

Leaves of *Ettingshausenia cuneifolia* (Bronn) Stiehler (Angiospermae) and Associated Carpels and Stamens from the Turonian of Southern Kazakhstan

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Abstract—An assemblage of plant fossils from the Kyzyl-Jar locality (southern Kazakhstan, Turonian) including polymorphic leaves of *Ettingshausenia cuneifolia* (Angiospermae), dispersed carpels, and solitary stamens, is studied. The morphology of the *E. cuneifolia* leaves resembles that of representatives of the Platanaceae. The dispersed carpels, *Platanocarpelia kyzyljarica* gen. et sp. nov. (Platanaceae), have an oval ovary with a long persistent style, and lack a hair tuft at the carpel base. Solitary stamens are morphologically similar to those of the extant genus *Platanus*. *E. cuneifolia* leaves show significant damage by various agents, mainly arthropods. The problem of classification of these plant fossils is discussed.

Keywords: morphological variability of leaves, leaf damage, Kyzyl-Jar flora, *Platanocarpelia* gen. nov., Platanaceae, Late Cretaceous

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INTRODUCTION

The flora of the Kyzyl-Jar locality (southern Kazakhstan, Turonian) was studied for the first time by Jarmolenko (1935), who recognized 24 species including a fern of the family Marsileaceae and flowering plants belonging to the families Juglandaceae, Betulaceae, Fagaceae, Ulmaceae, Menispermaceae, Lauraceae, Platanaceae, Rhamnaceae, Vitaceae, Araliaceae, and Ebenaceae. Subsequently, additional collections from this locality were obtained and studied, that significantly increased the taxonomic diversity of the Kyzyl-Jar flora (Samsonov, 1964, 1966, 1967; Shilin, 1986). A number of the species described in the Kyzyl-Jar flora (or Kzyl-Jar, Kyzyl-Zhar, Kyzylzhar according to different authors) reached 146 (Samsonov, 1966, 1967). In the flora composition, horse-tails (*Equisetum* L.), gymnosperms of the families Ginkgoaceae, Araucariaceae, Cupressaceae, and Podocarpaceae, and angiosperms belonging to the families Magnoliaceae, Cercidiphyllaceae, Moraceae, Salicaceae, Fabaceae, Sapindaceae, Celastraceae, Myricaceae, Apocynaceae, Elaeagnaceae, and Cornaceae were also identified. According to all previous researchers, *Platanus*-like leaves assigned mainly to several extinct species of the genus *Platanus* L. domi-

nated the plant fossil assemblages of the locality, comprising up to 60% of all collected material (Jarmolenko, 1935; Vachrameev, 1952; Samsonov, 1964, 1966). Within platanoids, Samsonov (1966, 1967) indicated eight species of *Platanus* based on leaves as well as species of genera *Credneria* Zenker, *Aspidiophyllum* Lesquereux, *Protophyllum* Lesquereux, *Pseudoprotophyllum* Hollick, and *Platanophyllum* Fontaine. Besides, dispersed carpels were described as a new genus, *Platanocarpus* Jarm., assigned to the family Platanaceae (Jarmolenko, 1935). The systematic affinity of some fossil plants from Kyzyl-Jar was subsequently revised by the authors of *Fossil Flowering Plants of USSR (Iskopaemye...*, 1974, 1982) publications. A critical review based on modern taxonomic concepts is needed for a reasonable assessment of the composition of the Cretaceous Kyzyl-Jar flora, which according to published data consists largely of species of extant genera.

This paper aims to analyze the variability of *Platanus*-like leaves from the Kyzyl-Jar locality based on a large amount of existing material, to study the dispersed carpels and stamens associated with these leaves using a scanning electron microscope (SEM),



Fig. 1. Kyzyl-Jar locality on north-eastern slopes of Karatau Ridge, Southern Kazakhstan. Basic map is on the web-site <https://www.freeworldmaps.net/asia/kazakhstan/map.html>.

and to discuss the problems of classification of these fossils.

MATERIALS AND METHODS

The Kyzyl-Jar fossil site is located in southern Kazakhstan on the north-eastern slopes of Karatau Ridge, descending in a valley of lake Ashchykol' (Fig. 1). The stratigraphic section of Kyzyl-Jar hill is about 20 m thick and consists predominantly of red sandstones with gravelstone and clay interlayers. The unit of gray, gray-yellow, and ocher-yellow clays about three meters thick located near the middle part of the section contains numerous plant fossils (Jarmolenko, 1935; Samsonov, 1966; Shilin, 1986). The plant fossils are represented by well-preserved impressions without phytolites. The incrustations preserved on the surfaces of several leaves reflect some of their epidermal features. Moreover, the plant-bearing layers yielded insect and fish remains (Samsonov, 1966; Zherikhin, 1978). The age and stratigraphic position of these continental deposits have been controversial. Based on comparison of the Kyzyl-Jar flora with other Cretaceous floras, the sequence was assigned to the Cenomanian-Turonian (Jarmolenko, 1935; Vachrameev, 1952). Yanshin (1953) considered these deposits as Turonian in age, while Nikiforova (1960) assigned them to the lower part of the Turonian-Santonian Koturbulak Formation. Samsonov (1964, 1966) dated the fossiliferous deposits as the Turonian, based on comparison of the species composition of the Kyzyl-Jar flora with Cretaceous floras of Kazakhstan known

at the time. In subsequent years, the Turonian age of the Kyzyl-Jar locality became commonly accepted (Vachrameev et al., 1970; *Iskopaemye tsvetkovye rasteniya ...*, 1974, 1982; Shilin, 1975, 1986). Currently, these deposits are assigned to the Kyzyl-Jar sequence of Turonian age (Stratigraficheskie skhemy, 1996).

Our study is based on the following collections: (1) no. 5536, impressions of leaves and dispersed carpels of Platanaceae, kindly donated in 2001 by P.V. Shilin (Institute of Botany and Phytointroduction CS MES RK, Almaty, Kazakhstan) to N.P. Maslova; (2) nos. 2383, 3289, collections of entomological expeditions of Borissiak Paleontological Institute of Russian Academy of Sciences (PIN RAS, Moscow); (3) no. 407, collected by E.P. Korovin (Central Asian State University, Tashkent) in 1934 and donated to Jarmolenko from the Komarov Botanical Institute of Russian Academy of Sciences (BIN RAS, St. Petersburg) for study; (4) SGM-1835, collected by M.A. Akhmetiev from Geological Institute of Russian Academy of Sciences (GIN RAS, Moscow) in 1964. The collections nos. 5536, 2383, and 3289 are deposited in PIN RAS, the collection no. 407 is deposited in BIN RAS, the collection SGM-1835 is deposited in Vernadsky State Geological Museum of Russian Academy of Sciences (SGM RAS, Moscow).

For the leaf descriptions, we use the terminology of Ellis et al. (2009). Leaf damage was classified using the guide of Labandeira et al. (2007). Photographs of plant fossils were taken using a Nikon Coolpix 8700 digital camera and Leica DFC420 camera on a Leica M165c stereomicroscope (LM). Photomicrographs

were made using a TescanVega XMU SEM (PIN RAS) in a low vacuum mode, without a coating.

SYSTEMATIC PALEONTOLOGY
DIVISION ANGIOSPERMAE

Genus *Ettingshausenia* Stiehler, 1857

Ettingshausenia cuneifolia (Bronn) Stiehler, 1857

Platanus cuneifolia (Bronn) Krysh.: Jarmolenko, 1935, p. 17, pls. 9–10, 3; Samsonov, 1966, p. 35, pl. 6, figs. 5–6.

P. cuneifolia Bronn f. *pseudoquillelmae* Krasser: Samsonov, 1966, p. 36, pl. 7, figs. 1, 3.

P. aff. cuneifolia Bronn: Samsonov, 1966, p. 37, pl. 7, fig. 2.

P. cuneiformis Krasser: Jarmolenko, 1935, p. 18, pl. 7, 4; pl. 8, 3; Samsonov, 1966, p. 33, pl. 5, fig. 3.

P. embicola Vachr.: Samsonov, 1966, p. 35, pl. 6, figs. 2–4.

P. aff. embicola Vachr.: Samsonov, 1967, p. 104, pl. 2, fig. 11.

P. latior Knowlton: Samsonov, 1966, p. 34, pl. 5, figs. 4–5.

P. aff. latior Knowlton: Samsonov, 1966, p. 33, pl. 6, fig. 1.

P. newberryana Heer: Jarmolenko, 1935, p. 14, pl. 8, 5.

P. palibinii Jarm.: Jarmolenko, 1935, p. 19, pl. 6, 4; pl. 7, 3.

P. populina Jarm.: Jarmolenko, 1935, p. 16, pl. 8, 1.

P. pseudoquillelmae Krasser: Shilin, 1986, pl. 19, 1.

P. raynoldsii Newb.: Samsonov, 1967, p. 103, pl. 2, fig. 9.

Platanus sp. 1: Jarmolenko, 1935, p. 15, pls. 9–10, 4–5.

Platanus sp. 2: Jarmolenko, 1935, p. 16, pls. 3–4, 2, 5; pl. 7, 2.

Platanus sp.: Samsonov, 1966, p. 38, pl. 7, figs. 4, 5.

Credneria archangelskii Vachr.: Samsonov, 1966, p. 38, pl. 7, fig. 6.

Credneria dentata Vachr.: Samsonov, 1966, p. 39, pl. 8, fig. 1.

Pseudoprotophyllum aff. *viburnifolium* Hollick: Samsonov, 1966, p. 42, pl. 9, fig. 1.

Betulites westii Lesq.: Jarmolenko, 1935, p. 8, pl. 2, 1–4.

Betulites cf. *westii* Lesq.: Jarmolenko, 1935, pl. 2, 5.

