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Platanaceous reproductive structures and leaves from the Cretaceous of Kundur, Amur Region, Russia

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ABSTRACT

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New platanaceous genera are described based on micromorphology of a capitate infructescence (*Kunduricarpus* Kodrul, N. Maslova, Tekleva & Golovneva) and staminate inflorescence (*Kundurianthus* Kodrul, N. Maslova, Tekleva & Golovneva) from the Campanian of Amur Region, Russia. The presence of common characteristic features implies possible affinities of these reproductive organs to the same plant.

Key–words—Cretaceous, Amur Region, Platanaceae, Reproductive structures, Pollen.

रूस में अमुर क्षेत्र के कुंडुर के क्रिटेशस से प्राप्त प्लेटेनेसीमय पुनर्उत्पादी संरचनाएं एवं पत्तियां

टैटीएना एम. कोडरूल, नतालिया पी. मासलोवा, मारिया वी टेकलेवा एवं लोना बी गोलोव्नेवा

सारांश

रूस के अमुर क्षेत्र के कंपेनियन से प्राप्त समुंड पुष्पक्रमीफलन (*कुंडरीकार्पस* कोडरूल, एन मास्लोवा, टेक्लेवा एवं गोलोव्नेवा) और पुंकेसरी पुष्पसमूह (*कुंडरीएन्थस* कोडरूल, एन मास्लोवा टेक्लेवा एवं गोलोवनेवा) के सूक्ष्मआकृतिविज्ञान पर आधारित नवीन प्लेटेनेसीमय वंश वर्णित किए गए हैं। सामान्य अभिलक्षणिक लक्षणों की विद्यमानता उपर्युक्त वनस्पति के इन पुनर्उत्पादी अवयवों की संभावना का संकेत करती है।

संकेत-शब्द—क्रिटेशस, अमुर क्षेत्र, प्लेटेनेसी, पुनर्उत्पादी संरचनाएं, पराग।

INTRODUCTION

THE geological history of the family Platanaceae continuously attracts palaeobotanists. It is known that the only modern genus *Platanus* L., 1754 is a remnant of the once diverse family with the peak in the Cretaceous. Among Cretaceous reproductive structures referred to the Platanaceae there are capitate infructescences (Manchester, 1986; Crane *et al.*, 1988; Friis *et al.*, 1988; Crane *et al.*, 1993; Magallón-Puebla *et al.*, 1997; Maslova & Herman, 2006; Tschan *et al.*, 2008; Wang, 2008; Maslova *et al.*, 2011; Wang *et al.*, 2011; Maslova & Tekleva, 2012) and capitate staminate inflorescences (Krassilov, 1973; Manchester, 1986; Crane *et al.*, 1988; Friis *et al.*, 1988; Pigg & Stockey, 1991; Crane *et al.*, 1993; Pedersen *et al.*, 1994; Krassilov & Shilin, 1995; Magallón-Puebla *et al.*, 1997; Maslova, 2002; Maslova & Kodrul, 2003; Mindell *et al.*, 2006; Tschan *et al.*, 2008). Maslova (2010) proposed a new system of fossil platanoids and hamamelids which includes both modern (Platanaceae and Hamamelidaceae) and extinct families (Bogutchantaceae, Sarbaicarpaceae and Kasicarpaceae). A number of fossil genera previously described within the Platanaceae were placed in extinct families. Associated findings of fossil platanoid capitate reproductive structures and leaves were considered earlier by Maslova (2008; 2010). In the present study capitate infructescences and staminate inflorescences are described as new Platanaceae genera, and their possible relationships with platanoid leaves are discussed. New findings extend our knowledge of the geological history of the Platanaceae.

MATERIAL AND METHODS

The studied material was obtained from the upper part of Kundur Formation, which is exposed along the Federal Highway 'Amur' Chita-Khabarovsk in the interfluve area of Mutnaya and Udurchukan rivers (Fig. 1) 10 km south-east of Kundur Town, Amur Region, Russian Far East (GPS coordinates: 49°03′46.7″N, 130°52′18.2″E, VGS 84). Remains of reproductive structures and associated leaves were collected during biostratigraphic studies of the Cretaceous-Paleogene continental deposits conducted during the last decade in the south-eastern part of Zeya-Bureya Basin (Bugdaeva *et al.*, 2001; Sun *et al.*, 2002, 2004, 2007, 2011; Golovneva *et al.*, 2004, 2008; Van Itterbeeck *et al.*, 2005; Markevich *et al.*, 2005a, b; Herman *et al.*, 2009; Krassilov & Kodrul, 2009; Krassilov *et al.*, 2010).

The upper unit of the Kundur Formation is represented by alternating sandstones, which are sometimes calciferous, siltstones and clays with thin coal seams in the uppermost part of the section (Bugdaeva *et al.*, 2001; Van Itterbeeck *et al.*, 2005). Lacustrine deposits in the lower part of the unit are characterized by freshwater mollusks, conchostracans

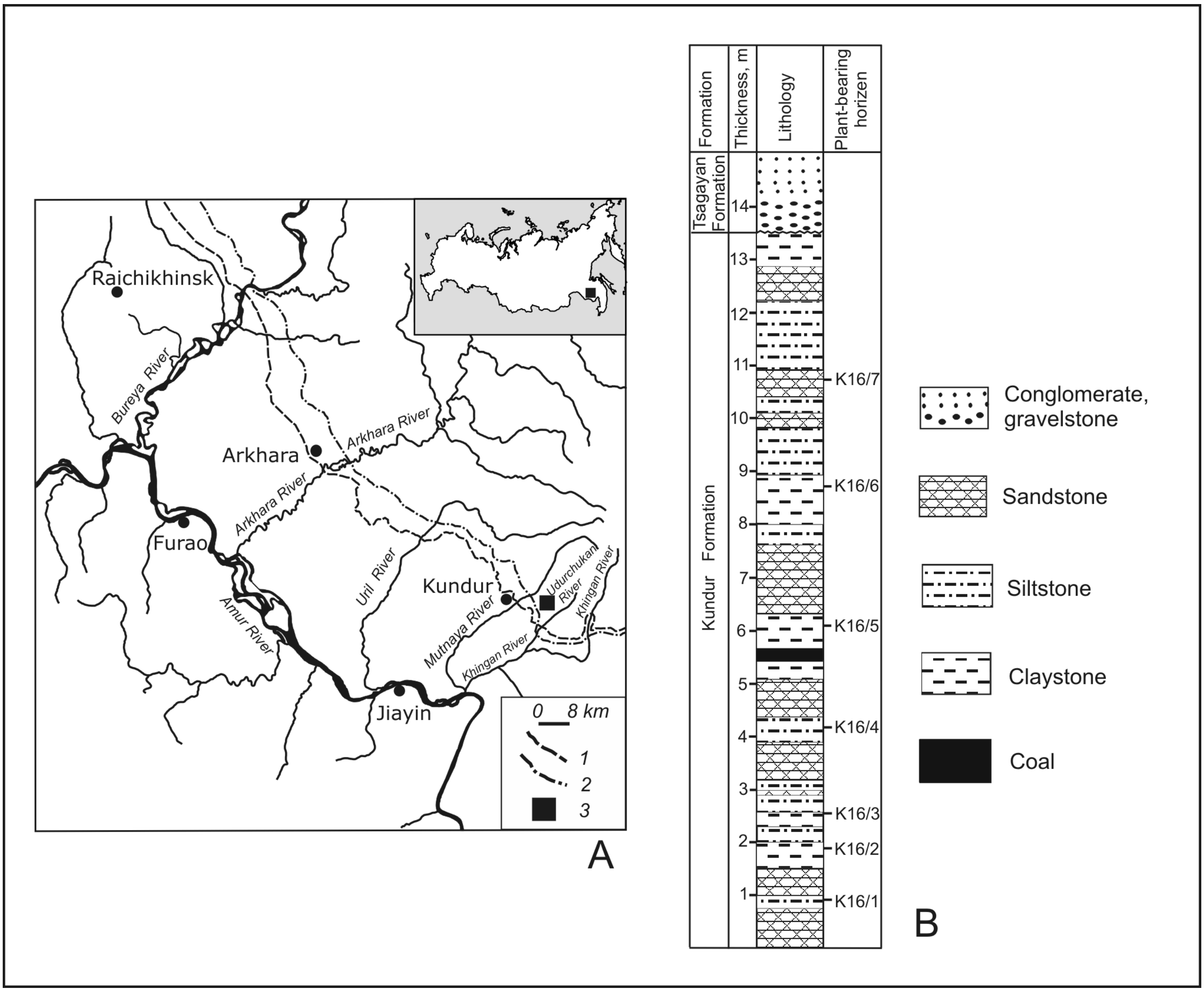

Fig. 1—Locality of the Kundur fossil site, Amur Region, Russian Far East (A) and the occurrence of fossil plant horizons in the upper part of the Kundur Formation (B). 1. Trans-Siberian Railroad. 2. Federal Highway 'Amur' Chita- Khabarovsk. 3. Kundur fossil plant locality.

and ostracods while alluvial deposits of channel, overbank/floodplain, and oxbow lake facies in the upper part of the unit contain numerous plant remains. Plant fossils under study come from several successive plant-bearing horizons in the uppermost part of Kundur Formation (Fig. 1) in the locality 16 (locality number after Bugdaeva *et al.*, 2001). The Kundur plant assemblage contains horsetails, ferns (including aquatic ferns), ginkgoaleans, conifers from the Cupressaceae *s.l.*, and angiosperms, among which platanoids, several *Trochodendroides* species and aquatic plants of *Quereuxia* and *Cobbania* predominate (Golovneva *et al.*, 2004, 2008; Markevich *et al.*, 2005a, b; Krassilov & Kodrul, 2009). According to palynological and macrofloristic data the upper part of the Kundur Formation is dated as Campanian (Markevich *et al.*, 2005a, b).

The morphology and anatomy of the reproductive structures were studied by scanning electron microscopy (SEM) after they were cleaned with hydrofluoric acid. Fragments of infructescences and inflorescences were macerated with Schulze's solution and alkali and then also observed under SEM. Digital photographs of the heads were taken using a Nikon Coolpix 8700. Scanning electron microscopes, CamScan and Tescan Vega XMU, were used at the Borissiak Paleontological Institute RAS.

Individual pollen grains and anther fragments were studied in light (Zeiss Axioplan-2), electron scanning (Hitachi, CamScan, JSM) and transmission (Jeol 100B and Jeol 1011) microscopes. Standard methods for transmission electron (TEM) study were followed (Meyer-Melikian *et al.*, 2004). Pollen grains were stained with osmium tetroxide, ultrathin sections were made with an LKB Ultratome V and stained after Reynolds (1963).

