

# ***Kunduriphyllum kundurense* gen. et comb. nov. (Platanaceae) and Associated Reproductive Structures from the Campanian of the Amur Region, Russia**

**T. M. Kodrul<sup>a, b, \*</sup> and N. P. Maslova<sup>c</sup>**

<sup>a</sup>*Sun Yat-sen University, Xingang Xi Road 135, Haizhu District, Guangzhou, 510275 China*

<sup>b</sup>*Geological Institute, Russian Academy of Science, Pyzhevsky per. 7, Moscow, 119017 Russia*

<sup>c</sup>*Borissiak Paleontological Institute, Russian Academy of Science, Profsoyuznaya ul. 123, Moscow, 117647 Russia*

*\*e-mail: kodrul@mail.ru*

Received April 24, 2017

**Abstract**—Fossil leaves and associated reproductive structures from the Kundur locality, Amur Region, are examined. A new genus of the unlobed platanaceous leaves, *Kunduriphyllum* gen. nov. (Platanaceae) is described based on distinctive morphological and epidermal features. The similarity of epidermal characteristics and identical biological damage suggest that the leaves *Kunduriphyllum kundurense* gen. et comb. nov., staminate inflorescences *Kundurianthus*, and infructescences *Kunduricarpus* could be assigned to a single plant.

**Keywords:** *Kunduriphyllum*, *Celastrinites*, *Arthollia*, *Kundurianthus*, *Kunduricarpus*, Platanaceae, Cretaceous, Amur Region

**DOI:** 10.1134/S0031030117140027

## INTRODUCTION

The Upper Cretaceous and Paleogene deposits of the Zeya–Bureya Basin in the Amur Region are interesting to researchers studying the florogenesis at the Cretaceous–Paleogene boundary. Various aspects of this problem were discussed in a number of papers (Konstantov, 1914; Kryshstofovich and Baikovskaya, 1966; Krassilov, 1976; *Flora i dinozavry...*, 2001; Akhmetiev et al., 2002; Herman et al., 2009; Sun et al., 2014). In recent years, due to intense morphological studies of the Cretaceous–Paleogene plants from this region, many previous plant identifications have been corrected and new taxa described, including a number of platanoid reproductive structures and leaves (Manchester et al., 2002; Maslova and Kodrul, 2003; Kodrul and Krassilov, 2005; Kodrul et al., 2006, 2013; Kodrul and Maslova, 2007; Maslova et al., 2007; Sun et al., 2007; Golovneva et al., 2008; Krassilov and Kodrul, 2008; Krassilov et al., 2009; Manchester et al., 2009; Manchester and Kodrul, 2014).

This paper contains an analysis of two morphotypes of fossil leaves of Platanaceae from the Campanian Kundur locality and considers possible assignment of the leaves previously described as *Celastrinites kundurensis* Golovneva, Sun et Bugdaeva (Golovneva et al., 2008), infructescences *Kunduricarpus* Kodrul, N. Maslova, Tekleva et Golovneva, and staminate inflorescences *Kundurianthus* Kodrul, N. Maslova,

Tekleva et Golovneva (Kodrul et al., 2013) to a single plant.

## MATERIAL AND METHODS

The material studied comes from the upper part of the Kundur Formation in a section along the federal “Amur” (Chita–Khabarovsk) highway in the interfluvium of the Mutnaya and Udurchukan rivers, 10 km southeast of the village of Kundur, Amur Region (49°04′ N, 130°52′ E, VGS 84). Remains of reproductive structures and associated leaves were collected during biostratigraphic research of continental deposits at the Cretaceous–Paleogene boundary conducted in various years in the southeastern regions of the Zeya–Bureya Basin (*Flora i dinozavry...*, 2001; Sun et al., 2002, 2007, 2011, 2014; Van Itterbeeck et al., 2005; Markevich et al., 2005a, 2005b; Golovneva et al., 2008; Krassilov and Kodrul, 2008; Herman et al., 2009; Krassilov et al., 2009). The upper unit of the Kundur Formation is composed of alternating sandstones, siltstones, and clay with thin coal seams in the terminal part of the section (*Flora i dinozavry...*, 2001; Van Itterbeeck et al., 2005). The mostly lacustrine deposits composing the lower part of this unit contain freshwater mollusks, conchostracans, and ostracods, while infrequent beds of alluvial sandstone contain plant remains. The section of the terminal part

of the Kundur Formation formed by alluvial deposits of the fluvial, floodplain, and oxbow lake facies contains several successive beds of clay, siltstone, or medium-grained sandstone with abundant plant remains (Fig. 1). The Kundur fossil plant assemblage includes horsetails, ferns (including aquatic ferns), ginkgophytes, conifers of the family Cupressaceae sensu lato, and angiosperms dominated by platanoids, Trochodendroides, and aquatic plants of the genera *Quereuxia* and *Cobbania* (Markevich et al., 2005a, 2005b; Golovneva et al., 2008; Krassilov and Kodrul, 2008). Based on palynological data and taxonomic composition of the plant macrofossil assemblage, the upper part of the Kundur Formation is dated as Campanian (Markevich et al., 2005a, 2005b).

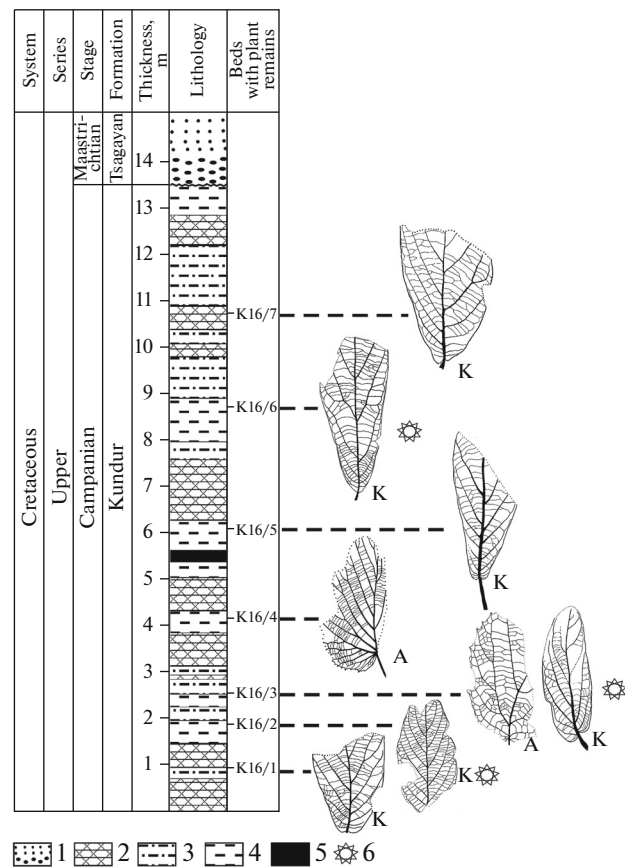
All fossil leaf impressions studied here commonly lack coaly organic matter. A few remains of cuticles and fragments of subcrustations (Krassilov and Makulbekov, 1996) were only found on the major veins and petioles of the leaves *Kunduriphyllum* gen. nov. Some parts of the leaf impressions had preserved thin mineral incrustations showing some characteristics of the epidermis. Details of the epidermis were observed using a Tescan Vega XMU scanning electron microscope (SEM) in the low vacuum regime (with no coating and with gold coating) and from the study of the cuticles preserved on the leaf veins after preparation using the standard method. The cuticles of modern leaves were obtained by treating leaf fragments for 24 hours with concentrated nitric acid and addition of potassium chlorate and subsequent complete removal of the mesophyll using dilute KOH solution. For leaf description terminology, we follow the *Manual of Leaf Architecture* (Ellis et al., 2009). Leaf photographs were taken using a digital Nikon Coolpix 8700 camera.

The collections are housed in the Geological Institute of the Russian Academy of Science (GIN), Moscow; coll. no. GIN 4867 and in the Botanical Institute of the Russian Academy of Science (BIN), St. Petersburg, coll. no. BIN 1538.

## RESULTS

Of the Kundur plant fossils, morphological characters typical of members of the family Platanaceae are observed in the leaves originally described as *Celastrinites kundurensis* (Golovneva et al., 2008) and, in this paper, assigned to the new genus *Kunduriphyllum* and also in the leaves *Arthollia tschernyschewii* (Konst.) Golovneva, Sun et Bugdaeva, infructescences *Kunduricarpus*, and staminate inflorescences *Kundurianthus*.