Description (Figs. 2–12). The leaves are simple, petiolate. The preserved petiole length reaches 50 mm, the petiole base is inflated (Figs. 7a, 7b, 7d, 7f). The leaves are polymorphic (Fig. 2), unlobed (Figs. 3a–3f, 4a–4d, 4f–4h, 7a, 7d) or palmately lobed (Figs. 5, a–h, 6a–6h), sometimes asymmetrical (Fig. 3e, 6a, 6b, 6f, 7c), elliptic (Figs. 3a–3f, 4g, 5c, 5e, 6c–6e, 6g), ovate (Figs. 4b, 4d, 4f, 5a, 5b, 5d, 5f, 5h, 6a, 6b, 6f, 6h), or obovate (Figs. 4h, 7a, 7d, 12a) in shape, with stipules (Figs. 7a, 7b) or without them. The lamina length varies from 2.2 to 15.0 cm (7.2 cm in average), the width varies from 2.5 to 15.5 cm (7.1 cm in average). The ratio of the length of the lamina to its width varies from 0.78 to 1.67 (mean value is 1.03). The leaf base angle is obtuse (Figs. 4c, 5a, 5b, 5e, 6a, 6c, 6d, 6f, 6g, 7a, 7c–7e, 7g) or acute (Figs. 4h, 5c, 5f, 5h, 7h, 7j, 8h); the base is cuneate (Figs. 4c, 4e, 5c, 5e, 6g, 7e, 7f), concave (Figs. 5a, 5f, 5h, 6h, 7h, 7j, 8h), rounded (Figs. 3a, 3d, 7a, 7c, 7d), or truncate (Fig. 4b; Fig. 8g), sometimes asymmetrical (Fig. 7i). The leaf apex angle is acute (Figs. 3a, 3e, 4c, 5a, 5c–5f, 6f, 6h) or obtuse (Figs. 3b, 3d, 3f, 4a, 4f), the apex is straight (Figs. 3a, 3f, 4c, 5a, 5c, 5e, 5f, 6f, 6h), rarely rounded (Figs. 4a, 4f). The lobes of the lobate leaves are small, sometimes asymmetrically placed (Figs. 5h, 6a, 6b, 6f), triangular in shape, with acute apices. The

leaf margin is toothed. The teeth are of three orders, different in size: large, terminating the secondary veins (first order teeth), intermediate, terminating the large branches of the secondary veins (second order teeth), and small, terminating the small branchlets (third order teeth). The teeth are concave/concave (Figs. 3e, 4c, 4e, 4g, 5a, 5e, 5g, 5h, 8b), concave/straight (Figs. 5c, 5e, 8f), concave/convex (Fig. 3b), or convex/convex (Figs. 3a, 7i) in shape. The teeth of different shape occur often within the same leaf. The tooth sinuses are rounded. The tooth apices are acute (Figs. 3e, 3f, 4g, 5a, 5d–5g), acuminate (Figs. 4c, 4d, 5c), rarely rounded (Figs. 4a, 4f), often glandular. Number of teeth per 1 cm of leaf margin is from two to four. The leaf base (up to 1/3 of the lamina proximal part) is untoothed.

The venation is actinodromous. The midvein is straight or slightly curved in the upper part. The lateral primary veins are suprabaasal, rarely basal, convex, almost equal in their thickness to the proximal pair of the secondary veins, diverge suboppositely (Figs. 3e, 3f, 4a, 4e, 4f, 5a, 5h, 6e, 6f, 6h, 7c, 7f, 7h, 7j, 8h) or with some shift relative to each other (Figs. 3d, 4b, 4c, 5b, 5e, 5f, 6a, 6c, 6d, 6g, 7a, 7d, 7e, 7g, 7i), extend upward or outward, reaching from one half to four fifths of the lamina length or slightly more, sometimes bifurcating at the margin (Figs. 3b, 3d, 4a, 4b, 7d). Agrophic veins are compound, occasionally simple, with the minor secondary veins branching from the lateral primary veins toward the leaf margin. Agrophic veins terminate at the tooth apex (Figs. 4b, 5h, 6a, 6b, 7a), or form brochidodromous loops at the margin (Figs. 3a, 4c, 5e, 6g). One or two pairs of thin infrabaasal veins are present (Figs. 3a, 3d, 3e, 4b, 4c, 5e, 5f, 5h, 7a, 7d, 7f, 7i). Secondary veins are craspedodromous, straight to somewhat curved, occasionally forking at the leaf margin. Three to six major secondaries arise from each side of the midvein, and up to three minor secondaries arise from the internal side of lateral primary veins (Figs. 3f, 5c, 5e–5h, 6a–6f). Tertiary veins are convex or straight, oppositely percurrent, up to nine per 1 cm of the secondary vein length. Higher-order veins form a fine orthogonal network. Leaf domatia occasionally occur on the lower leaf surface in the axils between the midvein and secondary or lateral primary veins (Figs. 8h, 8i).

The study of the leaf incrustations showed the numerous trichome bases on the upper leaf surface surrounded by radial cuticular striation (Fig. 10).

Remarks. Only taxa previously described from the Kyzyl-Jar flora were included in the synonymy of the species. Dispersed carpels described here as a new genus (Figs. 12–14) and stamens (Fig. 15) are associated with the leaves of *Ettingshausenia cuneifolia*.

Most of fossil leaves are damaged by various agents (Figs. 3a, 3e, 4b, 4c, 4e, 4g, 4h, 5d, 5e, 5g, 5h, 6c, 6d, 6f, 6h, 7a, 7b, 7f, 7g, 8g, 9a, 9b, 11a–11e; 12a–12d).

Material. In total, 205 samples were studied.

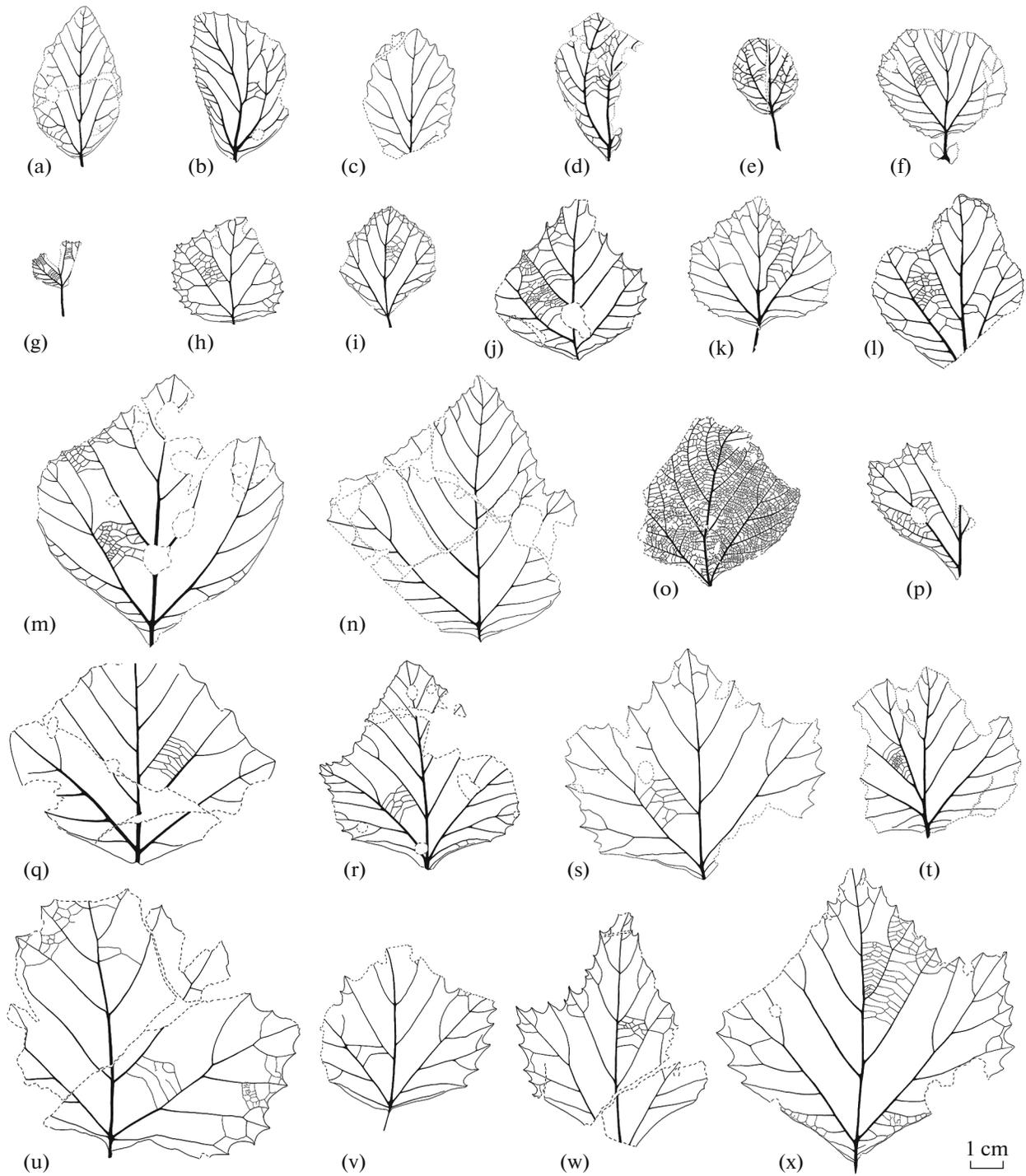


Fig. 2. Morphological variability of *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves: (a) specimen SGM-1835-14/FL-8607; (b) specimen SGM-1835-26/FL-8619; (c) specimen SGM-1835-16/FL-8609; (d) specimen SGM-1835-60/FL-8653; (e) specimen SGM-1835-11/FL-8604; (f) specimen SGM-1835-65/FL-8658; (g) specimen SGM-1835-27/FL-8620; (h) specimen SGM-1835-71/FL-8664; (i) specimen SGM-1835-10/FL-8603; (j) specimen SGM-1835-12/FL-8605; (k) specimen SGM-1835-50/FL-8643; (l) specimen SGM-1835-51/FL-8644; (m) specimen SGM-1835-19/FL-8612; (n) specimen SGM-1835-22/FL-8615; (o) specimen SGM-1835-08/FL-8601; (p) specimen SGM-1835-67/FL-8660; (q) specimen SGM-1835-37/FL-8630; (r) specimen SGM-1835-46/FL-8639; (s) specimen SGM-1835-34/FL-8627; (t) specimen SGM-1835-56/FL-8649; (u) specimen SGM-1835-31/FL-8624; (v) specimen SGM-1835-61/FL-8654; (w) specimen SGM-1835-45/FL-8638; (x) specimen SGM-1835-18/FL-8611.