Collections of the studied reproductive structures and associated leaves are housed at the Geological Institute, Russian Academy of Sciences (GIN RAS) under the number GIN 4867 and at the Botanical Institute, Russian Academy of Sciences (BIN RAS) under the number BIN 1538.

SYSTEMATICS

Family—PLATANACEAE Lestiboudois, 1826

Genus—KUNDURICARPUS Kodrul, N. Maslova, Tekleva & Golovneva gen. nov.

(Pl. 1-5)

Type species—*Kunduricarpus longistylium* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov.

Material—More than 100 specimens.

Diagnosis—Compound infructescence, consisting of an axis and heads on a peduncle. Epidermal cells of the axis transversally elongated, trapezoid, square and arranged in indistinct rows. Trichomes lacking on the axis. Fruit number in the head less than 30. Fruits lacking persistent perianth remains, tetra- or pentamerous, maturing nonsimultaneously, with long styles. Fruitlet epidermis lacks trichomes and stomata. Seed solitary in the fruitlet.

Etymology—From the locality Kundur.

Distribution—Kundur Formation, Campanian; Amur Region.

Discussion—Among the Platanaceae, *Kunduricarpus* gen. nov. shows most similarity to the modern genus *Platanus*, from which it differs in less numerous fruits per head, nonsimultaneous maturation and the lack of the basal hair bundles for dispersal. Among fossil Planataceae the new genus is most similar to the Eocene genus *Macginicarpa* Manchester, 1986 (Manchester, 1986), differing in less numerous fruits in the head, fruitlet number in the fruit (mostly four in *Kunduricarpus* gen. nov. and typically five in *Macginicarpa*), and absence of the perianth.

Kunduricarpus longistylium Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov.

(Pl. 1-5)

Diagnosis—Compound infructescence, consisting of an axis and heads on a peduncle. Epidermal cells of the axis transversally elongated, trapezoid, square and arranged in indistinct rows. Trichomes lacking on the axis. Head up to 15 mm (about 10 mm on average) in diameter consists of about 30 fruits. Fruits lacking perianth. Small swellings of the proliferous core tissue are between fruits. Fruits tetra- or pentamerous, fruitlets with long persistent curved styles. Individual fruitlets within the fruit reach different sizes while ripening. Ordinary epidermal cells of the fruitlets differ in size and shape, trichomes and stomata absent. Seed solitary in the fruitlet.

Description—The compound infructescence consists of an axis up to 1 mm in diameter and capitate heads, attached to the axis by peduncles up to 700 μm long (Pl. 1.1, 2, 6; Pl. 2.4, 7, 12). The total number of heads on the axis is unknown; the maximum visible number of heads is 4. The head diameter reaches up to 15 mm (about 10 mm on an average).

Ordinary epidermal cells of the infructescence axis vary in shape and size, they are transversally extended, trapezoid, square, from 10 to 18 μm in length and width, and are arranged in indistinct longitudinal rows (Pl. 4. 2). Trichomes are lacking on the axis (Pl. 4.1, 2).

The head consists of a central rounded core up to 6 mm in diameter and of fruits which are radially attached to the core (Pl. 1.1-12; Pl. 2.1-12; Pl. 3.1-9). Abscised fruits leave rounded or oval scars of different diameters, within the scars traces of the attachment of individual fruitlets can be seen in some specimens (Pl. 1.8, 9, 12). Adjacent fruits are clearly bordered by regions of a proliferous core tissue, which is most prominent in mature heads (Pl. 1.12).

The fruit number per head is less than 30. Fruits are mostly tetramerous, less often pentamerous (Pl. 1.8, 9, 12) with fruitlets in one whorl. The fruitlet size differs within the head and presumably within the fruit. No persistent perianth remains are observed.

Infructescences in different developmental stages were studied. In immature heads fruitlets are of about the same size, narrowly elliptic. In mature infructescences fruitlets differ in size. The maximum length of a mature fruitlet body is 2·6 mm (1·7 mm on average), the maximum width is 1·2 mm (0·8 mm on average). The shape of a mature fruitlet is from elliptic to widely elliptic and obovate (Pl. 2.3; Pl. 3.10, 11; Pl. 5.1, 2, 4). The ventral suture is running from the top of the ovary to the tip of the style. Styles are long, up to 3·2 mm (2·7 mm on average), persistent, curved to a different extent (Pl. 1.4, 10; Pl. 2.1, 6; Pl. 3.4-6). The fruitlet cuticle is thin. The fruitlet epidermis consists of differently shaped cells. The cells are longitudinally extended, mostly rectangular, often with oblique end walls, from 20 to 45 µm long and from 10 to 20 µm wide (Pl. 4.3-6; Pl. 5.6), in the apical region they are square and polygonal, from 20 to 45 µm long and from 15 to 30 µm wide (Pl. 4.7, 8; Pl. 5.3). Trichomes and stomata are absent. The inner layer of the fruitlet wall is formed by isodiametric, mostly square cells (Pl. 5.5). Seed is solitary in the fruitlet (Pl. 5.7, 8).

Numerous pollen grains and pollen clusters were found on the fruitlet surface (Pl. 3.12, 13; Pl. 11.6, 9, 14); they are identical in morphology and size to those studied from *Kundurianthus mirabilis* gen. *et* sp. nov. anthers.

Etymology—From long styles.

Holotype—GIN 4867-K16/3-66; capitate infructescence; Amur Region, road cut of the Federal Highway 'Amur' Chita-Khabarovsk between the rivers Mutnaya and Udurchukan, near Kundur Town; Kundur Formation, Campanian (Pl. 1.2, 3), designated here.

Occurrence—Amur Region, area between the rivers Mutnaya and Udurchukan, near Kundur Town; Kundur Formation, Campanian.

Genus—KUNDURIANTHUS Kodrul, N. Maslova, Tekleva & Golovneva gen. nov.

(Pl. 6-11)

Type species—Kundurianthus mirabilis Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov.

Material—More than 70 specimens.

Diagnosis—Staminate heads up to 10 mm in diameter, sessile or pedunculate. Epidermal cells of the axis transversally elongated, trapezoid, square and arranged in indistinct rows. Trichomes lacking on the axis. The flower number per head about 30. Flowers lacking perianth. Flowers are mostly tetramerous, less often pentamerous. Stamens differing in size. Stamen filaments are not pronounced. Pollen sacs narrow, spindle-shaped, pointed apically, different in size. Connective lacking apical extension. Rare, irregularly arranged fruitlets with long styles occur in the head, the fruitlets are developed to a different extent. Occasionally the mature fruitlet can reach or exceed the inflorescence diameter. Pollen grains small, finely reticulate, semitectate, tricolpate or tricolporate, with indistinct ora, columellate.

Etymology—After Kundur locality.

Distribution—Kundur Formation, Campanian; Amur Region.

Discussion—No close similarity to *Kundurianthus* gen. nov. is observed among the modern Platanaceae and related fossil genera. The principle characteristic of the new genus is the presence of variously developed and irregularly arranged fruitlets in the staminate inflorescences, mostly with one large mature fruitlet which is equal to or exceeds the whole inflorescence length. Rudimentary carpels were described for the Eocene genus *Gynoplatananthus* Mindell, Stockey & Beard, 2006 (Mindell *et al.*, 2006) and for some species of modern *Platanus* (Boothroyd, 1930; Schwarzwalder & Dilcher, 1981). While in modern *Platanus* rudimentary carpels occur sporadically in flowers, in *Gynoplatananthus* they are five per flower and permanently present. In *Kundurianthus* gen. nov. there are rare fruitlets in the head, more often there is one gigantic mature fruitlet per inflorescence, which is most probably extrafloral. Such giant fruitlets were not observed in every inflorescence. It is to be noted that the presence of fully developed male and female flowers in the same inflorescence was shown for modern *Platanus racemosa* Nuttall, 1842 (Floyd *et al.*, 1999). Besides, the new genus differs in the unique epidermal structure of the inflorescence axis and in low density of pollen grains in pollen sacs.

Kundurianthus mirabilis Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov.

(Pl. 6-11)

Diagnosis—Staminate heads 5-10 mm in diameter, sessile or on a peduncle. Epidermal cells of the axis transversally elongated, trapezoid, square and arranged in indistinct rows. Trichomes lacking on the axis. Flower number about 30 per head. Flowers lacking perianth. Flower attachment scars distinct on the globular receptacular core, marked by small swellings of the proliferous core tissue. Flowers are mostly tetramerous, less often pentamerous. Stamens differing in size. Stamen filaments not pronounced. Pollen sacs spindle-shaped, pointed apically, differently sized in the flower. Pollen density in the sacs low. Apical extensions of the connectives not developed. One or rarely several fruitlets with long curved styles in the head, the fruitlets are developed to a different extent. The mature fruitlet sometimes reaches or exceedes the head diameter. The fruitlet body widely ovoid, ventral suture from the fruitlet base to the style tip. Pollen small, finely re-