**Reproductive structures.** We previously described two types of capitate reproductive structures from the Kundur locality: infructescences *Kunduricarpus* and staminate inflorescences *Kundurianthus* (Kodrul et al., 2013). The compound infructescence *Kunduricarpus* is composed of an axis and heads on a pedun-



**Fig. 1.** Beds with plant fossils in a geological section of the upper part of the Kundur Formation, Kundur locality, loc. 16 (after *Flora i dinozavry...*, 2001); Amur Region. Explanations: (1) conglomerate, gravelstone, (2) sandstone, (3) gravelstone, (4) clay, (5) coal, (6) reproductive structures *Kundurianthus* and *Kunduricarpus*, (K16/1–7) numbers of beds with fossil plants, (K) *Kunduriphyllum* leaves, (A) *Arthollia* leaves.

cle. The epidermal cells of the axis lack trichomes and have square cells with transverse anticlinal walls oriented at an angle to the longitudinal cell axis. The number of fruits in a head does not exceed 30. The fruit have no persistent perianth remains, are tetra- or pentamerous, with long styles, maturing nonsimultaneously. The carpel epidermis lacks trichomes and stomata. The ovule is solitary in the carpel.

The staminate heads *Kundurianthus* are up to 10 mm in diameter, pedunculate or almost sessile. The epidermal cells of the inflorescence's axis are the same as in the infructescence *Kunduricarpus*. The flower number per head does not exceed 30. The flowers lack a perianth. Stamens vary in size within one head. Stamen filaments are not pronounced; pollen sacs are narrow, spindle-shaped, and different in size. A distinctive feature of *Kundurianthus* is the sporadic presence in inflorescences of functional, variously developed carpels with long styles. Occasionally the carpel diameter can reach the size of the inflorescence *Kun-*

*durianthus*. Pollen grains are small, finely reticulate, semitectate, tricolpate, or tricolporate, with indistinct ora. Identical pollen grains were found on the surface of the *Kunduricarpus* carpels.

***Arthollia tschernyschewii* leaves.** Leaves assigned to *A. tschernyschewii* (Golovneva et al., 2008) are very rare in the Kundur oryctocoenoses. The leaves are simple, unlobed, elliptic, or ovate, up to 8 cm wide and 15 cm long, with a reflex or obtuse base angle and cordate or rounded base shape, acute apex angle, and straight apex shape (Pl. 8, figs. 1–5). The margin of leaves is toothed from the leaf base, with densely spaced (three–four per 1 cm), regular teeth of two orders, mainly concave/concave or with straight distal and proximal flanks, 1–2 mm high, with a rounded sinus and nonspecific apex. The venation is suprabasal or basal actinodromous, craspedodromous. The primary lateral veins are slightly thicker than the secondary veins and produce compound agrophic veins. The secondary suprabasal veins are in 5–7 pairs and 1–3 pairs of infrabasal veins are present. The tertiary venation is mixed percurrent; the venation of higher orders is reticulate. No epidermal data exist for *A. tschernyschewii*.

**Leaves of *Kunduriphyllum* gen. nov.** Leaves previously assigned to the formal genus *Celastrinites* Saporta (Golovneva et al., 2008) dominate in many Kundur oryctocoenoses. They are characterized by a complex of morphological features variable within a broad range and observed in both Platanaceae and some Altingiaceae. Based on the morphological and epidermal characters, we recognize a new genus, *Kunduriphyllum*, for these leaves. Due to a peculiarity of the plant fossil preservation, a very important character, anomocytic stomata, was revealed in only a single specimen; we consider this specimen as the epitype.

## SYSTEMATIC PALEONTOLOGY

### Family Platanaceae Lestiboudois, 1826

#### *Kunduriphyllum* Kodrul et N. Maslova, gen. nov.

**Etymology.** From the Kundur locality.

**Type species.** *Celastrinites kundurensis* Golovneva, Sun et Bugdaeva

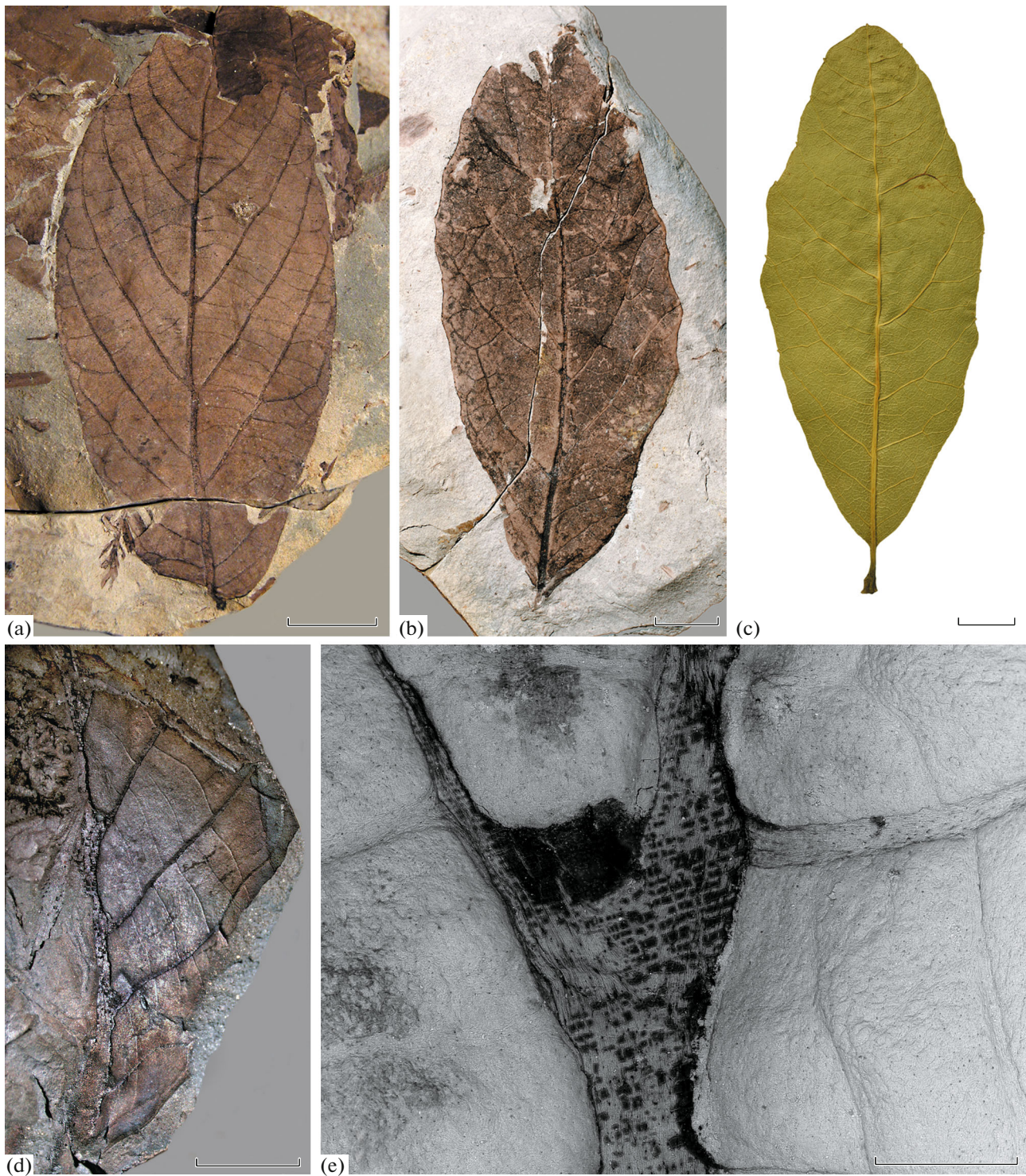
**Species composition.** Type species.

**Diagnosis.** Leaves simple, unlobed; petiole short. Lamina elliptic, rarely obovate, occasionally asymmetrical. Base angle of lamina acute, rarely obtuse; base shape rounded, slightly cordate or cuneate, asymmetrical. Apex angle of lamina acute, rarely obtuse; apex shape rounded or straight, often mucronate, rarely spinose. Margin entire or serrate in upper part of lamina, rarely toothed from lower third part of leaf. Tooth spacing irregular, one order of teeth; sinus shape rounded, tooth shape concave/convex to straight/straight, tooth apex nonspecific. Primary venation pinnate brochidodromous, often semicraspedodromous in upper part of lamina or mix craspe-

dodromous/brochidodromous. Secondaries alternate to subopposite, often irregular, with simple agrophic veins in middle part of lamina; intersecondaries rarely present. Tertiaries alternate percurrent to mixed opposite–alternate percurrent. Fourth order vein fabric reticulate. Ordinary epidermal cells of costal area of lower lamina surface with straight anticlinal walls of various sizes and shapes: square, polygonal, rectangular or with transverse anticlinal walls oriented obliquely to longitudinal axis of cell; stomata anomocytic, with four subsidiary cells. Epidermal cells of upper leaf surface rectangular, rarely polygonal, stomata and trichome bases absent.