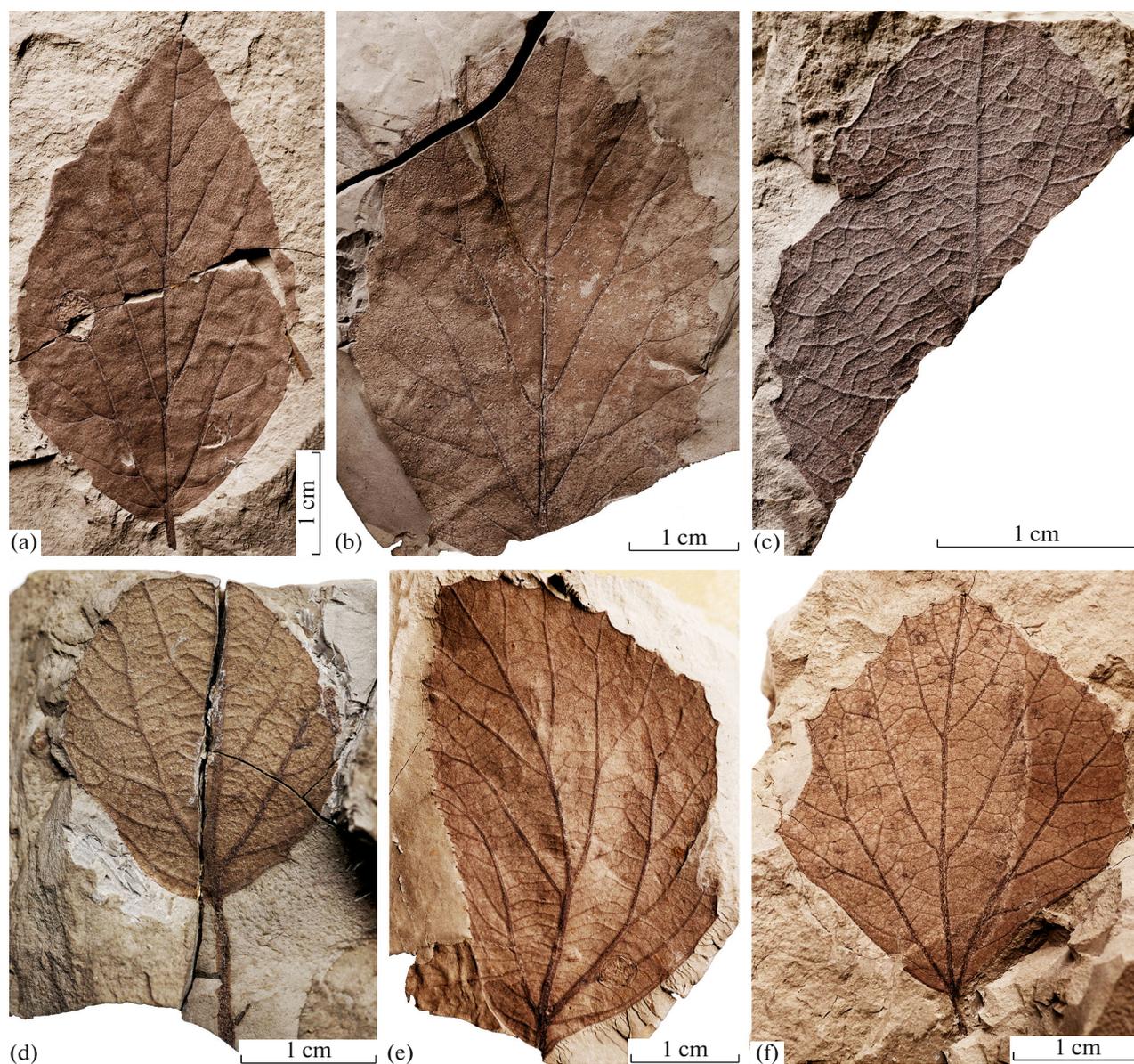


Fig. 3. *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves with unlobed laminae: (a) specimen SGM-1835-14/FL-8607; (b) specimen SGM-1835-16/FL-8609; (c) specimen SGM-1835-25/FL-8618; (d) specimen SGM-1835-11/FL-8604; (e) specimen SGM-1835-26/FL-8619; (f) specimen SGM-1835-10/FL-8603.

Family Platanaceae Lestiboudois, 1826

Genus *Platanocarpelia* N. Maslova et Kodrul, gen. nov.

Etymology. From *Platanus*, the generic name of the plane-tree, and the Latin *carpellum* (carpel).

Species composition. The type species.

Diagnosis. Carpels dispersed. Ovary oval, about 1 mm wide, up to 2 mm long. Style persistent, up to 4 mm long. Ovary epidermal cells elongated quadrangular.

Comparison. The new genus is most similar to *Macginicarpa* Manchester from the Eocene of North America (Manchester, 1986) in the ovary shape, persistent style, and lack of a hair tuft at the carpel base.

The carpels of the new genus differ in the longer style exceeding the ovary length and lesser size of the ovary. Besides, the genus *Macginicarpa* was described based on a head infructescence, the morphology and anatomy of which were studied in detail. The morphology of the infructescences produced *Platanocarpelia* remains unknown.

***Platanocarpelia kyzyljarica* N. Maslova et Kodrul, sp. nov.**

Etymology. From the Kyzyl-Jar locality.

Holotype. Specimen no. 5536-5, aggregation of carpels; Southern Kazakhstan, Karatau Ridge, Kyzyl-Jar; Turonian; designated here, Figs. 13b, 13c, 13f, 13g.

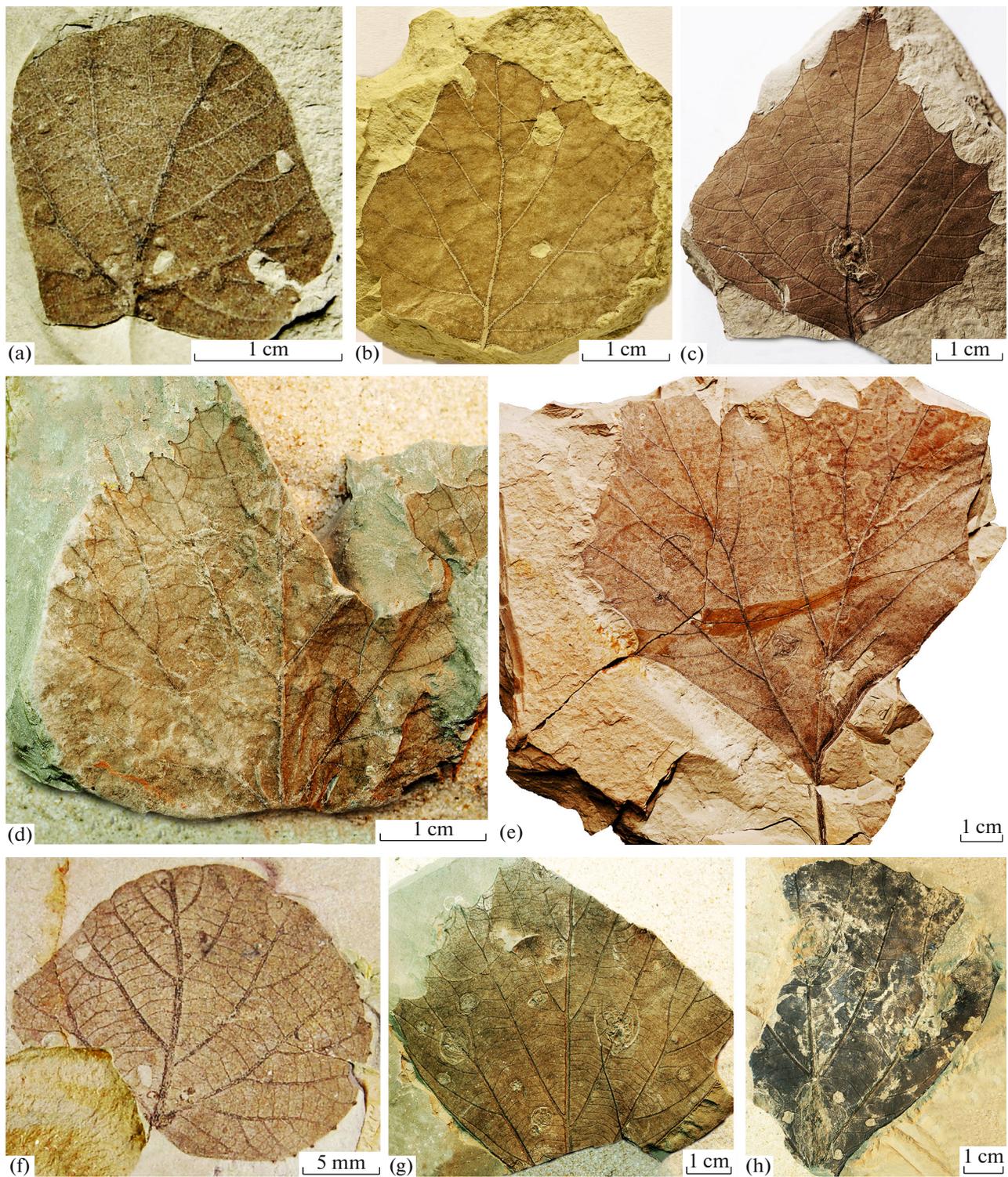


Fig. 4. *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves with unlobed (a–d, f–h) and lobed laminae (e): (a) specimen SGM-1835-13a/FL-8606; (b) specimen no. 5536-15, hole feeding and a margin feeding are visible; (c) specimen SGM-1835-12/FL-8605, large gall on a vein is visible; (d) specimen no. 407-159, teeth different in shape and size are visible; (e) specimen SGM-1835-20/FL-8613, large gall and round mine are visible; (f) specimen SGM-1835-13b/FL-8606; (g) specimen no. 407-69, large galls are visible; (h) specimen no. 407-3, large galls are visible

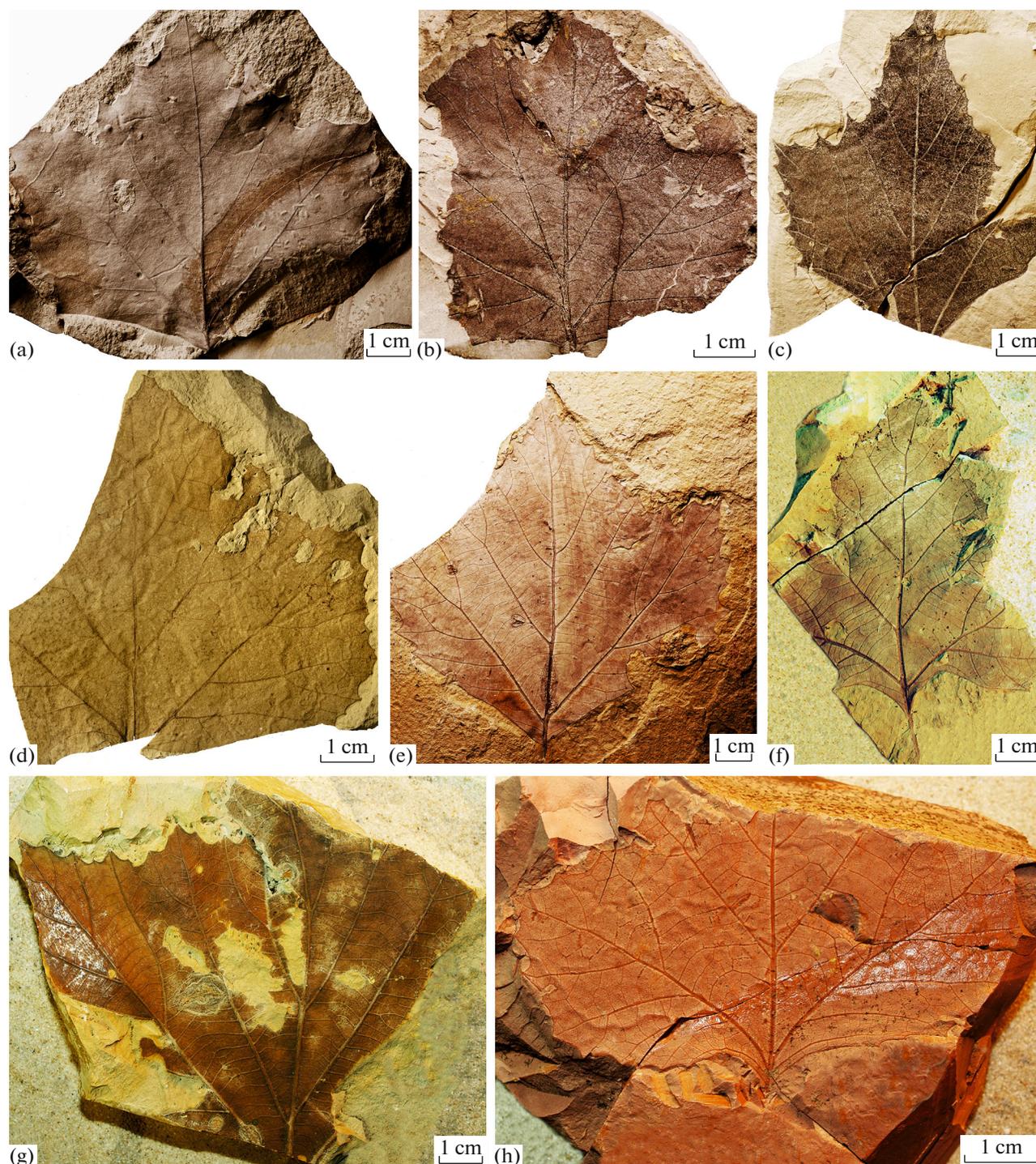


Fig. 5. *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves with lobed laminae: (a) specimen SGM-1835-34/FL-8627, hole feeding is visible; (b) specimen SGM-1835-56/FL-8649; (c) specimen SGM-1835-45/FL-8638; (d) specimen no. 5536-75, hole feeding and margin feeding are visible; (e) specimen SGM-1835-18/FL-8611, margin feeding and galls are visible; (f) specimen no. 407-92; (g) specimen no. 407-B-626, galls are visible; (h) specimen no. 407-106, margin feeding is visible.