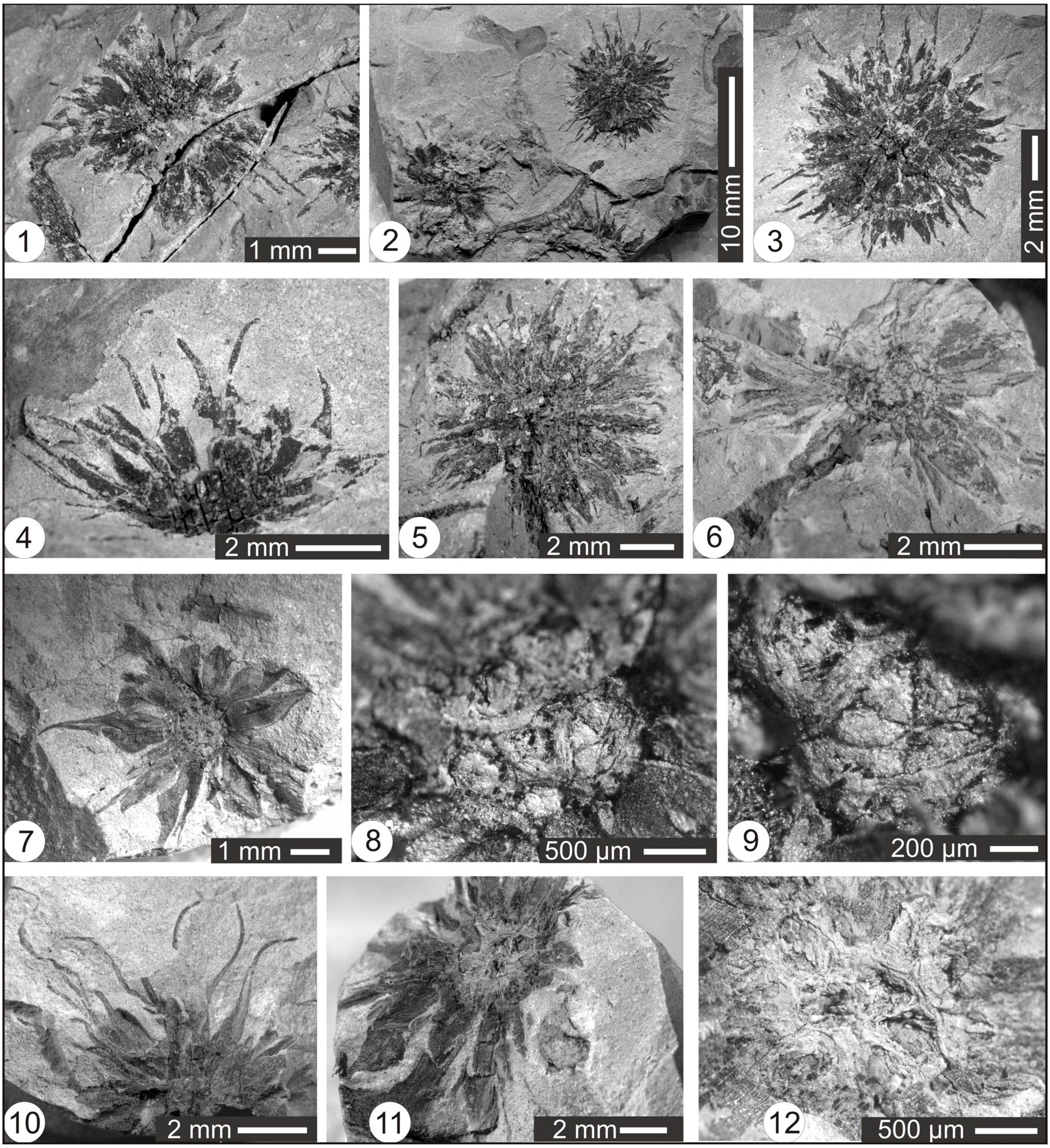

PLATE 1

Morphology of infructescences of *Kunduricarpus longistylium* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov.

1. Specimen GIN 4867-K16/3-65, head.
2. Holotype GIN 4867-K16/3-66, infructescence fragment with three heads.
3. Holotype GIN 4867-K16/3-66, enlargement of the head from fig. 2.
4. Specimen GIN 4867-K16/3-97, head fragment.
5. Specimen GIN 4867-K16/3-63, head.
6. Specimen GIN 4867-K16/3-61, head.
7. Specimen GIN 4867-K16/6-14, head.
8. Specimen GIN 4867-K16/6-14, head core, scars of abscised fruits are visible.
9. Specimen GIN 4867-K16/6-14, head core, scar of an abscised fruit of five fruitlets is visible.
10. Specimen GIN 4867-K16/3-94b, head fragment.
11. Specimen GIN 4867-K16/6-74, infructescence on a peduncle, architecture.
12. Specimen GIN 4867-K16/6-74, core fragment, fruit bases and tissue regions between fruits.

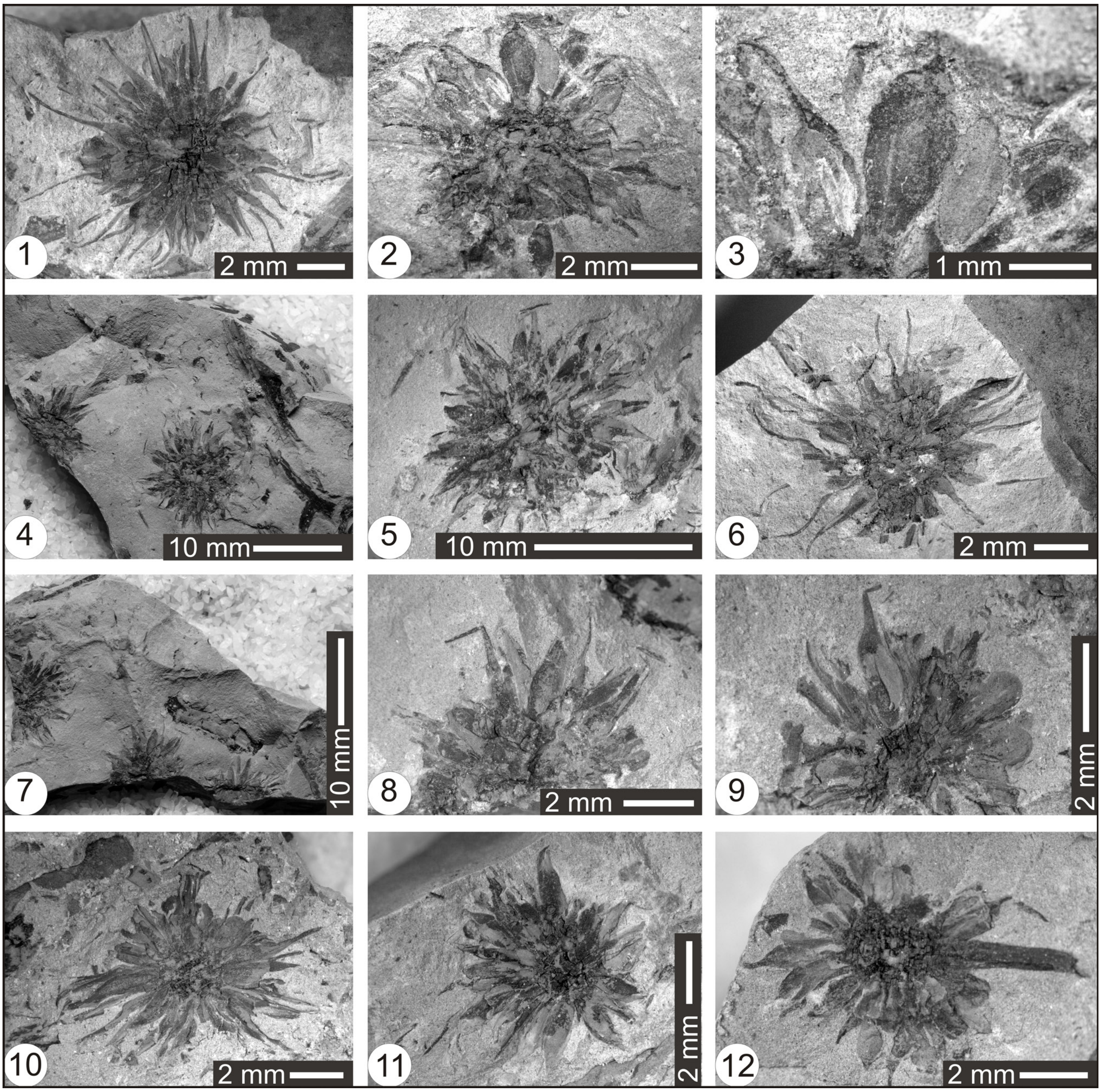

PLATE 2

Morphology of infructescences of *Kunduricarpus longistylium* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov.

1. Specimen GIN 4867-K16/6-9, head.
2. Specimen GIN 4867-K16/6-17-1, head.
3. Specimen GIN 4867-K16/6-17-1, enlargement of fig. 2, differently sized fruitlets are visible.
4. Specimen GIN 4867-K16/6-18a, two heads.
5. Specimen GIN 4867-K16/6-18a, head, enlargement of fig. 4.
6. Specimen GIN 4867-K16/3-94a, head.
7. Specimen GIN 4867-K16/6-18b, fragments of three heads.
8. Specimen GIN 4867-K16/6-18b, enlargement of fig. 7, head fragment.
9. Specimen GIN 4867-K16/6-18b, head fragment.
10. Specimen GIN 4867-K16/6-52a, head.
11. Specimen GIN 4867-K16/6-21, head.
12. Specimen GIN 4867-K16/6-58, head.

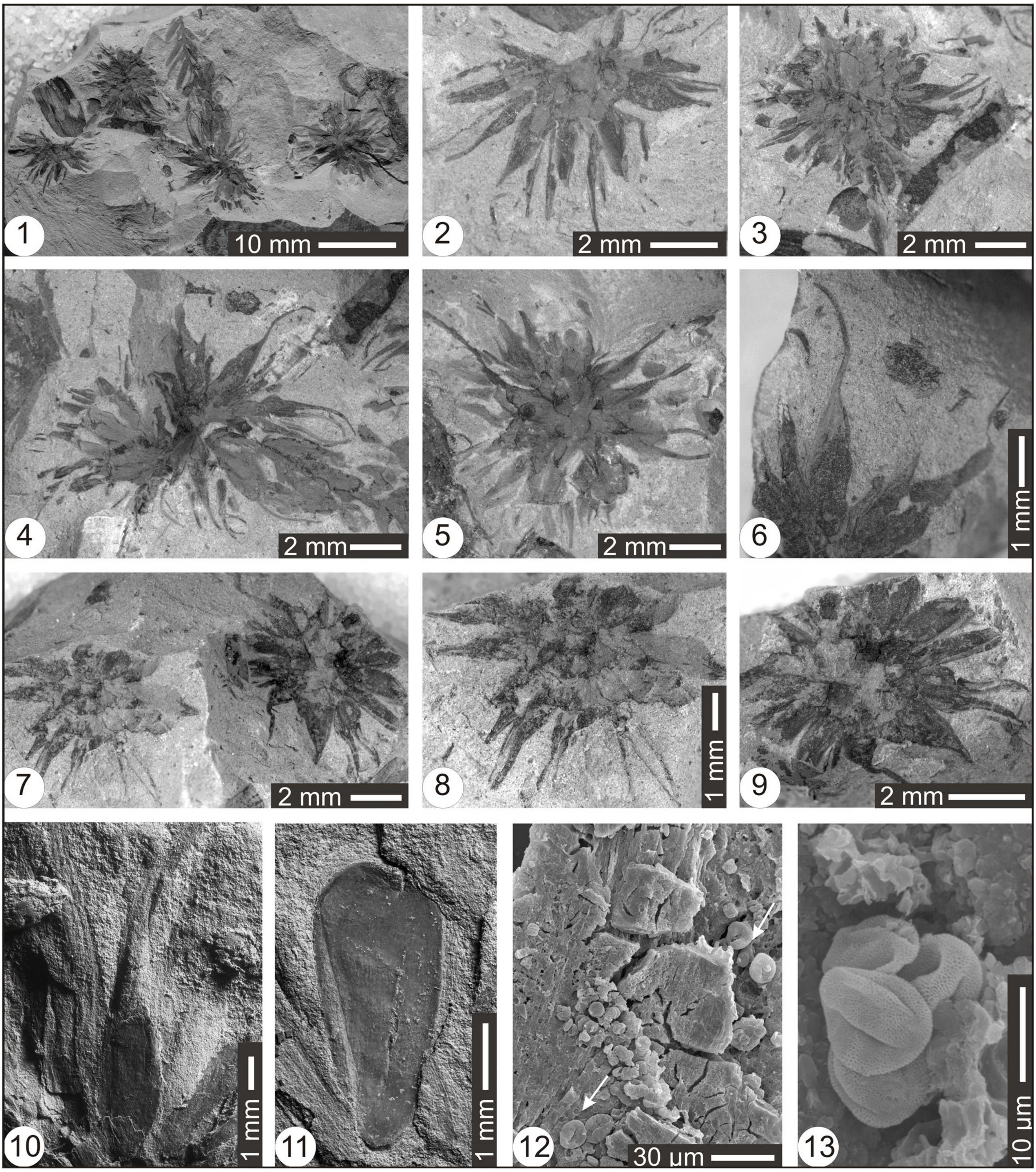

PLATE 3

Morphology of infructescences (1 - 9) and a fruitlet (10, 11) of *Kunduricarpus longistylium* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov., and pollen grains (12, 13) adhered to the fruitlet surface; (10 - 13) - SEM.