**Comparison.** Among extant and extinct Platanaceae, unlobed elliptical leaves are observed in some species of the genus *Platanus* L. Most species of the extant genus *Platanus*, the only surviving member of the family Platanaceae, have lobed leaves, except for *Platanus kerrii* Gagnepain from southeastern Asia, which has unlobed leaves. Leaves of the new genus are distinguished from the leaves of *P. kerrii* by the greater polymorphism of leaf laminae expressed in the presence of asymmetrical and untoothed morphotypes, and by the epidermal characters (presence of ordinary cells with transverse anticlinal walls oriented at an angle to the longitudinal cell axis). Leaves of the new genus also show morphological similarity to unlobed leaves of the extant species *P. acerifolia* (Aiton) Willd. (Figs. 2b, 2c), differing in the above mentioned characters of the epidermal structure. Of all extant species of the genus *Platanus*, the fossil species is distinguished by the absence of trichomes in the leaf epidermis (*Platanus* has both nonglandular and glandular trichomes).

Simple unlobed elliptical leaves are also observed in *Platanus neptuni* (Ettingshausen) Bůžek, Holy et Kvaček, originally described from the Oligocene and Miocene deposits of northern Bohemia (Bůžek et al., 1967). Subsequently, knowledge of morphological variations of leaves of this species considerably expanded due to the occurrence in the Cenozoic deposits of Western and Central Europe of compound leaves with three or five leaflets, similar in epidermal characters to the leaves of *P. neptuni* (Walter, 1985). Kvaček and Manchester (2004) showed that simple, ternate, and pentamerous leaves of this fossil *Platanus* are found together in many localities. They are characterized by the identical epidermal characters and accompanied by the same reproductive structures. Based on these data, Kvaček and Manchester (2004) proposed the general specific name *P. neptuni* for the entire complex of these phytofossils. Simple, unlobed leaves of *P. neptuni* are similar to the leaves of the new genus in general morphology, differing in the more densely spaced marginal teeth and in the different epidermal features (epidermal cells on the upper surface of the leaves of *P. neptuni* are polylobate in shape, with sinuous anticlinal walls; cells of the lower epidermis of leaves are polygonal with slightly sinuous anticlinal



**Fig. 2.** Leaves of (a, b, d, e) *Kunduriphyllum kundurense* gen. et comb. nov. and (c) *Platanus acerifolia* (Aiton) Willd., herbarium of N.P. Maslova: (a) holotype BIN, no. 1538-95; (b) specimen GIN, no. 4867-16/3-116b-2, elliptical leaf with an acute, cuneate in shape base, small irregular marginal teeth, beginning from the lower third of the leaf lamina and mixed craspedodromous–camptodromous secondary venation; (c) unlobed leaf with a basally expanded petiole; (d) epitype GIN, no. 4867-16/6-34a-1; (e) specimen BIN, no. 1538-88, SEM, domatia. Scale bar: (a–c) 1 cm, (d) 5 mm, (e) 1 mm.

walls; stomata anomocytic (laterocytic); compound bases of trichomes are present). In addition, morphotypes of compound leaves are not known for the new genus.

**Remarks.** A number of morphological characters (shape of the leaf lamina and petiole, type of venation and tooth morphology) and newly obtained epidermal data (anomocytic stomata) suggest that the leaves *Kunduriphyllum* gen. nov. are closely related to the Platanaceae. In addition, this taxonomic assignment is supported by the similarity of the unique epidermal characters of these leaves and associated reproductive structures (the epidermis of the costal zone of the leaves and axes of compound capitate inflorescences and infructescences is formed of cells of different shapes not organized in longitudinal rows and lacking trichomes).

All known species of *Celastrinites* are recognized based on the leaf morphology only, while epidermal data for these are absent. In macromorphology, leaves of the new genus are similar to those of *Celastrinites septentrionalis* (Krysht.) Golovneva from the Campanian–Danian floras of the Koryak–Anadyr region and Paleocene Barentsburg flora of Spitsbergen, in particular, to the leaves of the “longifolia” morphotype, one of five morphotypes recognized by Golovneva (1994) within this species. The main distinguishing characters of *Celastrinites kundurensis* include (Golovneva et al., 2008) the shape of the leaf lamina (in the “longifolia” morphotype, the maximum leaf width is in the lower third) and the type of secondary venation (secondary veins in the “longifolia” morphotype are more widely spaced and irregular, branching from the midrib at various distances from one another and at slightly different angles).

The leaves *Kunduriphyllum* gen. nov. in the shape of the leaf lamina and venation type are similar to those of some species of the genus *Liquidambar* L. (Altingiaceae): *L. chinensis* Champ., *L. gracilipes* (Hemsl.) Ickert-Bond et Wen, *L. chingii* (Metcalf) Ickert-Bond et Wen, *L. obovata* (Merrill et Chun) Ickert-Bond et Wen, and *L. excelsa* (Noronha) Oken. The main difference is the type of stomata (anomocytic in *Kunduriphyllum* gen. nov. and paracytic in *Liquidambar*).

*Kunduriphyllum kundurensis* (Golovneva, Sun et Bugdaeva)  
Kodrul et N. Maslova, comb. nov.

Plate 8, figs. 6–12; Plate 9

*Celastrinites kundurensis* Golovneva, Sun et Bugdaeva: Golovneva et al., 2008, p. 104, text-figs. 3 and 4.

**Holotype.** Specimen BIN, no. 1538/95, Amur Region, federal highway Chita–Khabarovsk, loc. 16 (after *Flora i dinozavry...*, 2001); upper part of the Kundur Formation, Campanian (Fig. 2a).

**Epitope.** Specimen GIN, no. 4867-16/6-34a-1; Amur Region, loc. 16 (after *Flora i dinozavry...*, 2001); upper part of the Kundur Formation, Campanian; designated here, Fig. 2d.

**Diagnosis.** As for the genus.

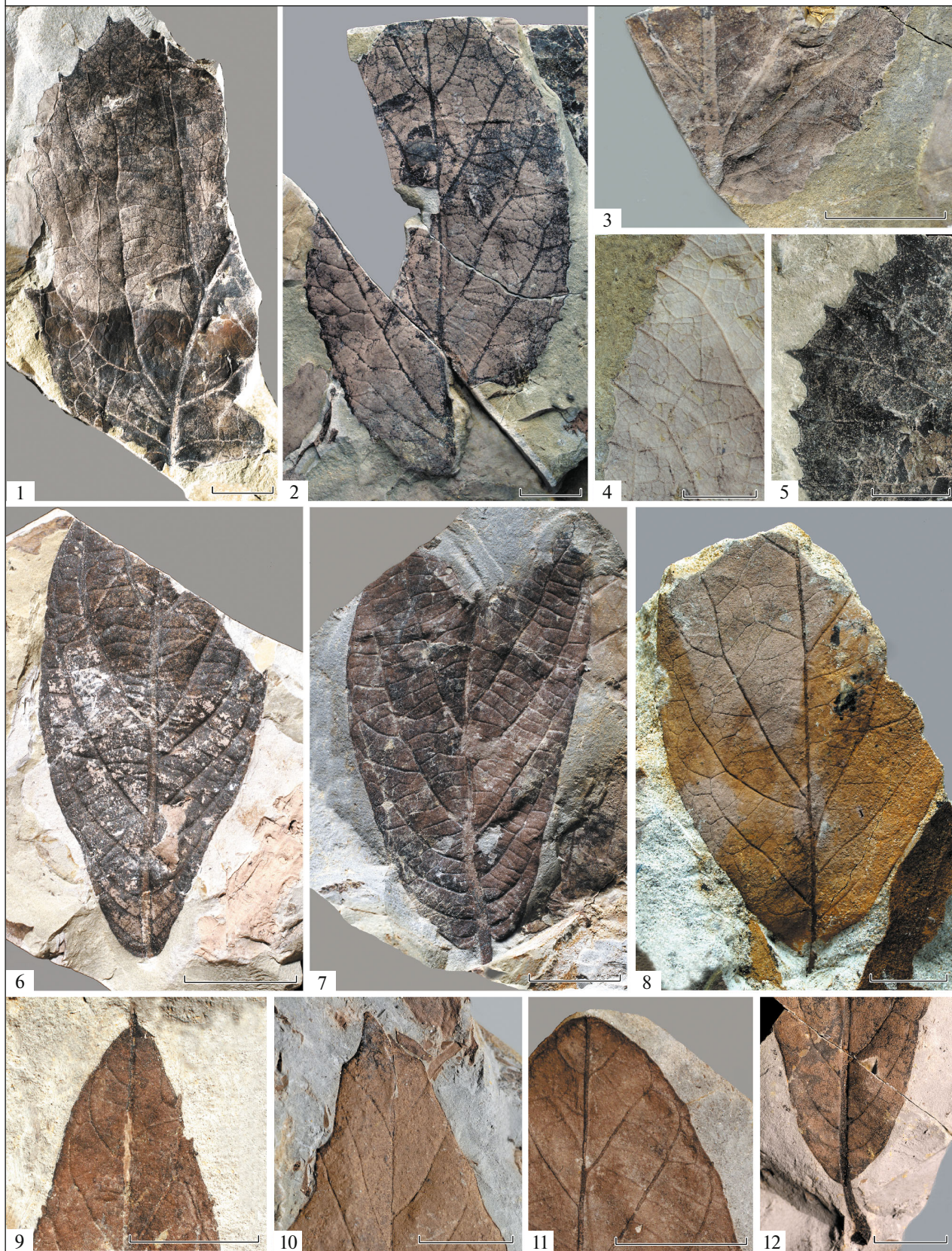
**Description** (Figs. 2–5). Leaves are simple, unlobed; leaf lamina is mainly elliptical, rarely ovate, 3–18 cm long and 1–8.7 cm wide, sometimes asymmetrical. The leaf lamina base is acute, rarely obtuse, weakly cordate, rounded or narrowly cuneate in shape, usually asymmetrical (Pl. 8, figs. 6–8, 12); the apex angle of lamina is acute, rarely obtuse; the apex shape is rounded or straight, often mucronate, rarely spinose (Pl. 8, figs. 9–11). The petiole is thick, expanding basally (Pl. 8, fig. 12), short (1–2 cm). The leaf lamina margin is untoothed or toothed in the upper part, less commonly serration begins from the lower third of the leaf; the base is always untoothed. The teeth are of one order, irregular, two–three teeth per 1 cm, low, with a rounded sinus, concave/convex or with straight distal and proximal flanks. The tooth apices are usually with callous thickenings resembling glands. Often only vein projections extend beyond the leaf margin (Pl. 8, figs. 9–11). The venation is pinnate brochidodromous, often semi-craspedodromous in the upper part of the leaf lamina or mixed craspedodromous–camptodromous. The secondary veins (6–14 pairs) are alternate, less commonly almost opposite, often irregular (Pl. 8, figs. 6–8; Fig. 2b). Two three lower pairs of secondaries are usually thinner and shorter, with reduced spacing between these veins that branch off from the midrib at almost right angles and join brochidodromously. Secondary veins in the middle of leaf lamina (usually