Diagnosis. As for the genus.

Description (Figs. 11–13). The carpels are dispersed, clustered in groups, oriented in different directions in the same plane. The length of a mature

ovary is 1.2–2.0 mm, the width is 0.7–1.1 mm. The ovaries are oval in shape. The dorsal side of the ovary in a mature carpel is convex, the ventral one is straight (Fig. 14e). The styles are persistent, exceeding in



Fig. 6. *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves with lobed laminae: (a) specimen no. 2383-212b; (b) specimen no. 2383-212a; (c) specimen no. 5536-80a, hole feeding and viral or bacterial damage are visible; (d) specimen no. 5536-80b, hole feeding and viral or bacterial damage are visible; (e) specimen SGM-1835-08/FL-8601; (f) specimen SGM-1835-22/FL-8615, hole feeding is visible; (g) specimen SGM-1835-37/FL-8630; (h) specimen SGM-1835-46/FL-8639, galls are visible.

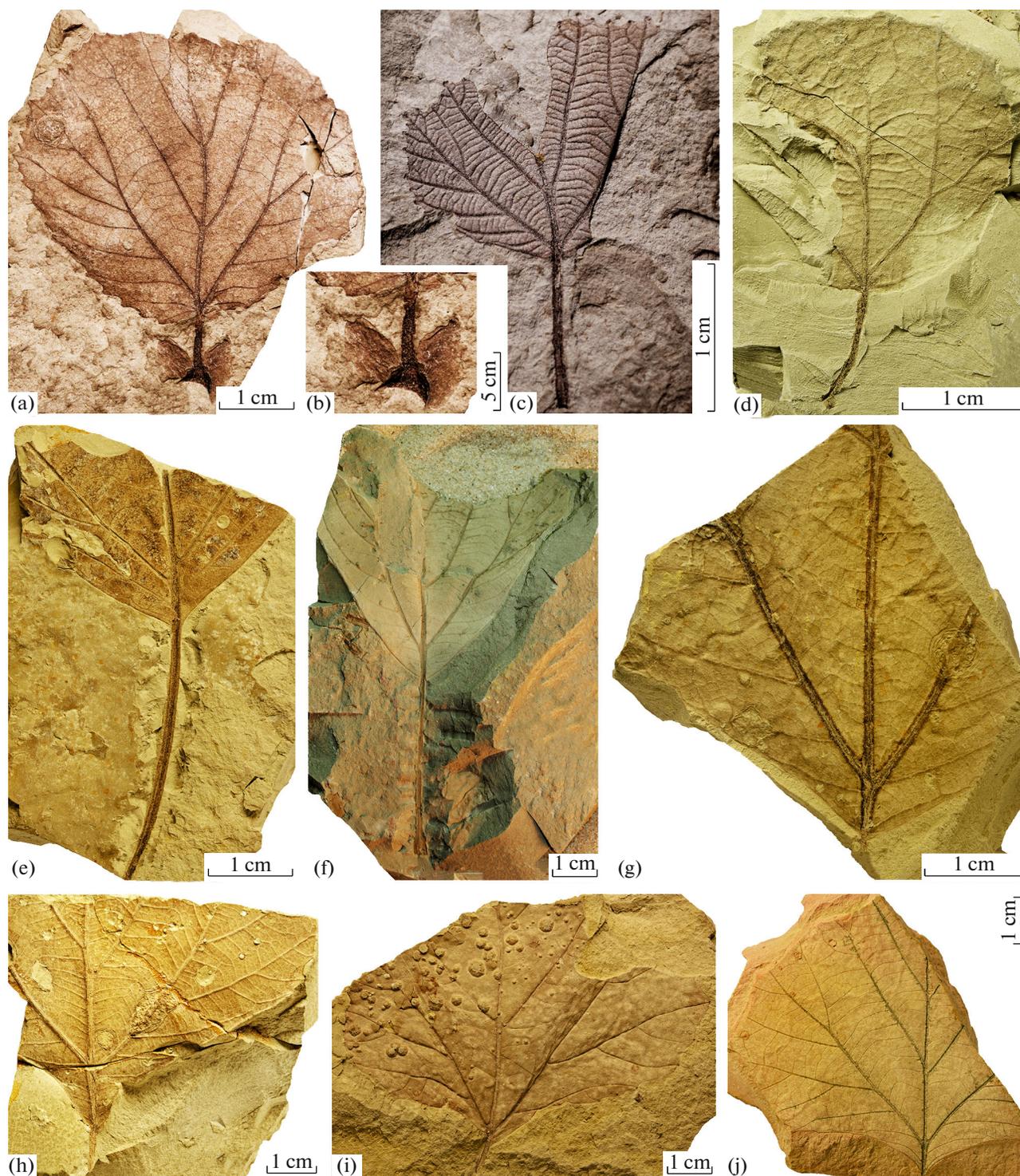


Fig. 7. Petioles and bases of *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves: (a) specimen SGM-1835-65/FL-8658, leaf with short petiole with inflated base and stipules, base shape is rounded, gall is visible; (b) specimen SGM-1835-27/FL-8620, leaf asymmetrical, base shape is rounded, margin feeding is visible; (c) specimen no. 3289-48, leaf with rounded base; (d) specimen no. 5536-6, lower part of leaf with asymmetrical cuneate base; (e) specimen no. 407-82, lower part of leaf with cuneate base; (f) specimen no. 5536-21, lower part of leaf with asymmetrical cuneate base, galls are visible; (g) specimen no. 5536-65, lower part of leaf with concave base, galls are visible; (h) specimen no. 5536-37, leaf fragment with asymmetrical concave base; (i) specimen no. 5536-23, leaf fragment with concave base.

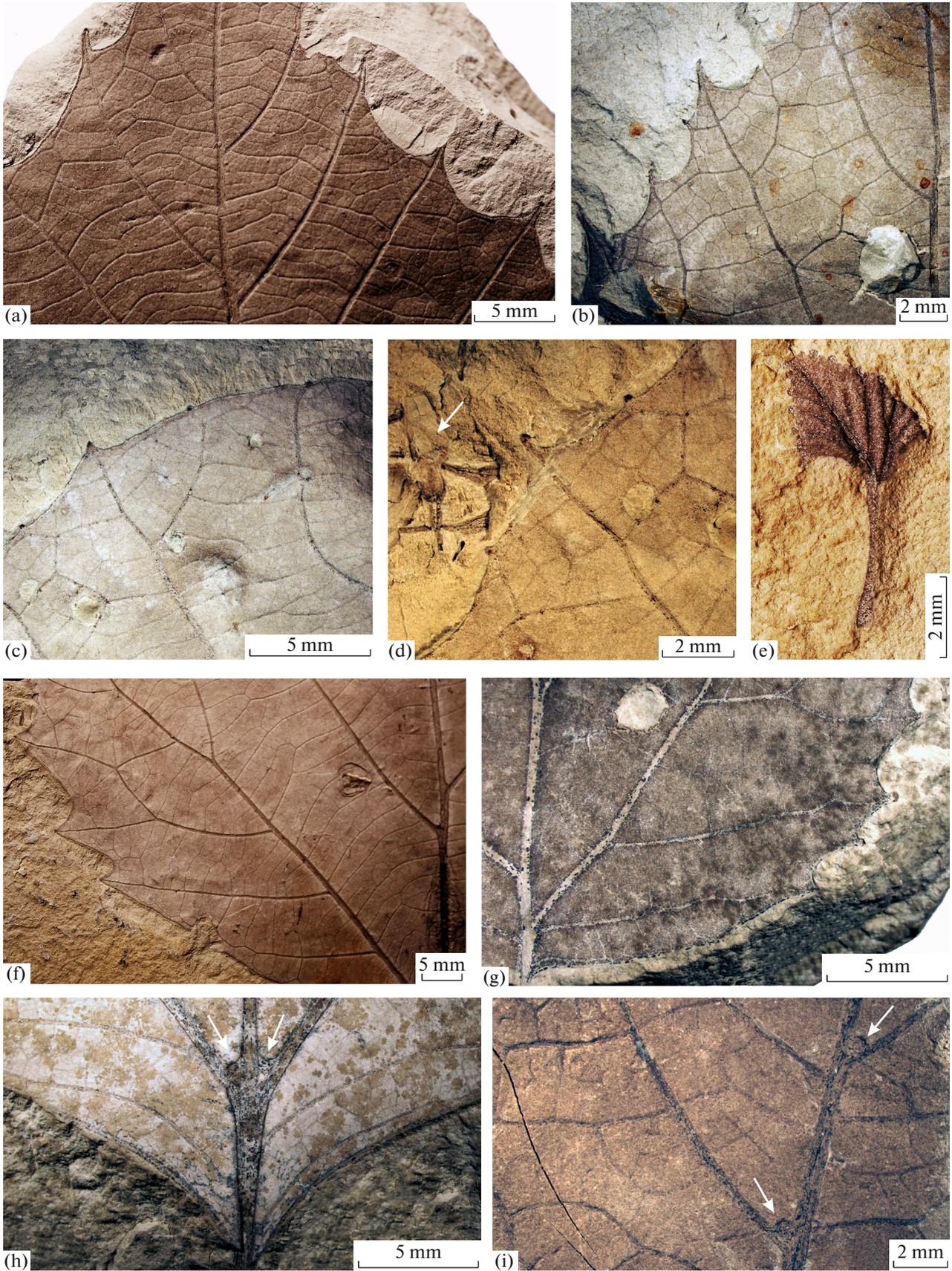


Fig. 8. Morphological details of *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves: (a) specimen SGM-1835-12/FL-8605, tertiary venation and shape of the first order teeth; (b) specimen no. 5536-25, tertiary venation and shape of teeth of the first and second orders; (c) specimen no. 5536-17, tertiary venation and shape of teeth of the first and second orders; (d) specimen no. 5536-17, teeth of different shape and size, carpels of *Platanocarpelia kyzyljarica* gen. et sp. nov. lying nearby are visible (arrow); (e) specimen SGM-1835-15/FL-8608, fragment of immature leaf with glandular teeth; (f) specimen SGM-1835-18/FL-8611, tertiary venation and agrophic veins terminating at the tooth apex or forming brochidodromous loops at the margin; (g) specimen no. 5536-15, lower part of leaf, primary lateral veins extend at different distance from the base, a hole feeding is visible; (h) specimen no. 5536-23, domatia in axils of primary lateral veins (arrows); (i) 5536-68, domatia in axils of secondary veins (arrows).