1-6. Specimen GIN 4867-K16/6-102, fruitlets in different stages of maturation.
7-9. Specimen BIN 1538/386, fruitlets in different stages of maturation.
10. Specimen GIN 4867-K16/6-17-2, fruitlet.
11. Specimen GIN 4867-K16/6-66b, body of a mature fruitlet with broken style.
12. Specimen GIN 4867-K16/6-18b, pollen cluster (arrows) on the fruitlet surface.
13. Specimen GIN 4867-K16/6-61-2, pollen cluster on the fruitlet surface.

ticulate, semitectate, tricolpate or tricolporate with indistinct ora, columellate, the inner layer (foot layer and/or endexine) unequal in thickness throughout the pollen grain. Colpi long, about 0·6-0·7 of the polar axis length, the colpus margin with a sporopollenin rim, aperture membrane presumably smooth.

Description—The staminate inflorescence consists of an axis up to 1·5 mm in diameter and heads 5-10 mm in diameter excluding projecting fruitlets (Pl. 6.1-12; Pl. 7.1-15; Pl. 8.1, 5). The heads are sessile (Pl. 7.13) or on a peduncle up to 500 µm long (Pl. 8.1). The maximum diameter of the head was observed for the presumably most mature inflorescence. Smaller, probably immature inflorescences are denser while larger (mature) inflorescences are loose with more freely arranged stamens.

The epidermis of the inflorescence axis consists of transversally elongated, trapezoid or square cells, up to 18 µm length and up to 15 µm width, arranged in indistinct longitudinal rows (Pl. 9.2). Trichomes are lacking on the axis (Pl. 9.1, 2).

Most fragments of inflorescences are single heads, occasionally three heads occur on the axis, but the maximum number of inflorescences on the axis was not determined. The central core is up to 4 mm in diameter. The flower number per head is defined by scars remained after the flowers fell out and is up to 30. Individual flowers are of different sizes and there are flowers which considerably exceed in size the majority of inflorescence flowers (Pl. 9.5, 6).

No evidence of perianth was found. In mature inflorescences, individual flowers on the core are clearly seen due to the development of the interflower tissue, as well as circular swellings about 100 µm high (Pl. 8.6-8).

Flowers are mostly tetramerous (Pl. 8.2), less often pentamerous (Pl. 8.3, 4). Stamens are supposedly tetrasporangiate (Pl. 9.3, 4; Pl. 10.3, 5). Head fragments easily disintegrate into individual pollen sacs that considerably vary in dimensions (Pl. 10.6-10, 13). The stamen filament is not pronounced. Pollen sacs are spindle-shaped, often somewhat curved, slightly pointed, up to 1800 µm long and up to 150 µm wide. The pollen sac cuticle is very thin (Pl. 10.1), fragmentary preserved on the tops of pollen sacs, but mostly not preserved at all (Pl. 10.2). Pollen density in sacs is low; the sacs are loose and easily break up into small fragments (Pl. 10.2, 6, 12-14).

There is at least one mature fruitlet in staminate head (Pl. 6.1, 2, 4, 5, 7, 10, 11), sometimes there are several small fruitlets per head (Pl. 7.4). The fruitlet body is broadly elliptic to widely ovoid, up to 4 mm long and 3 mm wide (Pl. 6.2). The whole length of the style is unknown, preserved fragments reach up to 3 mm. Thereby, the whole length of the fruitlet is almost equal to or exceeding the head diameter. The ventral suture runs from the base of the fruitlet to the style tip.

Pollen grains are small, the polar axis from 13·5 to 20·5 µm with the average from 15·5 to 17·5 µm, ellipsoidal, finely reticulate, tricolpate or tricolporate with indistinct ora (Pl. 11.1, 2, 11). The lumina are rounded and elongated, 3-4-5-angular with the similar sculpture on apo- and mesocolpia (Pl. 11.4-9, 14). The colpus margin is formed by a solid sporopollenin rim (Pl. 11.4, 5, 7, 8, 14). Colpi are long, the aperture membrane appears to be smooth (Pl. 11.7, 16). The exine is semitectate (Pl. 11.3, 10, 13). Three layers can be distinguished in the sporoderm: the tectum, columellate infratectum and the innermost layer (for convenience we will call this layer nexine, though the term is usually used for LM); in this concept, nexine probably includes the foot layer and endexine (Pl. 11.10-13, 15). If there are two layers present in the sporoderm it is impossible to distinguish them consistently on the studied material, though there is a thin, 0·03 µm thick, somewhat less electron dense layer, which probably represents remnants of the endexine. The nexine is unequal in thickness over the pollen grain (Pl. 11.10, 12, 13). The measurements are in a table (Fig. 2).

Etymology—From miraculous, unusual.

Holotype—GIN 4867-K16/6-39; capitate inflorescence; Amur Region, road cut of the Federal Highway 'Amur' Chita-Khabarovsk between the rivers Mutnaya and Udurchukan, near Kundur Town; Kundur Formation, Campanian (Pl. 6.1, 2; Pl. 10.1, 2, 4, 6, 8-12); designated here.

Occurrence—Amur Region, area between the rivers Mutnaya and Udurchukan, near Kundur Town; Kundur Formation, Campanian.

DISCUSSION

Pistillate reproductive structures

Infructescence architecture—Fossil platanoid infructescences differ in size, presence/absence of the developed style and the attachment mode. The study of their micromorphology reveals more details which allow to refer these species to different genera and even families.

PLATE 4

Anatomical characters in *Kunduricarpus longistylium* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov., SEM; (1-6) - cuticles after maceration, (7, 8) - fruitlet after HF cleaning, without maceration.

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1. Specimen GIN K16/6-102, epidermis of infructescence axis, external view.
2. Specimen GIN K16/6-102, epidermis of infructescence axis, internal view.
3. Specimen BIN 1538/386, epidermis of central part of a fruitlet, cells with oblique ends.
4. Specimen BIN 1538/386, epidermis in fruitlet base, longitudinally elongated cells are visible.
5. Specimen BIN 1538/386, epidermis of lower part of a fruitlet.

6-8. Specimen BIN 1538/378, epidermis of apical part of a fruitlet, differently shaped cells are visible.