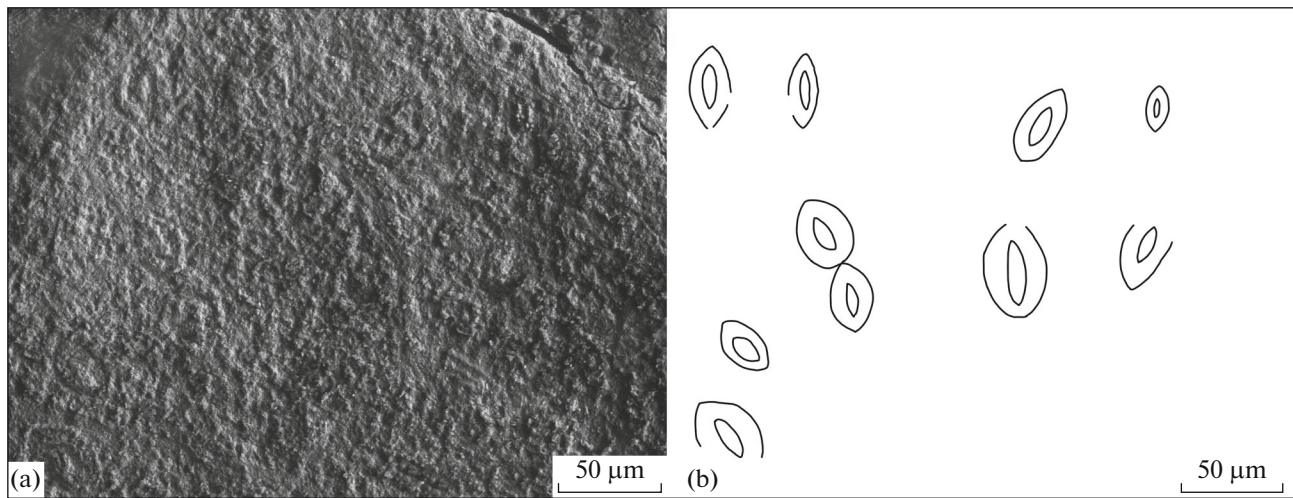
#### Explanation of Plate 8

**Figs. 1–5.** *Arthollia tschernyschewii* (Konst.) Golovneva, Sun et Bugdaeva: (1) specimen GIN, no. 4867-16/3-108a, elliptical leaf with a cordate base and suprabasal actinodromous venation; (2) specimen GIN, no. 4867-16/3-112-1, elliptical leaf with a rounded base; (3) specimen GIN, no. 4867-16/3-109, weakly cordate base of the leaf with marginal teeth; (4, 5) leaf margin with regular teeth of two orders: (4) specimen GIN, no. 4867-16/3-113 and (5) specimen GIN, no. 4867-16/3-112-2.

**Figs. 6–12.** *Kunduriphyllum kundurensis* gen. et comb. nov.: (6) specimen GIN, no. 4867-16/3-92, elliptical leaf with an untoothed margin, narrow rounded base, and pinnate brochidodromous venation; (7) specimen GIN, no. 4867-16/6-221, elliptical leaf with an untoothed margin and weakly cordate base; (8) specimen GIN, no. 4867-16/7-5, elliptical leaf with an untoothed margin, obtuse, cuneate in shape base and irregular secondary venation; (9) specimen GIN, no. 4867-16/6-24, acute, slightly rounded in shape leaf apex with a spine on a top and small irregular marginal teeth; (10) specimen GIN, no. 4867-16/6-39, acute, straight in shape leaf apex with irregular concave/convex marginal teeth; (11) specimen GIN, no. 4867-16/6-213, obtuse, rounded in shape leaf apex with vein projections extending beyond the leaf margin; (12) specimen GIN, no. 4867-16/6-45b, acute, rounded in shape leaf base with a short and thick petiole expanding basally. Scale bar, 1 cm.

Plate 8





**Fig. 3.** Arrangement of stomata on the lower surface of a leaf *Kunduriphyllum kundurensis* gen. et comb. nov., specimen GIN, no. 4867-16/3-115a: (a) incrustation, SEM, showing stomata varying in size; (b) drawing over figure 3a.

fifth and sixth pairs) often produce agrophic veins. Intersecondary veins are sometimes observed between the developed secondaries. The lower surface of the leaf often has domatia (Fig. 2e). Tertiaries are alternate percurrent to mixed opposite–alternate percurrent; the veins are oriented at a right angle or slightly obliquely to the secondary veins. The venation of the fourth order is reticulate.

The leaf epidermal characters are studied in subcrustations, incrustations, and cuticles incompletely preserved only on the leaf major veins and petioles. Ordinary epidermal cells of costal area with straight anticlinal walls (Pl. 9, figs. 1–6) vary in size and shape from rectangular 20–57 µm long and 8–20 µm wide, often with a transverse anticlinal wall oriented obliquely to the longitudinal axis of the cell, to square or polygonal up to 20 µm long and 8–12 µm wide. The anomocytic type of stomatal apparatus was observed in subcrustation preserved on the midvein. A stoma has four subsidiary cells, somewhat varying in shape, but not different from ordinary epidermal cells (Pl. 9, figs. 3, 4).

The incrustations allowed the epidermal features of the upper leaf surface to be studied (Pl. 9, fig. 8) and the arrangement and size of the stomata on the lower leaf surface (Fig. 3). The epidermis of the upper leaf surface is composed mainly of isodiametric quadrangular cells, less commonly polygonal cells, while stomata and trichome bases are absent. The stomata are from 12.1 to 42.2 µm long and from 12.0 to 30.0 µm wide.