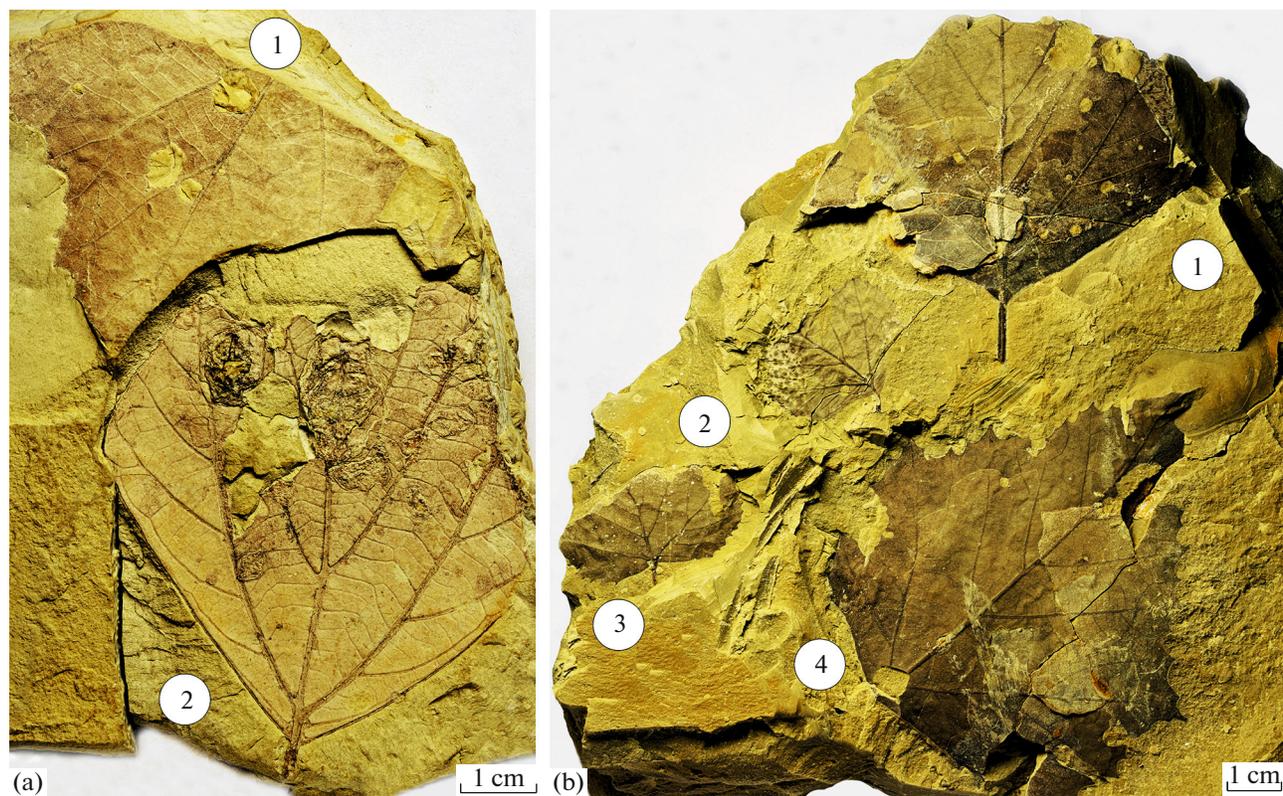


Fig. 9. Different morphotypes of *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves: (a) specimen no. 5536-36-1, specimen no. 5536-36-2; (b) specimen no. 3289-56-1, specimen no. 3289-56-2, specimen no. 3289-56-3, specimen no. 3289-56-4.

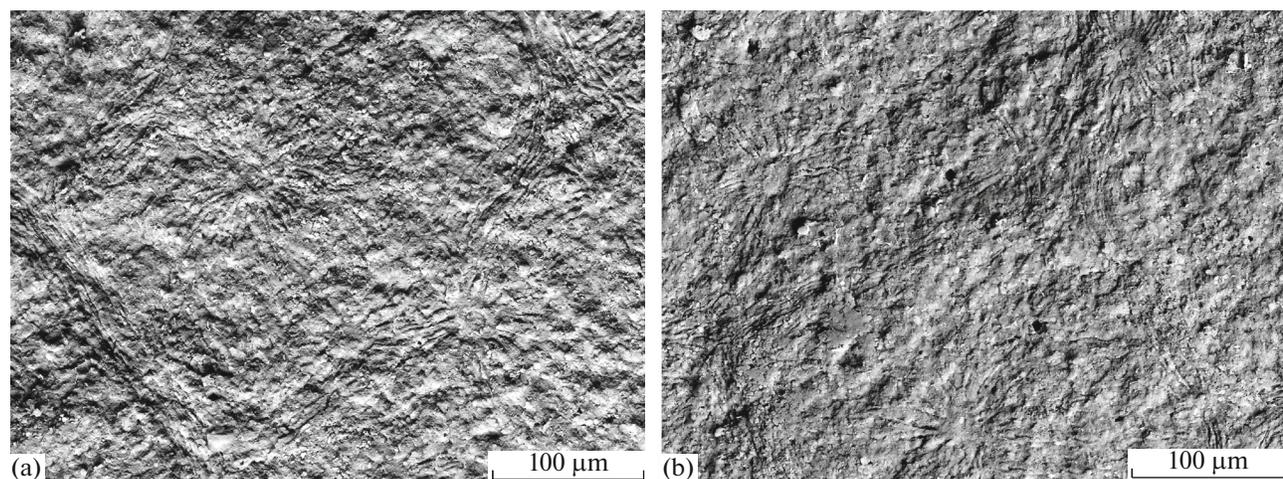


Fig. 10. Incrustations on *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves, cuticular striation radiating from trichome bases are visible, SEM: (a) specimen no. 2383-212a; (b) specimen no. 3289-42.

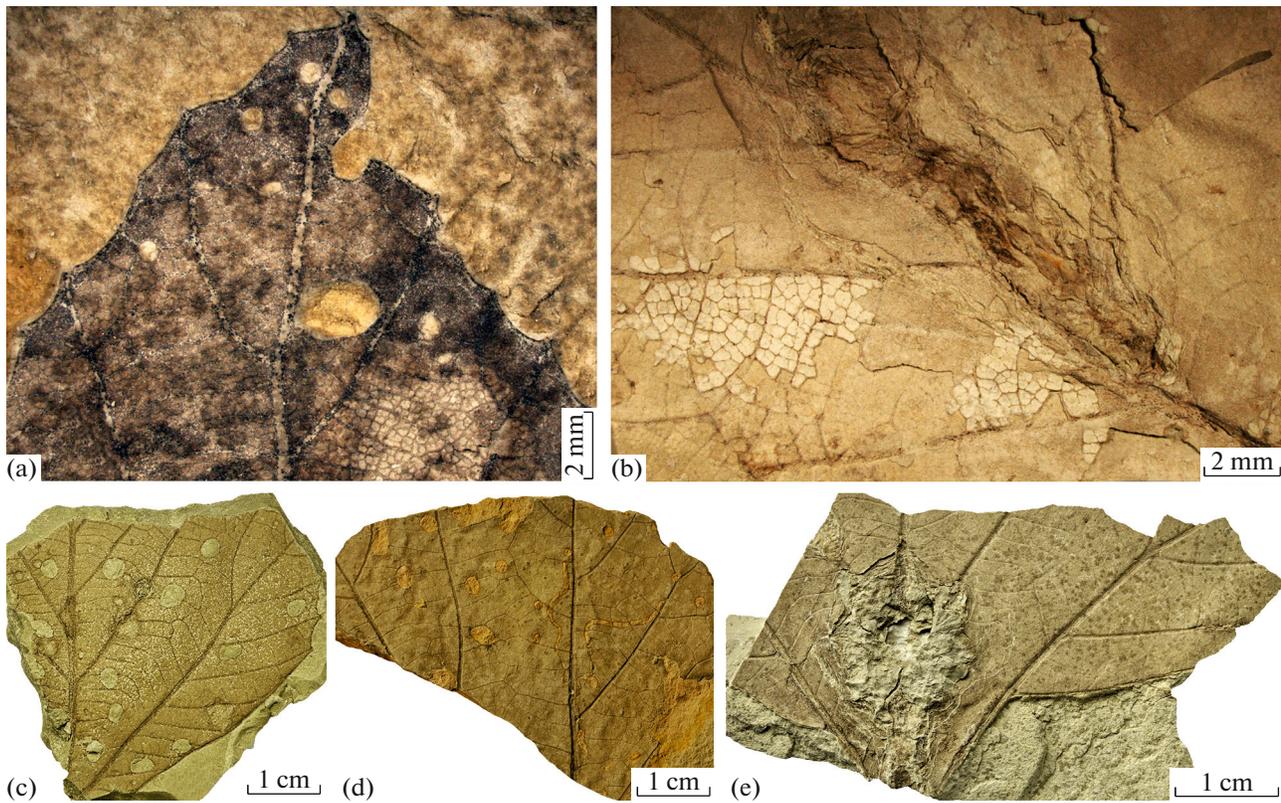


Fig. 11. Damage on *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves: (a) specimen no. 5536-42, margin feeding, hole feeding, and skeletonization; (b) specimen no. 5536-17, skeletonization and galls on vein; (c) specimen no. 3289-59, hole feeding and galls; (d) specimen no. 5536-34, hole feeding and serpentine mine; (e) specimen no. 5536-85, galls on veins.

length the ovary, reach 4.0 mm in length. The ventral suture is expressed from the ovary base, observed along the entire length of the style (Figs. 13b, 13f, 13g). The ovary epidermis is composed of elongated rectangular cells up to 100 μm long, up to 40 μm wide (Fig. 14d).

Material. 16 specimens.

Stamens

Within the clusters of the carpels (Fig. 13e) as well as on the surface of the leaves of *Ettingshausenia cuneifolia* (Fig. 15a), solitary stamens were found. The length of the filament reaches 450 μm , the length of the stamen is 3 mm, the width of the stamen is 800 μm , the width of the connective reaches about 300 μm . The extension of the connective is not completely preserved.

DISCUSSION

To the systematics of leaves of *Ettingshausenia*. When the first results of the study of Kyzyl-Jar flora began to be published (Jarmolenko, 1935; Samsonov, 1964, 1966), the Cretaceous *Platanus*-like leaves were assigned to the extant genus *Platanus* or to the fossil

genera *Protophyllum*, *Pseudoprotophyllum*, *Aspidiophyllum* Lesquereux, *Pseudoaspidiophyllum* Hollick, *Credneria* which were sometimes also included in the family Platanaceae (e.g., Hollick, 1930; Vachrameev, 1952). Later Vachrameev (1976) proposed the term platanomorphs (essentially the same as platanoids) for this group of the Cretaceous genera, which indicated the morphological similarity of the fossil leaves with the leaves of Platanaceae but did not postulate their affinity to this family. Numerous new species of plane-trees and platanoids have been described based on variations of morphological features of leaves. The Cretaceous floras of Kazakhstan, with numerous *Platanus* species, as well as other genera related to Platanaceae, were called “platanaceous floras” (Kornilova, 1966).