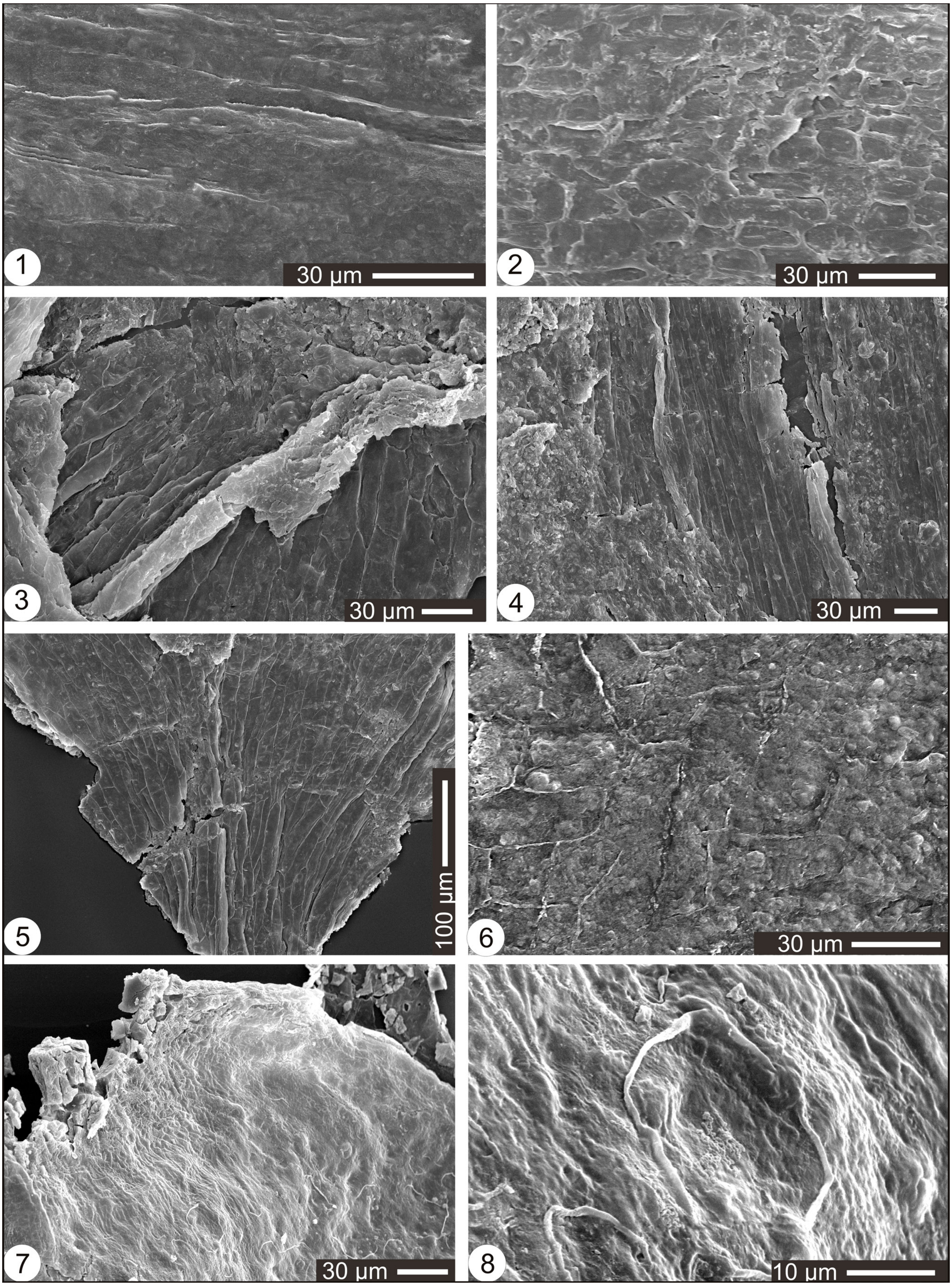

PLATE 4

Specimen	Holotype GIN 4867-K16/6-39 Average (min-max), µm	Specimen BIN 1538/369 Average (min-max), µm	Pollen adhered to ***Kunduricarpus*** Average (min-max), µm
Polar axis/equatorial diameter	1.22 (1.03-1.42)	1.3 (1.11-1.57)	1.29 (1.0-1.58)
Polar axis	15.27 (13.46-17.45)	17.76 (14.62-20.0)	17.52 (14.59-20.36)
Equatorial diameter	12.51 (11.74-15.0)	13.76 (11.75-18.0)	13.7 (10.91-16.13)
Colpus length	8.85 (5.0-10.42)	12.19 (5.5-18.4)	10.35 (6.36-13.21)
Exine thickness	0.7 (0.29-1.13)	0.6 (0.33-0.73)	-
Tectum	0.16 (0.06-0.27)	0.25 (0.17-0.33)	-
Columella height	0.25 (0.11-0.43)	0. 13 (0.1-0. 17)	-
Columella width	0.11 (0.06-0.15)	0.08 (0.07-0.1)	-
Nexine	0.25 (0, 0.03-0.53)	0.23 (0, 0.07-0.67)	-

Fig. 2—Measurements of pollen grains from *Kundurianthus* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov. and those adhered to *Kunduricarpus* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov.

All known fossil capitate infructescences are smaller than those of the modern plane tree (except *P. kerrii* Gagnepain, 1939). Infructescence diameter in *Platanus* can reach 4 cm (more often 2-3 cm). The maximum diameter of *Kunduricarpus* gen. nov. infructescences is 15 mm (about 10 mm on average). The compound infructescence of *K. longistylium* gen. *et* sp. nov. consists of an axis and pedunculate heads. The maximum visible number of heads on the axis in *Kunduricarpus* gen. nov. is four, but the specimens are incomplete and the full number of infructescences may have been greater. Modern *Platanus* species differ in head number and how they are attached to the axis (see a discussion in Nixon & Poole, 2003). Heads of fossil *Platanus* species can be sessile or pedunculate. Among extinct Platanaceae the infructescences of *Macginicarpa* have peduncles. Species of the Late Cretaceous genus *Friisicarpus* N. Maslova & Herman, 2006 (Friis *et al.*, 1988; Maslova *et al.*, 2011; Maslova & Tekleva, 2012) are characterized by sessile heads.

In a number of the fossil Platanaceae and related taxa the axis of the compound infructescence has a longitudinal striation seen in a stereo microscope which is formed by cutin strands and bears numerous trichomes. As a rule, epidermal cells of the axis are tetragonal and arranged in regular longitudinal rows. This is true for Cretaceous genera *Friisicarpus* (Maslova *et al.*, 2011; Maslova & Tekleva, 2012), *Sarbaicarpa* N. Maslova, 2009, Sarbaicarpales (Maslova, 2009) and modern *Platanus*. Trichomes on the axis of reproductive structures are described for the modern Platanaceae and some Proteaceae (Carpenter *et al.*, 2005).

Kunduricarpus gen. nov. is characterized by a unique epidermal structure of the infructescence axis, which differs from that in all the known platanoid reproductive structures. As a rule, reproductive structures similar in macromorphology have a thin axis, covered by trichomes in a varying degree. So, the axis is strongly hairy in Albian-Cenomanian *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova, 2011 (Maslova *et al.*, 2011) and Senonian *F. sarbaensis* N. Maslova & Tekleva, 2012 (Maslova & Tekleva, 2012). On the contrary, trichomes are absent on the axis of *Kunduricarpus longistylium* gen. *et* sp. nov. Besides, epidermal cells of known fossil Platanaceae species are strongly cutinized, rather uniform in their shape (square or rectangular) and size, and are arranged in distinct longitudinal rows, while in the new genus the cutinization is weaker and the axis epidermis consists of differently shaped (transversally elongated, trapezoid, square) and sized cells, arranged in indistinct rows.

K. longistylium gen. *et* sp. nov. heads at our disposal probably represent different stages of maturation. Less mature heads have slightly smaller sizes, more compact arrangement of narrowly elliptic carpels with shorter styles. More mature infructescences differ in the larger diameter, looser arrangement of the fruitlets/fruits (apparently, due to the overgrowth of the core tissue between fruits), widely elliptic (up to obovate) fruitlets with longer styles. *Kunduricarpus* gen. nov. is similar to modern *Liquidambar orientalis* Miller, 1768 (Ickert-Bond *et al.*, 2005) in the presence of the considerably proliferated tissue around adjacent fruits.

Differently shaped and sized fruitlets occur in infructescences of *Kunduricarpus longistylium* gen. *et* sp. nov. This can indicate their nonsimultaneous maturation. Such phenomenon is known for *Macginicarpa* (Manchester, 1986) and for some modern Hamamelidaceae (Bogle, 1986), as well as for a number of fossil taxa with capitate infructescences combining features of the Platanaceae and Hamamelidaceae (Maslova & Krassilov, 1997; Maslova & Golovneva, 2000; Maslova & Herman, 2004; Maslova *et al.*, 2005).

The new genus of infructescence is quite isolated from all fossil Platanaceae and modern *Platanus* in the low number of fruit per head. The infructescence of *Kunduricarpus* gen. nov. contains less than 30 fruits, whereas *Friisicarpus* species

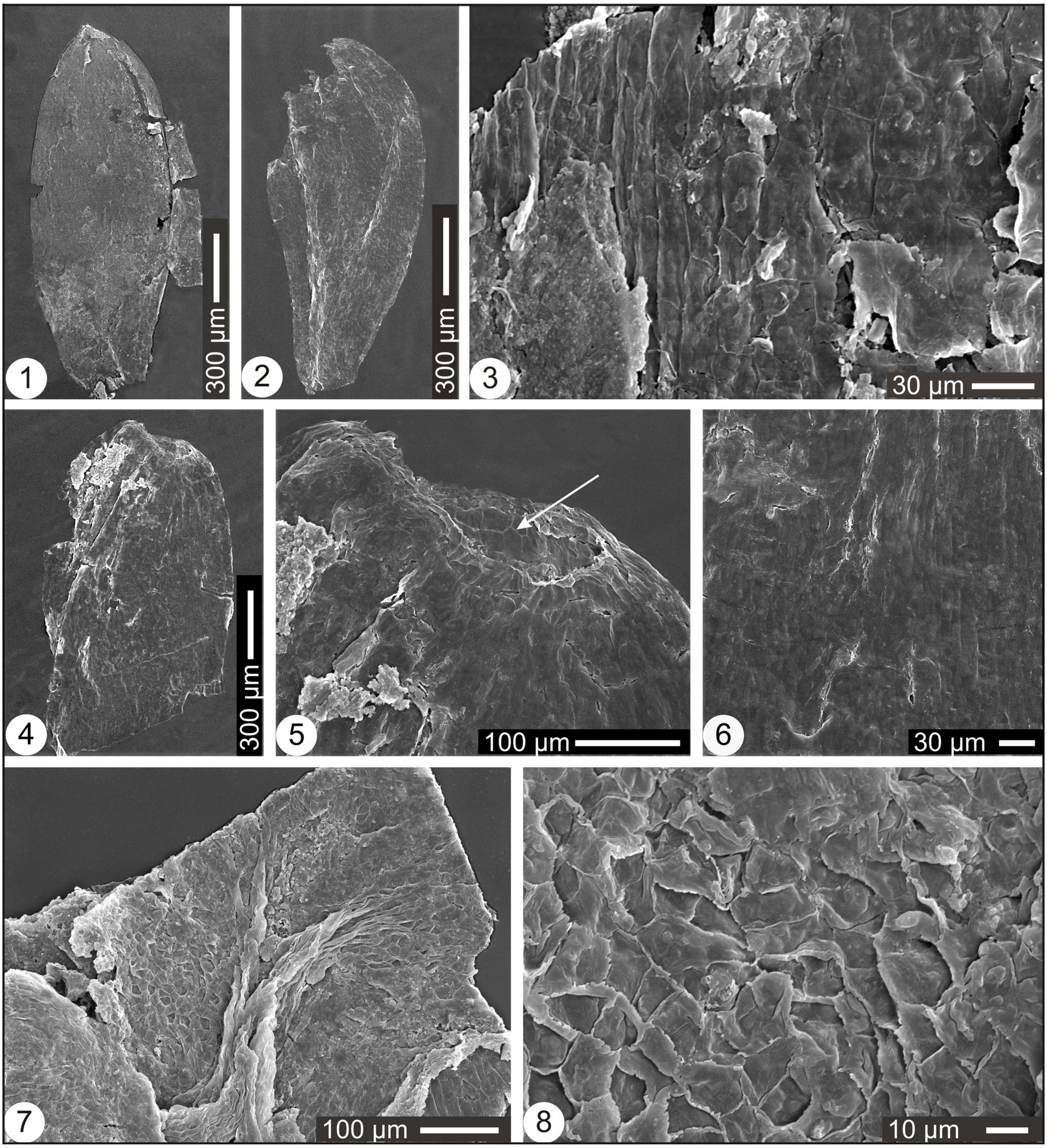

PLATE 5

Morphological and epidermal characters of *Kunduricarpus longistylium* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov., SEM.

1. Specimen BIN 1538/378, cuticle of fruitlet body, style is detached off.
2. Specimen BIN 1538/386, cuticle of fruitlet body without apical part.
3. Specimen BIN 1538/386, epidermis of apical part of a fruitlet, narrow elongated cells in the suture region (on the left) and tetragonal cells (on the right) of central part of a fruitlet.

4, 5. Specimen GIN 4867-K16/6-22, cuticle of apical part of a fruitlet, style is detached off, polygonal cells (arrow) of the inner wall layer of the fruitlet are visible.