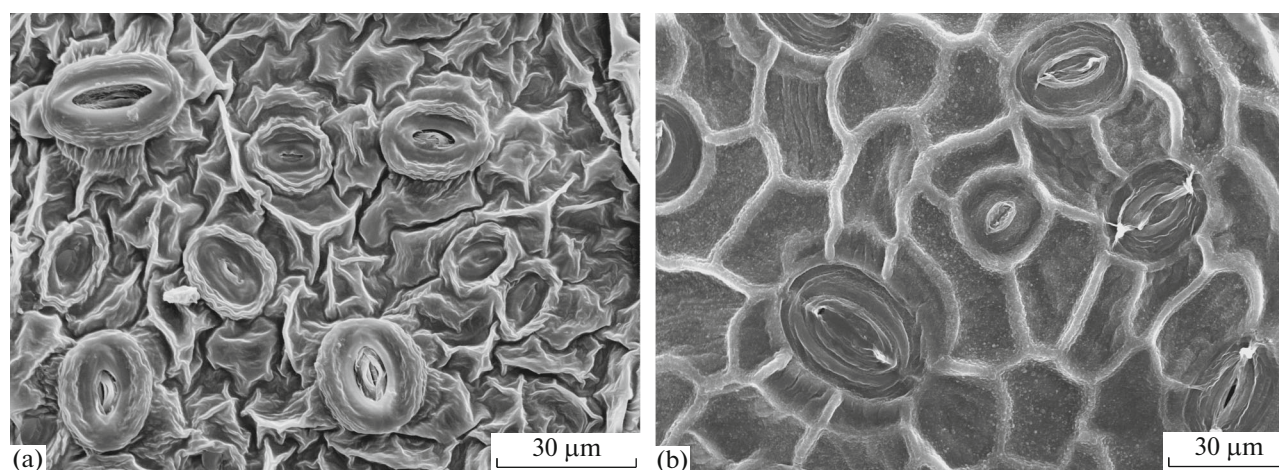
**Material.** Seventy-two specimens in collection BIN, no. 1538 and 96 specimens in collection GIN, no. 4867.

## DISCUSSION

**Systematic affinity of plant fossils.** Based on micro-morphological characters, the inflorescences *Kundurianthus* and infructescences *Kunduricarpus* were assigned to Platanaceae (Kodrul et al., 2013). Leaves of the genus *Arthollia* (Herman and Golovneva, 1988) were originally considered within the formal group of platanoids proposed by Vachrameev (1976) for dispersed angiosperm leaves morphologically similar to extant *Platanus*. Epidermal characters typical of the family Platanaceae were shown for leaves *A. anadyrensis* N. Maslova from the Eocene of Kamchatka (Maslova, 2003). Later (Golovneva et al., 2008), the genus *Arthollia* was assigned to the family Platanaceae.

The genus *Celastrinites*, with the type species *C. venulosus* Saporta, was described from the Paleogene deposits of France for dispersed angiosperm leaves similar in morphology and venation to the leaves of some modern species of the genus *Euonymus* L. (Saporta, 1865). Based on this, the genus *Celastrinites* was for some time considered within the family Celastraceae (Wonnacott, 1955). However, palynological data suggest that the first representatives of Celastraceae did not appear before the Miocene (Muller, 1970). In addition, the absence in earlier floras of confirmed reproductive structures of this family and also a certain morphological variability of the leaves and manifestations of widespread parallelisms in their morphological evolution provide the basis for reconsidering the Cretaceous or Paleogene age of the first representatives of Celastraceae.

*Celastrinites kundurensis* was originally assigned to angiosperms of uncertain systematic affinity (Golovneva et al., 2008). Our study has shown that these



**Fig. 4.** Epidermis of a lower leaf surface of extant *Platanus acerifolia* (Aiton) Willd., herbarium of N.P. Maslova, SEM: (a) outer view showing stomata varying in size; (b) inner view showing differently sized anomocytic and laterocytic stomata.

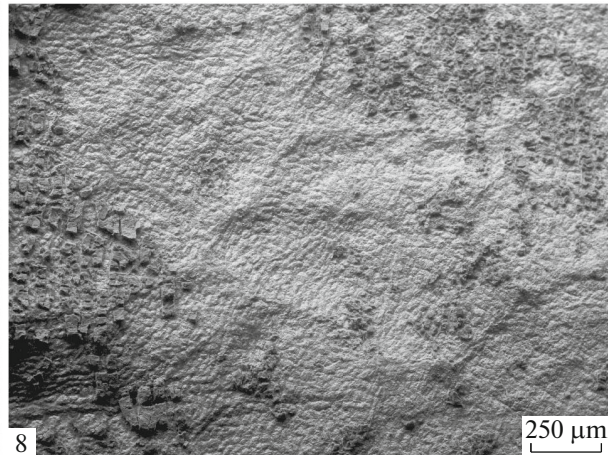
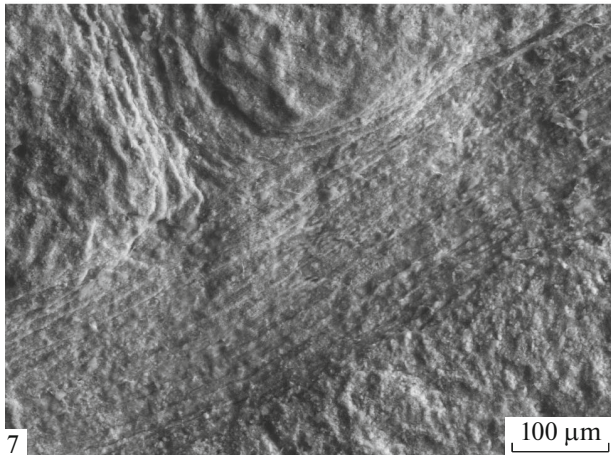
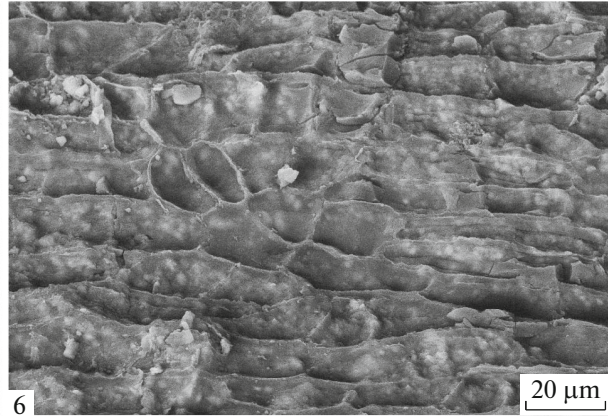
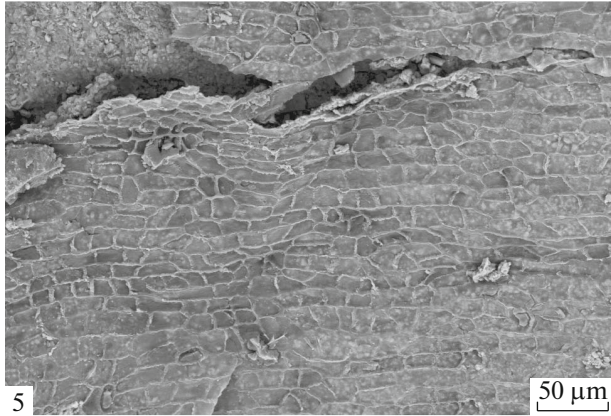
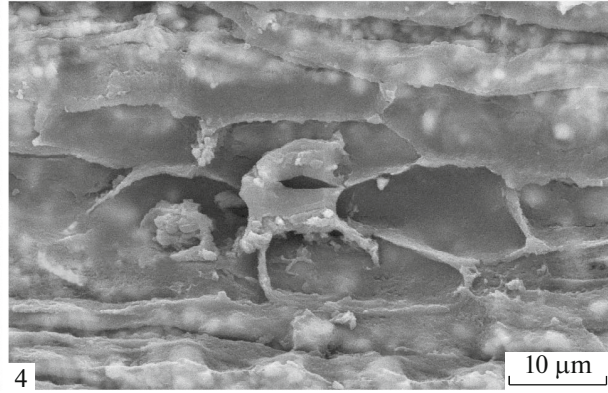
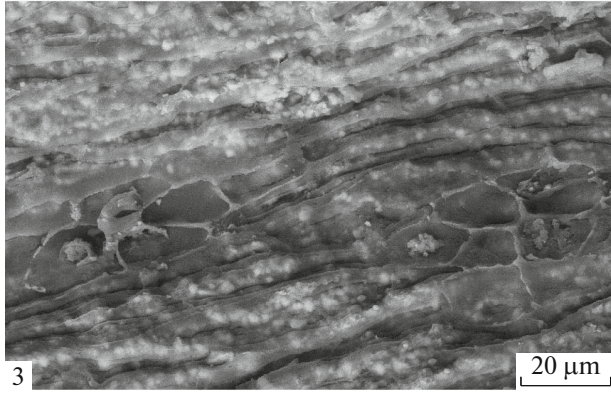
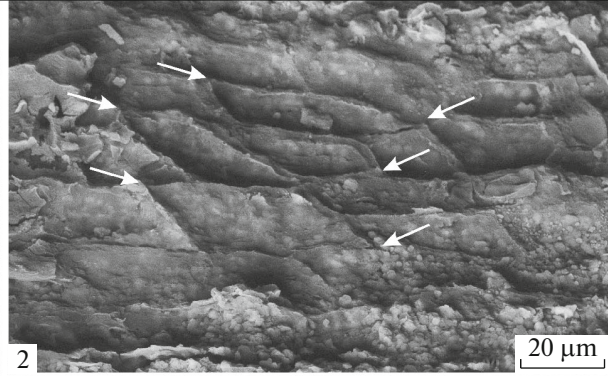
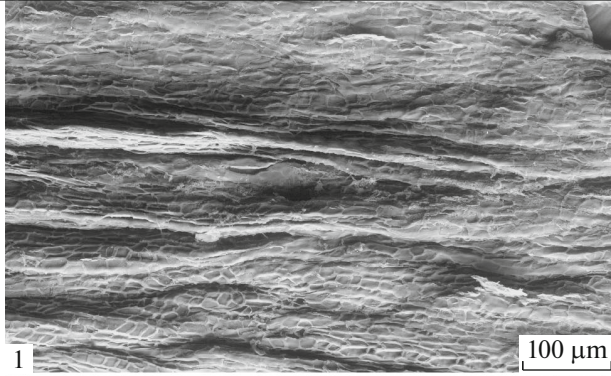
leaves differ from the type species of the genus *Celastrinities* in their venation (Saporta, 1868), but possess some morphological characters typical of leaves of the extant *Platanus*. For instance, in the shape of the leaf lamina, they are similar to the leaves of *Platanus kerrii* and also to the unlobed leaves of *P. acerifolia* (Fig. 2c). Leaf petioles of *Kunduriphyllum kundurensense* gen. et comb. nov. are expanded basally, although not forming a distinct cap protecting the axillary bud, as in most extant *Platanus* species. It is known that the untoothed leaves of *P. kerrii* also lack protection of the bud in a form of basally expanding cap-shaped petiole (Takhtajan, 2009). Leaves of *Kunduriphyllum kundurensense* gen. et comb. nov., *P. kerrii*, and unlobed leaves of *P. acerifolia* are also similar in venation – semicraspedodromous in the upper part of the lamina or mixed craspedodromous–camptodromous. Leaves of all these species are characterized by irregular intersecondary veins and similar types of teeth.