By now, the history of Platanaceae and taxa closely related to Platanaceae is well studied from the Cretaceous to the present day: new genera were described based on reproductive structures (Manchester, 1986, 1994; Crane et al., 1988, 1993; Friis et al., 1988; Pigg and Stockey, 1991; Pedersen et al., 1994; Krassilov and Shilin, 1995; Magallón-Puebla et al., 1997; Maslova, 2002; Maslova and Kodrul, 2003; Mindell et al., 2006, 2014; Maslova et al., 2007; 2012; Kodrul et al., 2013), and also examples of associations of *Pla-*

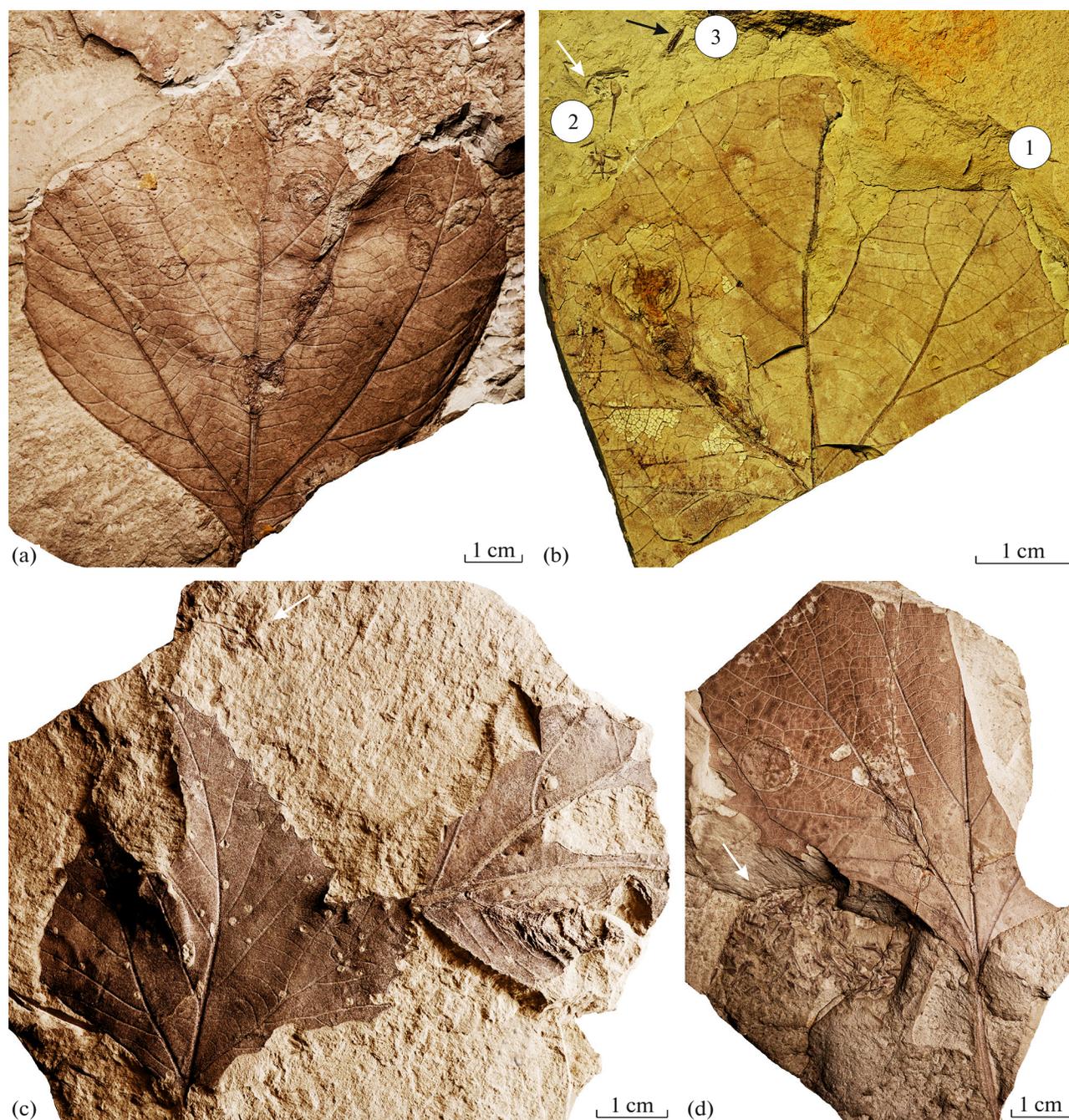


Fig. 12. *Etinghsausenia cuneifolia* (Bronn) Stiehler leaves and associated carpels of *Platanocarpelia kyzyljarica* gen. et sp. nov. and stamens: (a) specimen SGM-1835-19/FL-8612, leaf and cluster of carpels (white arrow); (b) specimen no. 5536-17-1, leaf, specimen no. 5536-17-2, carpels (white arrow), specimen no. 5536-17-3, stamen (black arrow); (c) specimen SGM-1835-57/FL-8650, specimen SGM-1835-42-2, leaves, specimen SGM-1835-42-3, carpels (white arrow); (d) specimen SGM-1835-05/FL-8598, leaf and cluster of carpels (white arrow).

tanus-like leaves and different staminate inflorescences and infructescences assigned to either Platanaceae or other families were demonstrated (Krassilov, 1976; Pigg and Stockey, 1991; Krassilov and Shilin, 1995; Maslova, 1997, 2010; Maslova and Herman, 2004, 2006; Maslova et al., 2005; Tschan et al., 2008;

Wang et al., 2011; Manchester et al., 2014; Huegele et al., 2020). Analysis of available data shows that all known Cretaceous reproductive structures related to Platanaceae are almost identical in external morphology to those of extant *Platanus*, but considerably differ in anatomical characters.



Fig. 13. Carpels of *Platanocarpelia kyzyljarica* gen. et sp. nov. associated with *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves, LM: (a) specimen no. 5536-2; (b, c, f, g) holotype no. 5536-5; (d) specimen no. 5536-90; (e) specimen no. 5536-89, carpels and stamens (arrow).

Assignment of the Cretaceous angiosperm leaves to recent genera based on morphological similarity alone was initially criticized by Wolfe (1973). Later Krassilov (1979) presented a preliminary version of classification of dispersed dicotyledonous fossil leaves for which only features of general morphology are known. Maslova and co-authors (2005) proposed to assign fossil dispersed leaves similar in morphology to leaves of the recent plane-tree to the genus *Ettingshausenia*,

classified within the morphological system. The use of the morphological system for dispersed fossil leaves of angiosperms is supported by the fact that leaves of similar morphology may belong to plants of different systematic groups, and identification of their generic or family affinity is problematic or impossible in the absence of information about diagnostically significant epidermal features.

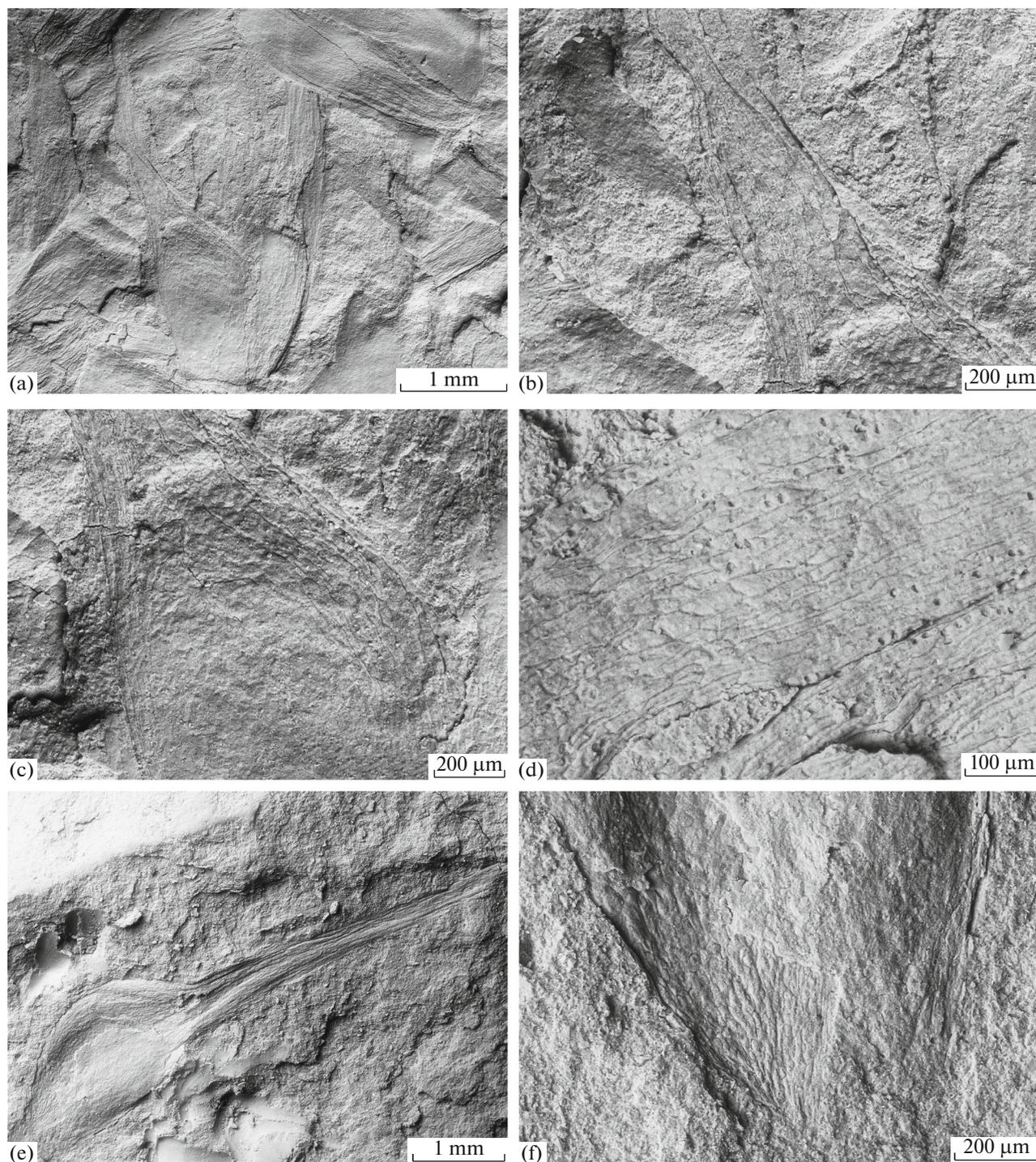


Fig. 14. Carpels of *Platanocarpelia kyzyljarica* gen. et sp. nov. associated with *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves, SEM: (a) specimen no. 5536-2, cluster of carpels; (b) specimen no. 5536-2, style, elongated epidermal cells are visible; (c, d) specimen no. 5536-2, ovary, elongated epidermal cells in rows without hair bases are visible; (e) specimen no. 5536-19; (f) specimen no. 5536-19, base of carpel ovary, epidermal cells without hair bases are visible; a hair tuft for dissemination lacks.