6. Specimen GIN 4867-K16/6-22, cuticle of lower part of a fruitlet.
7. Specimen BIN 1538/386, longitudinal split of fruit part through three fruitlets, the cavity of the leftmost fruitlet occupies by the tissue of the solitary seed.
8. Specimen BIN 1538/386, enlargement of fig. 7, seed tissue.

have from 50 to 100, *Macginicarpa* has about 60 and modern *Platanus* species may have more than 100. The new genus resembles *Altingia* Noronha, 1790 and *Liquidambar* L., 1753, which are considered as members of the Hamamelidaceae, Altingioideae (Endress, 1989) or Altingiaceae (Magallón-Puebla *et al.*, 1999; Pigg *et al.*, 2004; Ickert-Bond *et al.*, 2005, 2007), in having a similarly small number of fruits per head. So, in *Altingia* it is up to 25 fruits and in *Liquidambar* it is from 26 to 40 (Bogle, 1986; Ickert-Bond *et al.*, 2005, 2007). Miocene *L. changii* Pigg, Ickert-Bond & Wen, 2004 has about 25-30 fruits (Pigg *et al.*, 2004). In the infructescence of the Coniacian genus *Lindacarpa* N. Maslova & Golovneva, 2000 (Maslova & Golovneva, 2000) up to 30 fruits were described.

Quadriplatanus Magallón-Puebla, Herendeen & Crane, 1997 (Bogutchanthaceae after Maslova, 2010) from the Coniacian-Santonian with heads similar in macromorphology to the Platanaceae has about 40 fruits (Magallón-Puebla *et al.*, 1997), Turonian *Kasicarpa* N. Maslova, Golovneva & Tekleva, 2005, Kasicarpaceae (Maslova *et al.*, 2005) has 30-40 fruits per head.

Perianth—The degree of the perianth development in the flower is one of diagnostic features which helps to distinguish heads of the modern genus from macromorphologically similar fossil platanaceous heads. The maximum development of the perianth was observed for fossil genera *Friisicarpus* and *Macginicarpa*.

Linnaeus (1754, p. 433) in his first description of the genus *Platanus* interpreted perianth elements as tiny and hardly visible. The presence of the perianth in modern *Platanus* was discussed over a long time (Bretzler, 1924; Boothroyd, 1930; Ernst, 1963; Nixon & Poole, 2003; Douglas & Stevenson, 1998, and others). In the detailed study by von Balthazar and Schönenberger (2009) two circles of sterile structures in staminate and pistillate flowers were observed on the example of *P. hispanica* Münchh. The sterile structures surround the androecium and gynoecium and have different origin. Elements of the outer circle are no more than 500 μm and have numerous hairs in the apical part. These structures belong to the perianth while elements of the inner circle are staminodia. It is evident that detailed study of other modern species of *Platanus* is required to clarify the degree of the perianth development.

Kunduricarpus gen. nov. mature fruits lack a perianth. Poor preservation of pistillate inflorescences on the early developmental stages made it impossible to study their micromorphology and to indicate the presence or absence of the perianth in immature flowers. Maceration of fruit fragments resulted in no cuticles except those of the fruitlets. Also there were not any remnants of a perianth in the fruit bases on the specimens with fallen fruits. In this the new genus is similar to modern *Altingia* and *Liquidambar* with naked flowers in capitate infructescences.

Bogle (1986) hypothesized that altingioid ancestors could have developed perianths which later were transformed into a sclerotized tissue between fruits in mature infructescences. An assumption on the secondary origin of altingioid flowers received additional support from fossil findings (e.g. Maslova & Golovneva, 2000). The tissue proliferation between adjacent flowers in mature infructescences of *Kunduricarpus* gen. nov. might indicate the presence of a developed perianth in ancestral forms.

It should be noted that for a number of angiosperms a correlation between a degree of a perianth development and fixed number of flower elements was revealed (Endress, 1990). Such a correlation was also observed in the Platanaceae (Crane, 1989; Drinnan *et al.*, 1994; Magallón-Puebla *et al.*, 1997, and others). As a rule, in the fossil Platanaceae with a well-developed perianth the number of reproductive organs is constant within the flower (Manchester, 1986; Friis *et al.*, 1988; Pigg & Stockey, 1991; Crane *et al.*, 1993; Pedersen *et al.*, 1994; Maslova & Herman, 2006; Maslova *et al.*, 2011; Maslova & Tekleva, 2012, and others). On the contrary, *Platanus* species is characterized by a weakly developed perianth or its absence and by various number of reproductive organs in the flower (Boothroyd, 1930). In case of *Kunduricarpus* gen. nov. also a combination of an unstable number of fruitlets in the fruit (four or five) and perianth absence were shown.

Gynoecium—One of the most distinguishing flower characters of modern *Platanus* is an unstable number of the elements. Pistillate flowers have from five to nine apocarpous carples. On the contrary, extinct genera of the Platanaceae are characterized by stable number of carpels per flower. E.g., *Friisicarpus* and *Macginicarpa* have pentamerous fruits (there are exceptions, in *Macginicarpa* 6-merous fruits sometimes occur as reported in Manchester, 1986). Both tetra- and pen-

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PLATE 6

Morphology of inflorescences of *Kundurianthus mirabilis* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov.

⟶

1. Holotype GIN 4867-K16/6-39, two heads with a large fruitlet (arrow) in one of them.
2. Holotype GIN 4867-K16/6-39, head with prominent fruitlet.
3. Specimen GIN 4867-K16/6-66a, head fragment, note an abscised large fruitlet lying adjacently (arrow).
4. Specimen BIN 1538/369, two heads with a large fruitlet (arrow) in one of them.
5. Specimen BIN 1538/369, enlargement of fig. 4, fruitlet.
6. Specimen GIN 4867-K16/6-30a, head.
7. Specimen BIN 1538/374, head with a large fruitlet (arrow).
8. Specimen GIN 4867-K16/6-29a, head.
9. Specimen BIN 1538/381-1, head.
10. Specimen BIN 1538/381-2, head with a large fruitlet (arrow).
11. Specimen BIN 1538/381-2, enlargement of fig. 10, fruitlet.
12. Specimen BIN 1538/383b, head core, flowers are abscised, scars of flower bases and developed core tissue between them are visible.

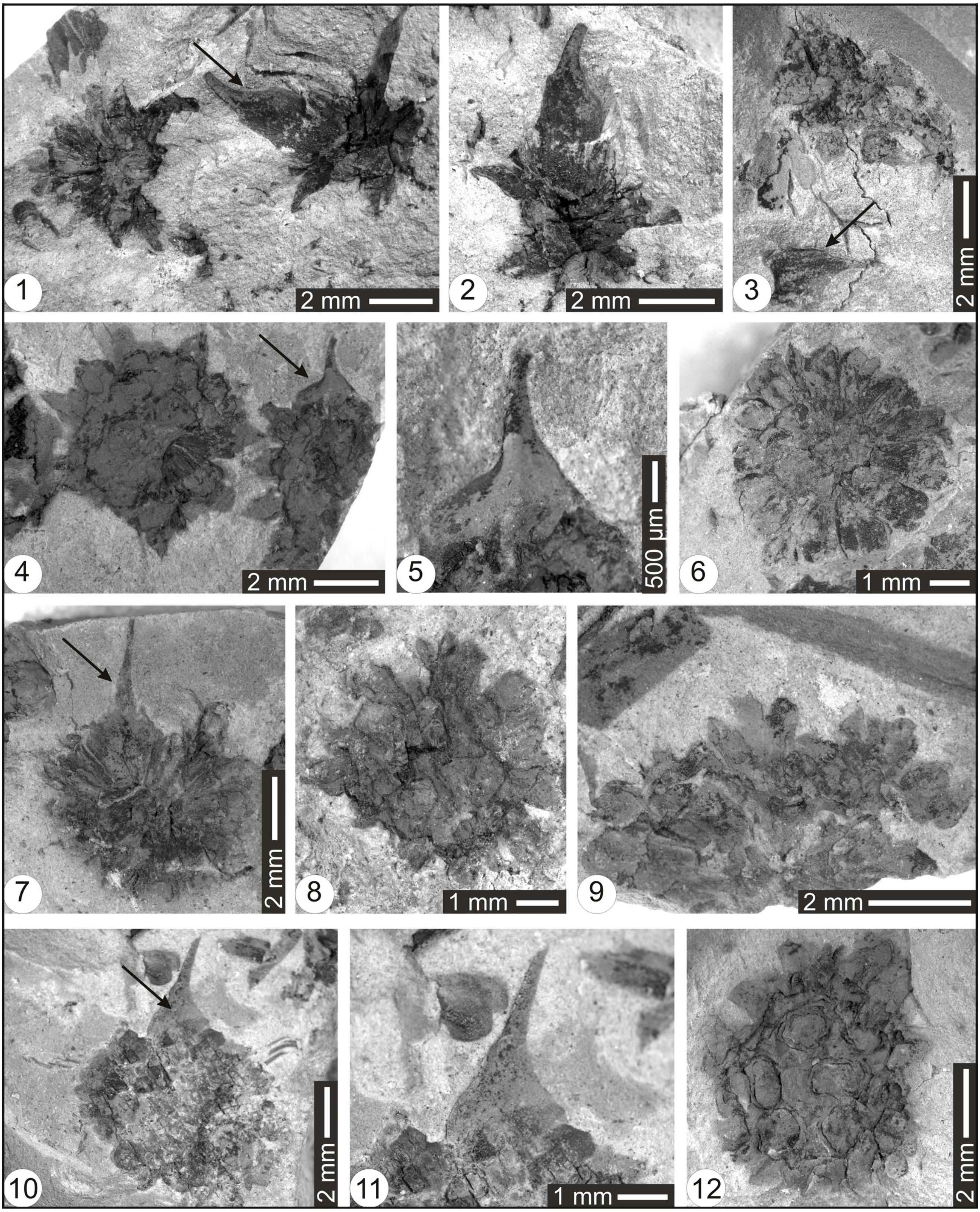
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PLATE 6

tamerous fruits were observed for *Kunduricarpus* gen. nov. Unfortunately, the preservation does not allow to be certain about the percentage of tetramerous and pentamerous merosity per head.

Differently matured individual fruitlets within the infructescence observed for *Kunduricarpus* gen. nov. were also shown for *Macginicarpa* (Manchester, 1986). While modern *Platanus* species differ in rather synchronous maturation of carpels, a nonsimultaneous maturation of carpels was shown for Eocene-Miocene *P. neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, 1968, subgenus *Glandulosa* (Kvaček & Manchester, 2004). In nonsimultaneous maturation of individual carpels within the head *Kunduricarpus* gen. nov. is similar to Cretaceous genera of the Hamamelidaceae—*Lindacarpa* (Maslova & Golovneva, 2000) and *Evacarpa* N. Maslova & Krassilov, 1997 (Maslova & Krassilov, 1997)-as well as to *Kasicarpa* (Maslova *et al.*, 2005), *Anadyricarpa* N. Maslova & Herman, 2004 (Maslova & Herman, 2004), and *Oreocarpa* N. Maslova & Krassilov, 2002 (Maslova & Krassilov, 2002) which have been placed in the extinct order Sarbaicarpales (Maslova, 2010). Note that modern genera *Altingia*, *Liquidambar* and *Semiliquidambar* H.T. Chang, 1962 have capitate infructescences and are also characterized by nonsimultaneous maturation of the fruits.