Epidermal characters of the leaves *Celastrinities kundurensis* have not been reported in the first description of the species (Golovneva et al., 2008). Our newly obtained epidermal data show a number of characters typical of the family Platanaceae: anomocytic stomata (Pl. 9, figs. 3, 4), presence of stomata of different size on the same leaf (Fig. 3, for comparison, see Fig. 4), and closely positioned (paired) stomata (Fig. 3, for comparison, see Fig. 4). Anomocytic type of the stomata (along with laterocytic) is typical of representatives of both extant and early (Cretaceous) Platanaceae. Epidermal characters typical of Platanaceae were formed in the Late Albian and remained in general unchanged, and morphologically similar types of leaves with an epidermis typical of Platanaceae were associated with substantially different reproductive structures (Maslova, 2010). In contrast to Platanaceae,

the leaf epidermis of Celastraceae possesses various types of stomata within the same leaf—paracytic, cyclocytic, laterocytic, and anisocytic (den Hartog née Van Ter Tholen and Baas, 1978). We found that a distinctive feature of the epidermis in *Kunduriphyllum kundurensense* gen. et comb. nov. is the absence of trichome bases both on the upper leaf surface (Pl. 9, figs. 8) and on veins and petioles (Pl. 9, figs. 1, 7). In addition, the epidermal characters of the costal zone of these leaves are unique; unlike most angiosperm leaves, in which elongated cells arranged in rows are present in the costal zone, the costal zone of *Kunduriphyllum* leaves is composed of cell varying in size and shape, including cells with transverse anticlinal walls obliquely oriented to the longitudinal cell axes (Pl. 9, figs. 2, 5, 6). Extant and fossil representatives of Platanaceae are characterized by a well-developed trichome cover both on the axes of the reproductive organs and on the leaves and also by epidermal characters of the leaf costal zone typical of angiosperms. Nevertheless, considering the similarity of some morphological and epidermal characters of the leaves of *K. kundurensense* gen. et comb. nov. with those in the extant and fossil Platanaceae, we suppose it appropriate to assign this species to the family Platanaceae.

**Evaluation of the probability of the inflorescences *Kundurianthus*, infructescences *Kunduricarpus*, and leaves *Kunduriphyllum kundurensense* gen. et comb. nov. belonging to the same plant.** In reconstructions of fossil plants, occurrence of various plant organs together in one locality or in several localities is an important argument for their belonging to the same plant. The assignment of isolated vegetative and reproductive organs to the same plant should be supported by the presence of similar characteristic structures. Previously (Kodrul et al., 2013), we proposed that the Kun-





dur inflorescences and infructescences belonged to the same plant. The infructescences *Kunduricarpus* and inflorescences *Kundurianthus* were found together in a number of phytotoxycoenoses in the upper part of the Kundur Formation and shared a number of characters: (1) capitate inflorescences and infructescences; (2) unique epidermal structure, with no trichomes, but with variously shaped cells not organized in longitudinal rows, which is uncharacteristic of the genera assigned to the family Platanaceae or related to this family; (3) nonsynchronous maturing of flower elements, carpels in *Kunduricarpus* and stamens in *Kundurianthus*; (4) distinctly developed ring of expanded plant tissue separating isolated fruits and flowers in the heads of *Kunduricarpus* and *Kundurianthus*; (5) similar body shape and morphology of styles in the carpels of *Kunduricarpus* and in carpels sometimes present in the staminate inflorescences *Kundurianthus*; (6) pollen grains from the pollen sacs of *Kundurianthus* are identical to those found on the carpels and axes of *Kunduricarpus*. In addition, the same oryctocoenoses found in different facies (fluvial, floodplain, and oxbow-lake) have persistent co-occurrence of reproductive structures *Kundurianthus* and *Kunduricarpus* and leaves *K. kundurensis* gen. et comb. nov. The plant fossils under consideration occur commonly in the Kundur locality and often the same samples contain impressions of the leaves *Kunduriphyllum* gen. nov., along with remains of inflorescences and (or) infructescences. The leaves assigned to the genus *Arthollia* are found in considerably lesser quantities in isolated beds with plant fossils and only in one oryctocoenosis are they associated with the reproductive structures *Kundurianthus* and *Kunduricarpus*.

In addition to the above-mentioned morphological and anatomical characters typical of Platanaceae, leaves *Kunduriphyllum kundurensis* gen. et comb. nov. and reproductive structures from the Kundur locality have features in common supporting their assignment to the same plant. Firstly, these are unique similar characters of the axial epidermis in compound capitate inflorescences and infructescences and the leaf coastal zone formed by variously shaped cells. A similar variety of shapes in epidermal cells is also observed in the epidermis of the carpels of *Kunduricarpus*. Another common feature in the epidermis of leaves and reproductive structures is the absence of trichomes. The lack of trichomes in the leaves *K. kundurensis* gen. et comb. nov., as in the inflorescences

*Kundurianthus* and infructescences *Kunduricarpus*, which have other characters typical of Platanaceae, we consider as an additional argument supporting their assignment to the same plant.

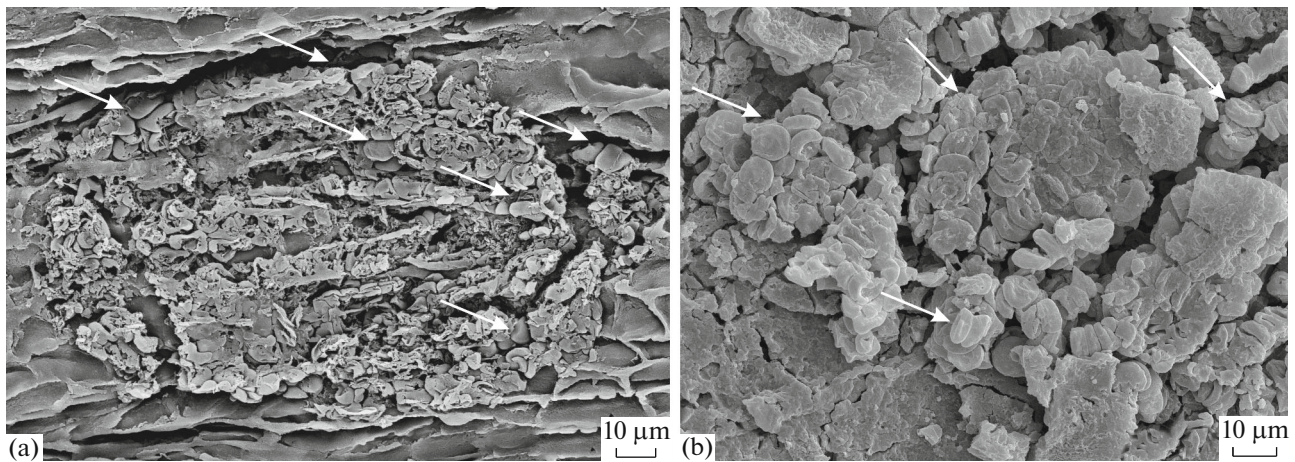
Another feature supporting the possible affinity of the structures discussed is the similarity of some morphological features of the Kundur leaves and reproductive structures with those in some representatives of Altingiaceae. Earlier, we noted that inflorescences and infructescences show some features in common with the reproductive structures of *Altingia* Noronha and *Liquidambar* (Kodrul et al., 2013). These include such characters as the capitate inflorescences and infructescences, flowers lacking perianth, nonsynchronous maturing of elements in staminate flowers and fruits, and the presence of reproductive structures of the opposite sex. In addition, the infructescences *Kunduricarpus*, like the infructescences of the genera *Altingia*, *Liquidambar*, and *Semiliquidambar* H.T. Chang, which are currently considered within the genus *Liquidambar* in the monotypic family Altingiaceae (Ickert-Bond, Wen, 2013), have overgrown plant tissues between the fruits visible to the naked eye. The epidermis of the carpels of *Liquidambar orientalis* L. is revealed to have rectangular cells with obliquely oriented transverse anticlinal walls (Ickert-Bond et al., 2005).