Identification of fossil leaves within natural system of plant classification is also complicated by repeated co-occurrence of isolated leaves of the same morpho-

type and reproductive structures that are uniform in morphology but different in anatomy. Co-occurrence of platanaceous leaves and capitate reproductive

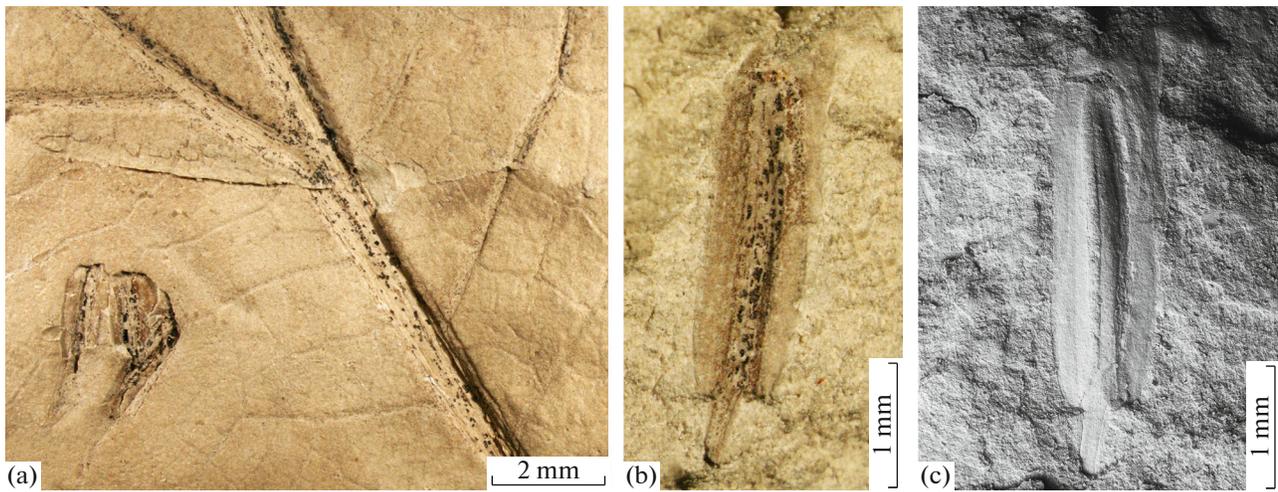


Fig. 15. Stamens associated with *Ettingshausenia cuneifolia* (Bronn) Stiehler leaves and carpels of *Platanocarpelia kyzyljarica* gen. et sp. nov.: (a) specimen no. 5536-16; (b) specimen no. 5536-17-3, LM; (c) specimen no. 5536-17-3, SEM.

structures assigned to different platanoid genera is recorded at numerous fossil localities (Krassilov, 1976; Maslova, 1997; Krassilov and Shilin, 1995; Maslova and Herman, 2004, 2006; Maslova et al., 2005, 2011, 2012; Wang et al., 2011; Maslova and Tekleva, 2012; Huegele et al., 2020).

The morphological leaf type characteristic of the extant genus might be recognized in the fossil record much earlier than its reproductive structures. The first appearance of *Platanus*-like leaves has been dated to the late Albian (Maslova, 2010), whereas the earliest currently known reproductive structures characteristic of this genus are from the Paleocene (Maslova, 1997; Kvaček et al., 2001). The earlier origin of the extant genus may be justified only by obtaining reliable evidence of existence of the Cretaceous reproductive structures of *Platanus*. The characteristic cuticular and epidermal features of the Platanaceae (predominantly anomocytic type of stomata, trichome bases associated with several underlying epidermal cells, radial cuticular striation around the stomata and trichome bases, and glandular trichomes) had also existed already in the Albian (Upchurch, 1984). However, the diagnostic significance of these features is different. The type of stomatal apparatus and specific trichomes are principal epidermal features of Platanaceae, whereas radial cuticular striation around stomata may be absent in Platanaceae, but be a characteristic feature of other taxa, for instance, some genera of Rosaceae (Kumachova et al., 2019). The microclimatic conditions under which the leaf developed also significantly affect the degree of cuticular striation. Additionally, some fossil leaves morphologically similar to those of Platanaceae are characterized by epidermal features which have not been observed in Platanaceae (Maslova and Shilin, 2011). Generally, epidermal

features substantially simplify identification of plant fossils, but they are not always available for study.

The history of study of the genus *Ettingshausenia*, as well as problems of identification of related genera, are reviewed comprehensively by Golovneva (2011). The synonymy of the type species *E. cuneifolia* was substantially extended by including a number of species of the genera *Ettingshausenia*, *Platanus*, *Credneria*, *Chondrophyllum* Bronn, and *Pseudoaspidiophyllum* from the Cretaceous of Western Europe (Czech Republic and Germany), Western Siberia, and Kazakhstan. The genus *Ettingshausenia* was accepted as monotypic and was considered within the natural system as belonging to the family Platanaceae. Along with the morphological features of leaves, Golovneva (2011) included in an extended diagnosis of the genus the epidermal characters of leaves obtained mainly from the Cenomanian Simonovo Formation (Kubaevo, Seversk, and Kas localities) in Western Siberia. Stomata in *E. cuneifolia* were characterized as anomocytic, laterocytic, and encyclocytic, and a predominance of the encyclocytic type of stomata was indicated (Golovneva, 2011; Golovneva and Nosova, 2012). It should be noted that *E. kubaensis* N. Maslova et Sokolova described also from the Kubaevo locality and defined as having only anomocytic stomata (Maslova et al., 2011) was included in the synonymy of *E. cuneifolia* (Golovneva and Nosova, 2012). Besides, *E. sarbaensis* N. Maslova et Shilin (Maslova and Shilin, 2011) from the Cenomanian-Turonian of Western Kazakhstan with a unique combination of stomatal types also was included in the extended synonymy of *E. cuneifolia* (Golovneva, 2011). This stomata type combination is not characteristic either of recent, or of other fossil representatives of the family Platanaceae. A complex of stomata identified for *E. sarbaensis* (Maslova and Shilin, 2011) includes encyclocytic,

incomplete amphicyclic, laterocytic, and more rarely paracytic types with complete absence of characteristic of Platanaceae anomocytic type. The anomocytic type of stomata predominates in the recent plane-tree as in fossil species of Platanaceae, both laterocytic and anomocytic types occur together more rarely (Kvaček et al., 2001; Carpenter et al., 2005; Maslova, 2010). Extrapolation of individual unique data (both uncharacteristic for Platanaceae encyclo-cytic type of stomata and a previously unknown combination of a few types of stomata, which has a significant diagnostic value by itself) on a species having a wide geographic and stratigraphic distribution and represented in most cases by impressions only was discussed earlier (Maslova and Herman, 2015).

Overall, the morphological and anatomical features characteristic of the *E. cuneifolia* leaves from the Kyzyl-Jar locality such as distinctive type of polymorphic foliage, expanded petiole base, presence of stipules, and radial cuticular striation around the trichome bases confirmed their platanaceous affinity. The absence of data on epidermal features of these fossil leaves, in particular, on the type of stomatal apparatus, prevents their taxonomic affinity from being identified with certainty. We suppose that the described leaves belong to a single species related to the family Platanaceae, however, we prefer to consider the Kyzyl-Jar leaves of *Ettingshausenia* within the morphological classification, until new data are obtained.

Morphological variability of leaves of *Ettingshausenia cuneifolia*. Leaves of high morphological variability assigned to *E. cuneifolia* (Golovneva, 2011), but previously described under different generic and specific names from localities in Europe (Bronn, 1838; Unger, 1849; Stiehler, 1857; Velenovský, 1882; Krasser, 1889, 1896; Kvaček and Váňová, 2006), Western Siberia (Lebedev, 1954, 1955, 1962; Golovneva, 2011; Maslova et al., 2011; Golovneva and Nosova, 2012), and Kazakhstan (Jarmolenko, 1935; Vachrameev, 1952; Samsonov, 1966, 1967; Shilin, 1986) show a number of similar morphological features. Polymorphism in *E. cuneifolia* leaves is observed in the petiole length, shape of the lamina and its base, and the size, shape and frequency of teeth. The *E. cuneifolia* leaves are predominantly unlobed with large teeth terminating lateral primary veins or, less frequently, with small lobes. Traditionally, the shape of these leaves has been defined as rhomboidal up to widely or narrowly cuneate or deltoid, more rarely hexangular (Bronn, 1838; Unger, 1849; Stiehler, 1857; Velenovský, 1882; Krasser, 1889, Vachrameev, 1952; Samsonov, 1966; Golovneva, 2011; Golovneva and Nosova, 2012). According to the terminology proposed for formalized description of leaf morphology (Ellis et al., 2009), the Kyzyl-Jar *E. cuneifolia* leaves are elliptic, ovate, or obovate in shape with cuneate, concave, rounded, or truncate base. In fossil and recent Platanaceae, the lamina shape is a substantially

variable feature not only on a specific, but also on an individual level within one plant (Fig. 16). The shape, size, and frequency of the teeth also may be different within shoots or even leaves of Platanaceae. *Ettingshausenia cuneifolia* combines leaves with small frequent teeth (Figs. 6a–6f), large teeth terminating agrophic or secondary veins (Figs. 3b; 4c; 5c) together with leaves with mixed type of teeth (Figs. 3e; 4; 5g). All variations in *E. cuneifolia* leaf morphology fall within a range of leaf morphological variability of extant Platanaceae (Maslova et al., 2008a; text-fig. 16).

Diagnostic value of a given feature may be different, and variability of features may be influenced also by ecological factors. Both morphological and epidermal features may vary appreciably within one plant, depending on, for example, placement of a leaf in the developed crown. Previously, we published the results of the study of sun and shade leaf variability in different taxa and discussed the possibility of using the data obtained for identification of plant fossils (Maslova et al., 2008a, 2008b, 2015, 2018, 2019). The principal morphological characters that depended on microclimatic conditions of leaves in the crown of the tree include the petiole length, the lamina length to width ratio, the degree of development of venation network, as well as size, shape, and distribution of teeth. The outlines of anticlinal walls of ordinary epidermal cells, number, and size of stomata and trichomes together with cuticular features (degree and type of cuticular striation, character of a peristomatic ring) are distinguished clearly in sun and shade leaves of many species of angiosperms (e.g., Zalusky, 1904; Larher, 1976).

The leaves of different morphotypes from the Kyzyl-Jar locality are considered to fall within a single species, *E. cuneifolia*, because of the presence of transitional forms between them. The leaf polymorphism of this species is also a diagnostic feature.