Pigg and Stockey (1991) revealed an evolutionary trend in the formation of the synchronous fruit maturation in the head. The authors noted that more ancestral members of the Platanaceae are more often characterized by independent fruit maturation, while modern *Platanus* shows synchronous maturation. This trend correlates to the tendency of the transition from biotic to abiotic pollination in the Platanaceae (Hesse, 1978; Friis *et al.*, 1988: Pigg & Stockey, 1991).

The shape of the fruitlet body in *Kunduricarpus* gen. nov. depends on its maturation stage. Less mature fruitlets have narrowly elliptic shape with gradual transition from the fruitlet body to the style and mostly straight styles. The shape of the body in more mature fruitlets is from elliptic to widely elliptic and obovate, the styles are often incurved. The fruitlet shape differs in the early Platanaceae—from narrowly triangular in Late Albian *Friisicarpus marylandensis* (Friis, Crane & Pedersen) N. Maslova & Herman, 2006 (Friis *et al.*, 1988), Early Albian *F. brookensis* (Crane, Pedersen, Friis & Drinnan) N. Maslova & Herman, 2005 (Crane *et al.*, 1993) and Santonian-Campanian *F. carolinensis* (Friis, Crane *et* Pedersen) N. Maslova & Herman, 2005 (Friis *et al.*, 1988) to narrowly elliptic in Paleocene *Platanus stenocarpa* N. Maslova (Maslova, 1997) and Santonian-Campanian *Friisicarpus* sp. (Friis *et al.*, 1988), from widely elliptic in Cretaceous *Platanus richteri* Knobloch & Mai, 1986 (Knobloch & Mai, 1986) to ovoid-elliptic in Eocene *Macginicarpa glabra* Manchester, 1986 (Manchester, 1986), obovate (up to triangular) in Middle Eocene *Platanus hirticarpa* Manchester, 1994 (Manchester, 1994) and oval (up to obovate) in Eocene *Tanyoplatanus cranei* Manchester, 1994 (Manchester, 1994).

One of the characteristic features of most extinct Platanaceae is absence of the hairs for fruitlet dispersal in pistillate heads. The only exclusion is the Eocene genus *Tanyoplatanus* Manchester, 1994 with numerous and rather large hairs in the fruitlet base. The bundle of hairs in pistillate flowers along with trichomes on carpel walls are characteristic features of the genus *Platanus*. For several *Platanus* species (*P. laevis* (Velenovský) Velenovský, 1882, *P. richteri*, *P. stenocarpa*, *P. neptuni*) no hairs in the fruitlet base were observed, but on the fruitlet surface. Trichomes in the fruitlet epidermis were also observed for *Friisicarpus* (Maslova *et al.*, 2011; Maslova & Tekleva, 2012). Interestingly, the bundle of hairs in the fruit base is present in the Cenomanian genus *Sarbaicarpa*, Sarbaicarpales (Maslova, 2009) with a mosaic combination of characteristic features of the both Platanaceae and Hamamelidaceae.

The fruitlet epidermis of *Kunduricarpus* gen. nov. consists of differently shaped and sized cells. The cells are strongly longitudinally elongated in the fruitlet base and rectangular, often with oblique margins in the central part. Identical epidermal cells of the fruitlet were shown for *Liquidambar orientalis* (Ickert-Bond *et al.* 2005, fig. 7, I).

There are areas of a wide, relatively smooth surface between adjacent fruits on the inflorescence core in mature heads of *Kunduricarpus* gen. nov. A similar core structure was observed for modern species of *Altingia* and *Liquidambar*

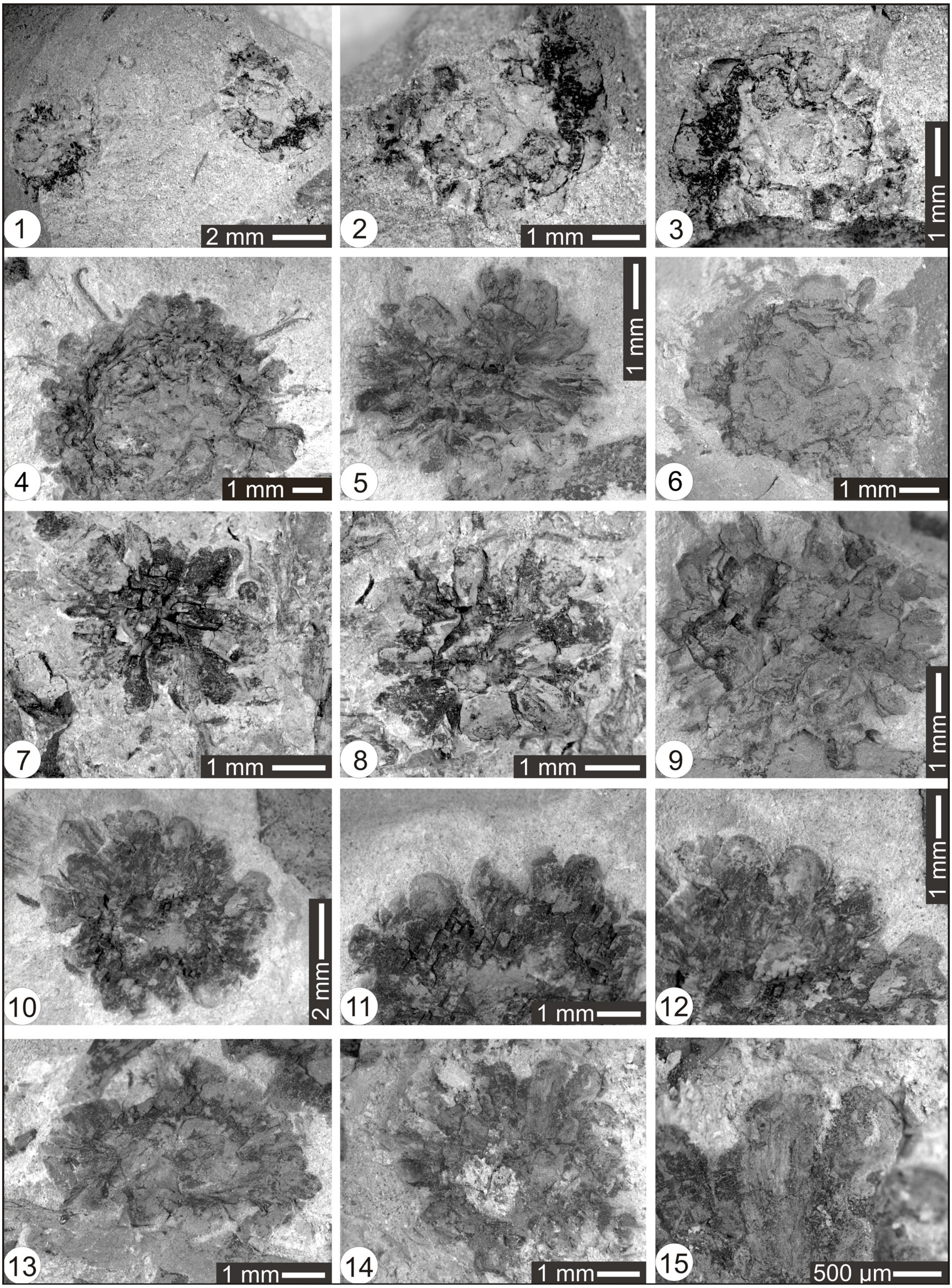
PLATE 7

Morphology of inflorescences of *Kundurianthus mirabilis* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov. ⟶

1. Specimen GIN 4867-K16/3-96, cores of two heads.
2. Specimen GIN 4867-K16/3-96, enlargement of fig. 1, head core, scars of abscised flowers and developed core tissue between them are visible.
3. Specimen GIN 4867-K16/3-96, enlargement of fig. 1, 270° turn in respect to fig. 2, head core, scars of abscised flowers and developed core tissue between them are visible.
4. Specimen BIN 1538/382, head, styles and scars of flower bases are visible.
5. Specimen BIN 1538/383a, sessile head on the axis.
6. Specimen GIN 4867-K16/6-60, head core, flowers are abscised; scars of flower bases and developed core tissue between them are visible.
7. Specimen GIN 4867-K16/3-77, head.
8. Specimen GIN 4867-K16/3-81, head.
9. Specimen BIN 1538/383b, head.
10. Specimen BIN 1538/380, head.

11, 12. Specimen BIN 1538/380, enlargement of fig. 10, head fragments.

13. Specimen GIN 4867-K16/6-34a, head on the axis.
14. Specimen GIN 4867-K16/6-29b, head.
15. Specimen GIN 4867-K16/6-29b, enlargement of fig. 14, head fragment.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15
500 µm

PLATE 7

with clear regions of smooth or reticulate sclerenchymous tissue between fruits (Ickert-Bond *et al.*, 2005; Ickert-Bond *et al.*, 2007).

The seed number per fruitlet in the studied fossil Platanaceae is one. *Kunduricarpus* gen. nov. also has one seed filling the whole fruitlet cavity.

Heads of modern *Platanus* are usually unisexual; sometimes the flowers additionally bear rudiments of reproductive structures (staminodia in infructescences and rudimentary pistils in staminate inflorescences). These rudimentary structures occur sporadically and were observed only in several species-*Platanus occidentalis* L., 1753, *P. acerifolia* (Aiton) Willdenow, 1797, *P. racemosa*, and *P. orientalis* L., 1753 (Boothroyd, 1930; Schwarzwalder & Dilcher, 1981). For *Altingia* and *Liquidambar* species with capitate infructescences the development of staminodia, which sometimes become stamens with fertile pollen, was described (Bogle, 1986; Ickert-Bond *et al.*, 2005). Neither staminodia, nor developed stamens were observed in *Kunduricarpus* gen. nov. infructescences.

Pollen grains associated with infructescences of Kunduricarpus longistylium gen. et sp. nov.—Pollen grains adhered to infructescence surface are identical in their morphology and size to those, extracted from *Kundurianthus* gen. nov. (Pl. 3.12, 13; Pl. 11.6, 9, 14).