The leaves *Kunduriphyllum kundurensis* gen. et comb. nov. are also characterized by a number of morphological characters common with those in leaves of the group of *Liquidambar* species (*L. chinensis* Champ., *L. gracilipes* (Hemsl.) Ickert-Bond et Wen, *L. chingii* (Metcalfe) Ickert-Bond et Wen, *L. obovata* (Merrill et Chun) Ickert-Bond et Wen, *L. excelsa* (Noronha) Oken), previously assigned to the genus *Altingia*: shape of the leaf lamina, developed domatia, semicraspedodromous venation, irregular branching of the secondary veins, presence of the weak intersecondary veins, and the shape of the teeth.

More support for the assignment of the leaves *K. kundurensis* gen. et comb. nov. and infructescences *Kunduricarpus* to the same plant is provided by unique damage of these plant remains by microorganisms. Bacteriomorphic structures found on the carpel walls of *Kunduricarpus* were previously described (Maslova et al., 2014). Remains of microorganisms were represented in two main states: organized in cylindrical chains and solitary forming mass aggregations (Fig. 5b). The chains are interpreted as an initial stage

#### Explanation of Plate 9

**Figs. 1–8.** Epidermal characters of the leaves *Kunduriphyllum kundurensis* gen. et comb. nov., SEM: (1) specimen GIN, no. 4867-16/6-34b-3, cuticle of the leaf veins after maceration, variety of cell shape in the costal zone, outer view; (2–6) GIN, no. 4867-16/6-34a-1, epitype, subcrustations: (2) cells of the costal zone with distinct obliquely oriented transverse anticlinal walls (arrows); (3) cells of the costal zone and a stoma; (4) anomocytic stoma; (5) cells of the costal zone, trichomes are absent; (6) cells of the costal zone, trichomes are absent; (7, 8) incrustations: (7) specimen GIN, no. 4867-16/3-115a, costal zone, trichomes are absent; (8) specimen GIN, no. 4867-16/6-34b-2, epidermal cells of the upper surface of the leaf lamina.



**Fig. 5.** Microorganisms (shown by arrows) discovered on the inner surface of the vein cuticle on a leaf *Kunduriphyllum kundurenses* gen. et comb. nov. (a) and on the carpel walls of *Kunduricarpus longistylum* Kodrul, N. Maslova, Tekleva et Golovneva (b) SEM, specimens GIN, no. 4867-16/6-34b-3 and GIN, no. 4867-16/6-18b, respectively.

in the development of the microorganisms; later they split into separate structures forming aggregates. The conclusion of the bacterial nature of the agents damaging the infructescences *Kunduricarpus* was based on analysis of their size, morphology, and organization. A bacterial infection was considered as a possible result of damage to the carpel by phytophagous insects.

We also found structures similar in shape and size on the inner side of a vein cuticle of the leaf *Kunduriphyllum kundurenses* gen. et comb. nov. (Fig. 5a). Presence of similar microorganisms on the cuticles of leaves and of reproductive organs can be indirect evidence of these organs belonging to the same plant. On the leaves *K. kundurenses* gen. et comb. nov. we found numerous damage apparently caused by insects. These include skeletonization of leaves, leaf margin feeding damage, hole feeding traces of various shapes (rounded and polylobate), and galls. The diversity of damage types suggests widespread plant–insect interactions, which could possibly have led to bacterial infections.

### CONCLUSIONS

Based on morphological and epidermal characters typical of the family Platanaceae, leaves originally described as *Celastrinites kundurensis* (Golovneva et al., 2008), are assigned to the new genus *Kunduriphyllum* in the family Platanaceae. These leaves are associated with the capitate staminate inflorescences *Kundurianthus* and infructescences *Kunduricarpus*, also assigned to this family. The co-occurrence of numerous leaves and reproductive structures in oryctocoenoses, similarity of their epidermal characters, and infection by the same bacteriomorphic microorganisms suggest that these plant fossils could have belonged to the same plant.

### ACKNOWLEDGMENTS

We are grateful to L.B. Golovneva (BIN) and A.B. Doweld (National Institute of Carpology, Gertner Institute) (NICAR) for constructive discussion of the results, valuable suggestions, and fossil material provided. We are also grateful to A.B. Herman (GIN) for critical remarks and fruitful discussions. The study was supported by the State project no. 0135-2016-0001 at the GIN (TMK), no. 0113-2014-0002 at the Boris- siak Paleontological Institute, Russian Academy of Sciences (NPM), and partly by the National Natural Science Foundation of China (NSFC), grant no. 41210001.

### REFERENCES

- Akhmetiev, M.A., Kezina, T.V., Kodrul, T.M., and Manchester, S.R., Stratigraphy and a flora of the Cretaceous–Paleogene boundary beds of the southeastern part of the Zeya–Bureya sedimentary basin, in *Pamyati chl.-korr. AN SSSR V.A. Vakhrameeva (k 90-letiyu so dnya rozhdeniya)* (In Commemoration of Corresponding Member of the Academy of Sciences of the USSR V.A. Vakhrameev, to the 90th Anniversary of His Birthday), Moscow: GEOS, 2002, pp. 275–315.
- Bůžek, Č., Holý, F., and Kvaček, Z., Eine bemerkenswerte Art der Familie Platanaceae Lindl. (1836) in nordböhmischen Tertiär, *Monat. Deutschl. Akad. Wissens. Berlin*, 1967, vol. 9, pp. 203–215.
- den Hartognee Van Ter Tholen, R.M. and Baas, P., Epidermal characters of the Celastraceae sensu lato, *Acta Bot. Neerl.*, 1978, vol. 27, pp. 355–388.
- Ellis, B.D., Daly, C., Hickey, L.J., et al., *Manual of Leaf Architecture*, Ithaca, New York: Cornell Univ. Press, 2009.
- Flora i dinozavry na granitse mela i paleogena Zeysko-Bureinskogo basseina* (Flora and Dinosaurs across the Cretaceous–Paleogene Boundary in the Zeya–Bureya Basin), Vladivostok: Dal'nauka, 2001.