Reproductive structures associated with *Ettingshausenia cuneifolia* leaves. The reproductive structures, which may be considered as belonging to the family Platanaceae based of morphological features, were found in association with the *E. cuneifolia* leaves at the Kyzyl-Jar locality. Dispersed carpels externally similar to those of some fossil representatives of Platanaceae and designated here as the new genus *Platanocarpelia* and solitary stamens resembling those of *Platanus* were recovered from this locality. Jarmolenko (1935) described a new genus *Platanocarpus* (Platanaceae) for fruitlets (as identified by Jarmolenko) with a long style and a tuft of long hairs arising from the base. Samsonov (1966) also reported the occurrence of spherical infructescences and numerous impressions of dispersed fruitlets similar to those described by Jarmolenko. These reproductive structures were assigned to *Platanocarpus* sp. (Samsonov, 1966).

The fruits of the recent plane-tree have a variable number of carpels (from five to nine) having hair tuft at the base for dissemination. The carpels are also cov-

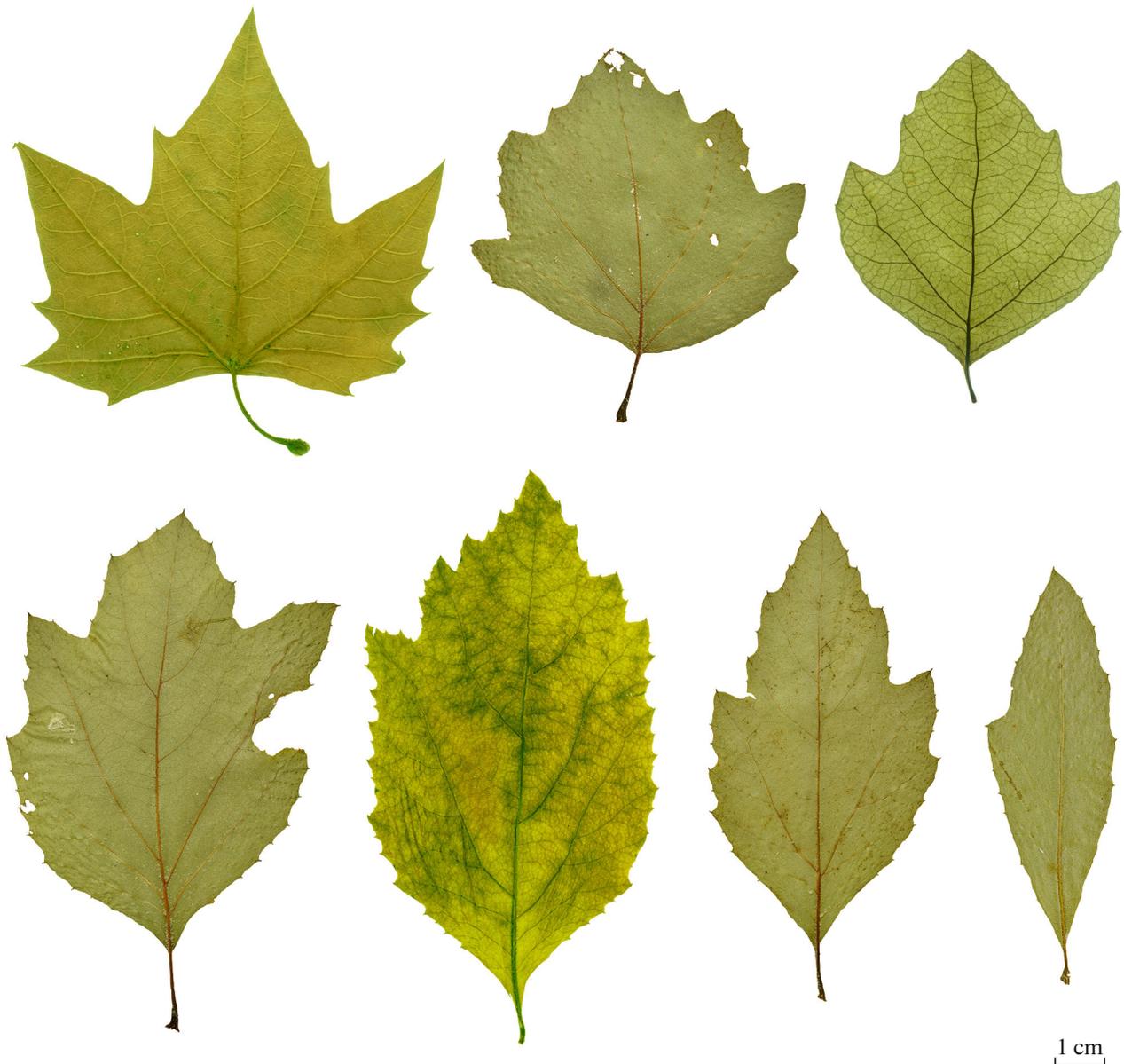


Fig. 16. Morphological variability of leaves of extant *Platanus acerifolia* Willd., the authors' herbarium.

ered with hairs. Fruits are organized in capitate infructescences (heads) borne solitary or in groups on the reproductive axis. Both a structure of fruits produced *Platanocarpelia* carpels and morphology of infructescences from Kyzyl-Jar remain unknown. The arrangement of carpels in the rock on a single plane but in different directions may indicate that they were loose in a fruit and could easily be released. The probability that the fruit consisted of a single carpel cannot be excluded, such fruits of Cretaceous platanoids have been described previously (e.g., *Anadyricarpa* N. Maslova et Herman, see Maslova and Herman, 2004; *Kasicarpa* N. Maslova, Golovneva et Tekleva,

see Maslova et al., 2005; and *Sarbaicarpa* N. Maslova, see Maslova, 2009). All listed genera differ in having pronounced perianth (sometimes with fusion of their elements in a tube tightly compressing the fruit), preserving/not abscising in mature fruits. By contrast, the fruits produced the *Platanocarpelia*, obviously, did not have developed perianth; at least, no elements of perianth were found together with the carpels. Therefore, easy disintegration of the carpels may be explained by the lack of a perianth. The loose arrangement of the carpels is also indicated by the lack of the hair tuft for dissemination at the carpel base, which, when hair interwoven, would hold the carpels in groups like in

extant *Platanus*. All known Cretaceous platanoid fruits differ in lack of dispersal hairs.

The lack of a hair tuft at the carpel base is the main feature distinguishing the carpels of the new genus *Platanocarpelia* from those of *Platanocarpus* described by Jarmolenko (1935). In Jarmolenko (1935; p. 19, text-fig. 3), there is a single drawing of a carpel with a tuft of long hairs at the base, by the artist S.P. Korovin. No other illustrations of *Platanocarpus* carpels were provided by Jarmolenko, or by subsequent researchers of the Kyzyl-Jar flora (Samsonov, 1966, 1967; Shilin, 1986). Jarmolenko did not indicate a holotype depositary of *Platanocarpus ovatus* Jarm., thus we were unable to study this specimen in detail. Our study of numerous Kyzyl-Jar carpels, including by SEM, showed the lack of a hair tuft at the carpel base and hairs on a carpel surface (Figs. 14a, 14d–14f). It is possible that depositional structures of the bedding surface could have been mistaken for a hair tuft in the first description of *Platanocarpus* because of technology limitations. However, there are no reasons to exclude the presence of the genus *Platanocarpus* in the Kyzyl-Jar flora without a detailed study of the holotype.

The styles of mature carpels of *Platanocarpelia* are persistent like those of extant *Platanus*. However, almost all known carpels of Cretaceous platanoids lack styles. This feature is known in several species of the genus *Friisicarpus* N. Maslova et Herman (Friis et al., 1988; Crane et al., 1993; Pedersen et al., 1994; Maslova and Herman, 2006; Maslova and Tekleva, 2012), and in the genera *Anadyricarpa* (Maslova and Herman, 2004), *Kasicarpa* (Maslova et al., 2005), and *Sarbaicarpa* (Maslova, 2009). The exceptions are Albian *Friisicarpus dakotensis* Wang, Dilcher, Schwarzwald et Kvaček (Wang et al., 2011), Albian-Cenomanian *F. kubaensis* N. Maslova, Tekleva et Sokolova (Maslova et al., 2011), and *Friisicarpus* sp. (Friis et al., 1988), having very short styles. Relatively long styles persistent at maturity were noted in the carpels of Cenozoic platanoids, such as *Platanites hybridicus* Forbes (Paleocene, Crane et al., 1988), *Macginicarpa glabra* Manchester (Eocene, Manchester, 1986), and *Tanyoplatanus cranei* Manchester (Eocene, Manchester, 1994).

The stamens associated with the *E. cuneifolia* leaves as well as the *Platanocarpelia* carpels are represented only by impressions. These reproductive structures morphologically similar to those of Platanaceae and leaves of *E. cuneifolia* from Kyzyl-Jar locality presumably belong to the same plant based on shared platanaceous affinity of vegetative and reproductive organs and co-occurrence even within one specimen. In Samsonov (1966; pl. 9, 2), a part of reproductive axis with two heads identified as *Platanocarpus* sp., in our opinion is most likely a fragment of a compound inflorescence with sessile stamen heads. We have been unable to study these reproductive structures, since Samsonov's collection from Kyzyl-Jar has been lost.

Damage of leaves *Ettingshausenia cuneifolia*. *Ettingshausenia cuneifolia* leaves show extensive damage by different agents, mostly arthropods. Leaf damage was classified into discrete DTs following Labandeira et al. (2007) as (1) margin feeding (DT12, D13, DT15, DT16, DT81; Figs. 4b, 4h, 5d, 5h, 6c, 6d, 7c, 11a), (2) hole feeding (DT1, DT2, DT3, DT4; Figs. 4b, 4f, 5a, 5d; 6c, 6d, 6f, 7e, 8b–8d, 8g, 11a, 11c, 11, 12c), (3) skeletonization (DT 16, Figs. 11a, 11b, 12b), (4) serpentine mines (DT 41, Fig. 11d), (5) blotch mines (DT 69, Figs. 4e, 12d), (6) galls (Figs. 3a, 3e, 4c, 4e, 4g, 4h, 5g, 6g, 6h, 7a, 7g, 7h, 9a, 11b, 11c, 11e, 12a–12d), and (7) viral or bacterial infection (Figs. 6c, 6d). None of these damage types are unique for *E. cuneifolia* leaves. Leaves of many taxa in the Kyzyl-Jar flora are noticeably damaged, and a combination of different damage types is frequently noted on the same leaf. The results of the study of the taxonomic composition of the Kyzyl-Jar flora and plant damage diversity will be published in a separate paper.

CONCLUSIONS

Based on the whole-plant concept (Kvaček, 2008), which aims to reveal an affinity between detached organs of extinct plants, we suppose that the Kyzyl-Jar fossils under study can be assigned to the same plant. This view is supported by the characteristic morphological features of the fossils studied, reflecting their similarity to fossil and recent representatives of Platanaceae, and co-occurrence of reproductive structures and leaves within one specimen. The polymorphic leaves of *E. cuneifolia* are classified within the morphological system due to a lack of epidermal data. This taxonomic decision is also supported by the association of the *E. cuneifolia* leaves with the dispersed carpels that are crucially distinguished from those of the recent plane-tree. The assemblage of plant fossils from the Kyzyl-Jar locality expands our understanding of taxonomic diversity of extinct Platanaceae and possible ancestors of the genus *Platanus*.

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