arctic Flora), Leningrad: Nauka, 1983.

Crane, P.R., Friis, E.M., Pedersen, K.R., and Drinnan, A.N., Platanoid Inflorescences Associated with *Sapindopsis* Leaves from the Potomac Group of Eastern North America, *Syst. Bot.*, 1993, vol. 18, pp. 328–344.

Fontaine, W.M., The Potomac or Younger Mesozoic Flora, *US Geol. Surv. Monogr.*, 1889, vol. 15, pp. 1–377.

Golovneva, L.B., Hvalj, A.V., and Krassilov, V.A., Leaves of *Liriodendropsis* and Associated Reproductive Structures from the Cretaceous of Siberia and Kazakhstan, *Abstracts of the Sixth Conference of the International Organization of Palaeobotany*, Qinhuangdao, 2000, p. 41.

Heer, O., Beiträge zur fossilen Flora Sibiriens und des Amurlandes, *Flora fossilis arctica*, 1878, vol. 5.

Heer, O., Die fossile Flora Grönlands. Theil I, *Flora fossilis arctica*, 1882, vol. 6, part 2, pp. 1–112.

Heer, O., Die fossile Flora Grönlands. Theil II, *Flora fossilis arctica*, 1883, vol. 7, pp. 1–275.

Hollick, A., Addition to the Palaeobotany of the Cretaceous Formation on Staten Islands, *Trans. N.Y. Acad. Sci.*, 1893, vol. 12, pp. 1–135.

Hollick, A., The Cretaceous Flora of Southern New York and New England, *US Geol. Surv. Monogr.*, 1906, vol. 50, pp. 1–219.

Hollick, A., The Upper Cretaceous Floras of Alaska, *US Geol. Surv. Prof. Pap.*, 1930, vol. 159, pp. 1–119.

Krassilov, V.A. and Golovneva, L.B., Inflorescence with Tricolpate Pollen Grains from the Cenomanian of Tschulymo–Yenisey Basin, West Siberia, *Rev. Palaeobot. Palynol.*, 2001, vol. 115, pp. 99–106.

Krassilov, V.A., Shilin, P.V., and Vachrameev, V.A., Cretaceous Flowers from Kazakhstan, *Rev. Palaeobot. Palynol.*, 1983, vol. 40, pp. 91–113.

Kvaček, I. and Dilcher, D.L., Comparison of Cenomanian Floras from Western Interior North America and Central Europe, *Acta Univ. Carolinae Geol.*, 2000, vol. 44, no. 1, pp. 17–38.

Lebedev, I.V., Cretaceous Beds of the Chulym–Yenisey Depression, *Izv. Tomsk. Politekh. Inst.*, 1958, vol. 90, pp. 3–11.

Lebedev, I.V., Cretaceous Plants, *Biostratigr. mezozoiskikh i tretichnykh otlozhenii Zapadnoi Sibiri. Tr. SNIIGGIMS. Vyp. 22* (Biostratigraphy of Mesozoic and Tertiary Deposits of Western Siberia: Proc. SNIIGGIMS, Issue 22), Leningrad: Gostoptekhizdat, 1962, pp. 237–282.

Meek, F.B. and Hayden, F.V., Remarks on the Lower Cretaceous Beds of Kansas and Nebraska together with Description of Some New Species of Carboniferous Fossile from the Valley of Kansas River, *Proc. Acad. Nat. Sci. Philad.*, 1858, vol. 265, pp. 1–129.

Newberry, J.S., The Ancestors of the Tulip-Tree, *Bull. Torrey Bot. Club*, 1887, vol. 14, no. 1, pp. 1–7.

Newberry, J.S., The Flora of the Amboy Clays, *US Geol. Surv. Monogr.*, 1895, vol. 26, pp. 1–260.

Seward, A.C., Notes sur la flore crétacé du Groenland, *Livre Jubil. Soc. Géol. Belgique*, 1925, vol. 1, fasc. 1, pp. 229–262.

Shaparenko, K.K., *Liriodendron*, a Tulip Tree, *Tr. Bot. Inst. Akad. Nauk SSSR*, 1937, no. 4, pp. 95–170.

Shilin, P.V., *Pozdnemelovye flory Kazakhstana* (Late Cretaceous Floras of Kazakhstan), Alma-Ata: Nauka, 1986.

Upchurch, G.R. and Dilcher, D.L., Cenomanian Angiosperm Leaf Megafossils, Dakota Formation, Rose Creek Locality, Jefferson County, Southeastern Nebraska, *US Geol. Surv. Bull.*, 1990, vol. 1915.

Vachrameev, V.A., Stratigraphy and Fossil Flora of the Cretaceous Beds of Western Kazakhstan, in *Regional'naya stratigrafiya SSSR. T. 1* (Regional Stratigraphy of the USSR: Vol. 1), Moscow: Akad. Nauk SSSR, 1952.

Vachrameev, V.A., *Yurskie i melovye flory i klimaty zemli: Tr. Geol. Inst. Akad. Nauk SSSR, Vyp. 430* (Jurassic and Cretaceous Floras and Climates of the Earth: Proc. Geol. Inst., USSR Acad. Sci., Issue 430), Moscow: Nauka, 1988.

Zabaluev, V.V., Slastenov, Yu.L., Kirichkova, A.I., and Budantsev, L.Yu., The Vilyui Syneclise and Verkhoyansk Trough: Their Age and Position in the Section of the Agrafena Formation, *Geologicheskoe stroenie i voprosy neftegazonosnosti Yakutskoi ASSR, Tr. Vses. Nauchno-Issled. Geologorazved. Inst., Vyp. 385* (Yakut Autonomous Soviet Socialist Republic: Its Geological Structure and the Presence of Oil and Gas: Proc. All-Russia Inst. Geol. Exploration, Issue 385), Leningrad: Gostoptekhizdat, 1976, pp. 163–168.