- Golovneva, L.B., Maastrichtian–Danian floras of the Koryak Highland, *Tr. Botan. Inst. Ross. Akad. Nauk*, 1994, vol. 13, pp. 1–147.
- Golovneva, L.B., Sun, G., and Bugdaeva, E.V., Campanian flora of the Bureya River Basin (Late Cretaceous of the Amur Region), *Paleontol. Zh.*, 2008, no. 5, pp. 96–107.
- Herman, A.B., Akhmetiev, M.A., Kodrul, T.M., Moiseva, M.G., and Yakovleva, A.I., Flora development in northeastern Asia and northern Alaska during the Cretaceous–Paleogene transitional epoch, *Stratigr. Geol. Korrelyatsiya*, 2009, vol. 17, no. 1, pp. 88–108.
- Herman, A.B. and Golovneva, L.B., A new genus of Late Cretaceous platanoids from the northeastern USSR, *Botan. Zh.*, 1988, vol. 73, no. 10, pp. 1456–1468.
- Ickert-Bond, S.M., Pigg, K.B., and Wen, J., Comparative infructescence morphology in *Liquidambar* (Altingiaceae) and its evolutionary significance, *Am. J. Bot.*, 2005, no. 92, pp. 1234–1255.
- Ickert-Bond, S.M. and Wen, J., A taxonomic synopsis of Altingiaceae with nine new combinations, *PhytoKeys*, 2013, no. 31, pp. 21–61.
- Kodrul, T. and Krassilov, V., New juglandaceous fruit morphotype from the Paleocene of Amur Province, *Russ. Far East Acta Palaeobotan.*, 2005, vol. 45, no. 2, pp. 139–144.
- Kodrul, T.M. and Maslova, N.P., A new species of the genus *Platimeliphyllum* N. Maslova from the Paleocene of the Amur Region, Russia, *Paleontol. J.*, 2007, vol. 41, no. 11, pp. 1108–1117.
- Kodrul, T.M., Maslova, N.P., Tekleva, M.V., and Golovneva, L.B., Platanaceous reproductive structures and leaves from the Cretaceous locality Kundur, Amur Region, Russia, *Palaeobotanist*, 2013, vol. 62, no. 1, pp. 123–148.
- Kodrul, T.M., Tekleva, M.V., and Krassilov, V.A., A new conifer species, *Mesocyparis rosanovii* sp. nov. (Cupressaceae, Coniferales), and Transberingian floristic connections, *Paleontol. Zh.*, 2006, no. 3, pp. 93–102.
- Konstantov, S.V., A Tertiary flora from Belogor'e outcrop at the lower reaches of the Bureya River, *Tr. Geol. Kom. Nov. Ser.*, 1914, vol. 113, pp. 1–27.
- Krassilov, V.A., *Tsagayanskaya flora Amurskoi oblasti* (Tsagayan Flora of the Amur Region), Moscow: Nauka, 1976.
- Krassilov, V. and Kodrul, T., In situ pollen of Alasia, a supposed staminate inflorescence of *Trochodendroides* plant, *Acta Mus. Nat. Pragae. Ser. B Hist. Natur.*, 2008, vol. 64, nos. 2–4, pp. 115–124.
- Krassilov, V.A. and Makulbekov, N.M., Subcrustations of plants, *Paleontol. Zh.*, 1996, no. 2, pp. 125–128.
- Krassilov, V.A., Kodrul, T.M., and Maslova, N.P., Plant systematics and differentiation of species over Transberingian land connections including a new species of cupressaceous conifer *Ditaxocladus* Guo et Sun, *Bull. Geol. Sci.*, 2009, vol. 85, no. 1, pp. 95–110.
- Krishtofovich, A.N. and Baikovskaya, T.N., Upper Cretaceous Tsagayan Flora in the Amur Region, in *A.N. Krishtofovich. Izbrannyye trudy* (A.N. Krishtofovich: Selected Works), Moscow–Leningrad: Akad. Nauk SSSR, 1966, vol. 3, pp. 184–320.
- Kvaček, Z. and Manchester, S.R., Vegetative and reproductive structures of the extinct *Platanus neptuni* from the Tertiary of Europe and relationships within the Platanaceae, *Plant Syst. Evol.*, 2004, vol. 244, pp. 1–29.
- Manchester, S.R., Akhmetiev, M.A., and Kodrul, T.M., Leaves and fruits of *Celtis aspera* (Newberry) comb. nov. (Celtidaceae) from the Paleocene of North America and eastern Asia, *Int. J. Plant Sci.*, 2002, no. 163, pp. 725–736.
- Manchester, S.R. and Kodrul, T.M., Morphology, affinities and phytogeographic history of *Porosia* Hickey in the Cretaceous and Paleocene of North America and Asia, *Acta Palaeobot.*, 2014, vol. 54, no. 1, pp. 77–99.
- Manchester, S.R., Xiang, Qiu-Yun (Jenny), Kodrul, T.M., Akhmetiev, M.A., Leaves of *Cornus* (Cornaceae) from the Paleocene of North America and Asia confirmed by trichome characters, *Int. J. Plant Sci.*, 2009, vol. 170, no. 1, pp. 132–142.
- Markevich, V.S., Golovneva, L.B., and Bugdaeva, E.V., Stratigraphy and flora of the Kundur Formation (Upper Cretaceous, Amur Region), in *Melovaya sistema Rossii: problemy stratigrafii i paleogeografii. Sbornik statei 2-go Vserossiiskogo soveshchaniya* (2nd All-Russia Conference on the Cretaceous System of Russia: Problems of Stratigraphy and Paleogeography), St. Petersburg: St. Peterb. Univ., 2005a, pp. 160–176.
- Markevich, V.S., Golovneva, L.B., and Bugdaeva, E.V., Floristic characterization of Santonian–Campanian deposits in the Zeya–Bureya Basin (Amur Region), in *Sovremennye problemy paleofloristiki, paleofitogeografii i fitostratigrafii. Trudy mezhdunarodnoi paleobotanicheskoi konferentsii Moskva, 17–18 maya 2005 g.* (Proceedings of the International Paleobotanical Conference on Current Problems of Paleofloristics, Paleophytogeography, and Phytostратigraphy, Moscow, May 17–18, 2005), Moscow: GEOS, 2005b, vol. 1, pp. 198–206.
- Maslova, N.P., Extinct and modern Platanaceae and Hamamelidaceae: Morphology, systematics, and phylogeny, *Paleontol. J.*, 2003, suppl. no. 5, pp. 467–589.
- Maslova, N.P., Systematics of fossil platanoids and hamamelids, *Paleontol. J.*, 2010, vol. 44, no. 11, pp. 1379–1466.
- Maslova, N.P. and Kodrul, T.M., *Archaranthus* gen. nov., a new genus of Platanaceae from the Maastrichtian–Paleocene beds of the Amur Region, *Paleontol. Zh.*, 2003, no. 1, pp. 92–100.
- Maslova, N.P., Kodrul, T.M., and Tekleva, M.V., A new staminate inflorescence *Bogutchanthus* gen. nov. (Hamamelidales) from the Paleocene beds of the Amur Region, Russia, *Paleontol. Zh.*, 2007, no. 5, pp. 89–103.
- Maslova, N.P., Kodrul, T.M., and Vasilenko, D.V., First find of the bacteriomorphic organisms in platanoid infructescences from the Campanian Kundur locality, Amur Region, *Paleontol. Zh.*, 2014, no. 5, pp. 110–116.
- Muller, J., Palynological evidence on early differentiation of angiosperms, *Biol. Rev.*, 1970, vol. 45, pp. 417–450.
- Saporta, G., Études sur la Végétation du Sud-Est de la France à L'Époque Tertiaire, Troisième: Partie 1, *Ann. Sci. Nat. Bot. Sér. 5e*, 1865, vol. 3, pp. 5–64.
- Saporta, G., Prodrome d'une flore fossile des travertins anciens de Sézanne, *Mém. Soc. Geol. France, Ser. 3e*, 1868, vol. 8, pp. 289–436.
- Sun, G., Akhmetiev, M., Dong, Z.M., et al., In search of the Cretaceous–Tertiary boundary in Heilongjiang River Area of China, *J. Geosci. Res. NE Asia*, 2002, vol. 5, no. 2, pp. 105–113.
- Sun, G., Akhmetiev, M., Golovneva, L., et al., Late Cretaceous plants from Jiayin along Heilongjiang River, North-

- east China, *Cour. Forschungsinst. Senckenb.*, 2007, vol. 258, pp. 75–83.
- Sun, G., Akhmetiev, M., Markevich, V., et al., Late Cretaceous biota and the Cretaceous–Paleogene (K-Pg) boundary in Jiayin of Heilongjiang, China, *Glob. Geol.*, 2011, vol. 14, no. 3, pp. 115–143.
- Sun, G., Dong, Z.M., Akhmetiev, M., et al., *Late Cretaceous–Paleocene Biota and the K-Pg Boundary from Jiayin of Heilongjiang, China with Discussion on the Extinction of Dinosaurs*, Shanghai: Shanghai Sci. Technol. Educ. Publ. House, 2014.
- Takhtajan, A.L., *Flowering Plants*, Heidelberg: Springer, 2009.
- Vakhrameev, V.A., Late Cretaceous Platanaceae, in *Ocherki geologii i paleontologii Dal'nego Vostoka* (Sketches on the Geology and Paleontology of the Far East), Vladivostok: Dal.–Vost. Nauchn. Tsentr Akad. Nauk SSSR, 1976, pp. 66–78.
- Van Itterbeeck, J., Bolotsky, Y., Bultynck, P., and Godefroit, P., Stratigraphy, sedimentology and ecology of the dinosaur-bearing Kundur section (Zeya-Bureya Basin, Amur Region, Far Eastern Russia), *Geol. Mag.*, 2005, vol. 142, pp. 735–750.
- Walter, H., Das Tertiär-Vorkommen der Gattung *Platanus* L. im Tertiär des Weibelster-Beckens (Bezirk Leipzig, DDR), *Hall. Jahrb. Geowiss.*, 1985, vol. 10, pp. 9–19.
- Wonnacott, F.M., Celastraceae, in *Fossilium Catalogus: II. Plantae, Pars 29*, Jongmans, W., Ed., S-Gravenhage: Uitgeverij Dr. W. Junk, 1955.

*Translated by S. Nikolaeva*