Staminate reproductive structures

Inflorescence architecture—Inflorescences of the genus *Kundurianthus* gen. nov. are represented by an axis with sessile and pedunculate heads. The maximum visible number of heads on the axis is three. Most Platanaceae are characterized by sessile staminate heads. Among fossil staminate inflorescences heads attached to the axis by a peduncle were described for *Platananthus* Manchester, 1986 (Platanaceae) - *P. scanicus* Friis, Crane & Pedersen, 1988 (Friis *et al.*, 1988) and *P. speirsae* Pigg & Stockey, 1991 (Pigg & Stockey, 1991), as well for the Paleocene genus *Archaranthus* N. Maslova & Kodrul, 2003 (Maslova & Kodrul, 2003) from the Bogutchanthaceae.

The axis structure of *Kundurianthus* gen. nov. inflorescence is similar to that of *Kunduricarpus* gen. nov., differing from known genera referred to the Platanaceae. The axis epidermis of *Kundurianthus* gen. nov. consists of trapezoid or square cells arranged in indistinct longitudinal rows. Like *Kunduricarpus* gen. nov., there are no trichomes on the axis epidermis of *Kundurianthus* gen. nov. This character distinguishes the new genus from modern *Platanus* and all known fossil Platanaceae genera. Trichomes on the reproductive axis of modern *Platanus* are rather abundant and epidermal cells of the axis are in clear longitudinal rows and always rectangular.

Both male and female flowers of *Platanus* are very dense, the flowers are tightly adpressed to each other. The borders of individual flowers are almost indistinguishable as perianth elements are either tiny or absent. In staminate inflorescences of the fossil Platanaceae with rather developed perianth the flower borders are distinct (e.g. *Platananthus*). In *Kundurianthus* gen. nov. borders of flowers in immature heads cannot be traced superficially due to the absence of the perianth and densely arranged flowers. In mature heads a nonsimultaneous development of individual flowers was observed when some flowers become considerably larger than others. The number of flowers can be determined only by scars of fallen flowers on the inflorescence core. Besides, individual flowers in mature heads of *Kundurianthus* gen. nov. are well marked by a proliferation of a core tissue, which occasionally forms small circular rollers engirdling the flower base. The tissue proliferation between adjacent fruits was also observed for *Kunduricarpus* gen. nov. heads.

The number of flowers per head is 30 in *Kundurianthus* gen. nov., which is about the same as observed in *Kunduricarpus* gen. nov. As a rule, staminate inflorescences of the Platanaceae have a larger number of flowers. So, in *Platananthus* inflorescences the number is from 50 to 100 flowers, in *Gynoplatananthus*, Platanaceae (Mindell *et al.*, 2006), *Bogutchanthus* N. Maslova, Kodrul & Tekleva, 2007 (Maslova *et al.*, 2007) and *Quadriplatanus* from the Bogutchanthaceae—at least, 40.

Perianth—No evidence of perianth in *Kundurianthus* gen. nov. was found. Maceration of head fragments resulted in no cuticles but that of pollen sacs only. In mature inflorescences the interflower tissue as well as circular swellings are well-developed. The possibility that these circular swellings are remnants of the perianth cannot be ruled out.

The extreme degree of the perianth reduction is observed in the flowers of staminate inflorescences of Paleocene Platanaceae *Platanites hybridicus* Forbes, 1851 (Crane *et al.*, 1988; Boulter & Kvaček, 1989) and *Chemurnautia staminosa*

PLATE 8

Morphology of inflorescences of *Kundurianthus mirabilis* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov., (6-8) - SEM. ⟶

1. Specimen GIN 4867-K16/3-88, inflorescence on a peduncle, flowers are abscised, scars of the flowers are seen on the core.
2. Specimen GIN 4867-K16/3-88, enlargement of fig. 1, head core, scars of abscised flowers of four stamens are visible.
3. Specimen GIN 4867-K16/3-96, head core, scars of abscised flowers are visible.
4. Specimen GIN 4867-K16/3-96, enlargement of fig. 3, flower base with scars of five stamens.
5. Specimen GIN 4867-K16/6-56a, architecture of a mature inflorescence.
6. Specimen GIN 4867-K16/6-56a, core fragment, proliferated tissue between flowers is visible.

7, 8. Specimen BIN 1538/383b, core fragment, proliferated tissue between flowers which forms circular rollers is visible.

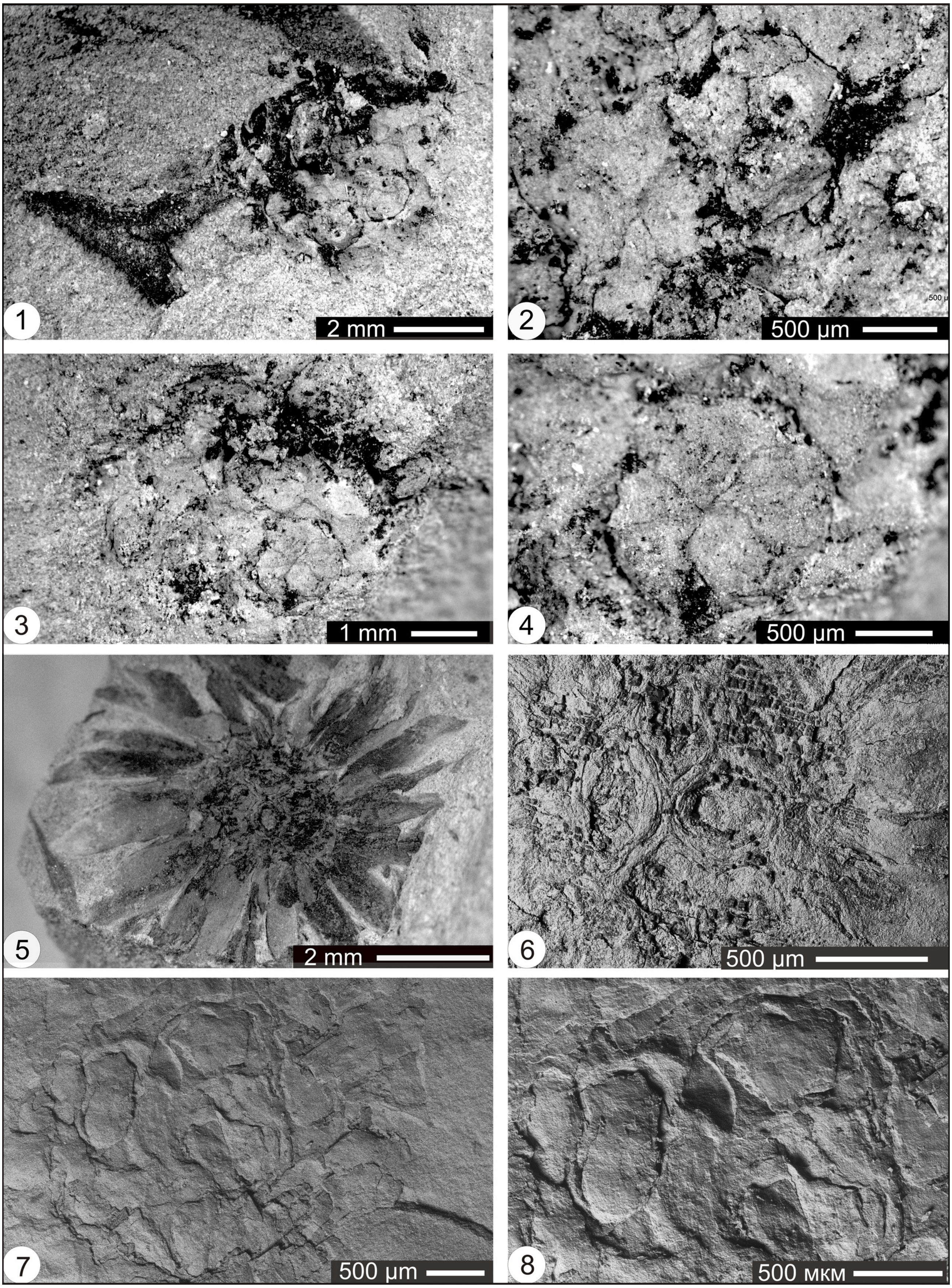

PLATE 8

N. Maslova, 2002 (Maslova, 2002). On the contrary, the perianth is well-developed, reaching an androecium length in the flowers of Cretaceous to Paleogene genus *Platananthus* (Manchester, 1986; Friis *et al.,* 1988; Pigg & Stockey, 1991), the Cretaceous genera *Aquia* Crane, Pedersen, Friis & Drinnan, 1993 (Crane *et al.*, 1993), and *Hamatia* Pedersen, Friis, Crane & Drinnan, 1994 (Pedersen *et al.*, 1994), and the Eocene *Gynoplatananthus* (Mindell *et al.*, 2006). The perianth is also well-developed in the flowers of Cretaceous genera *Quadriplatanus, Bogutchanthus*, and *Archaranthus*, which have been segregated as a distinct fossil family Bogutchanthaceae (Maslova, 2010). The Cretaceous genus *Sarbaya* Krassilov & Shilin, 1995 (Krassilov & Shilin, 1995) also placed in the Bogutchanthaceae, has a reduced perianth. A unique case with a well-developed perianth elements exceeding an androecium length was described for capitate staminate inflorescence *Krassilovianthus* N. Maslova, Tekleva & Remizowa, 2012; the familial attribution of this taxon is difficult due to a highly eclectic combination of characters (Maslova *et al.*, 2012).

The presence of a circle of tiny perianth elements partly fused in the base was shown in staminate flowers of modern *Platanus hispanica* (von Balthazar & Schönenberger, 2009). Douglas and Stevenson (1998) observed perianth development in staminate flowers of some *Platanus* species in the very early ontogenetic stages, but it was suppressed soon after their initiation.

Androecium—Due to insufficient preservation of the fossil material data on the androecium of *Kundurianthus* gen. nov. are incomplete. The number of stamens in the flower is mostly tetramerous, less often pentamerous.

Modern *Platanus* is characterized by unstable number of flower elements; the stamen number varies from three to five (Boothroyd, 1930; von Balthazar & Schönenberger, 2009). Fossil platanaceous genera mostly have flowers with a constant number of the androecial elements: *Platananthus*, *Gynoplatananthus*, and probably *Hamatia* have pentamerous flowers. Genera from the Bogutchanthaceae (*Bogutchanthus*, *Archaranthus*, *Sarbaya*, and *Quadriplatanus*) are characterized by tetramerous flowers, as well as staminate and pistillate heads from the Turonian of the Raritan formation, New Jersey with a combination of characters typical for the Platanaceae and Hamamelidaceae (Crepet *et al.*, 1992). A unique androecial structure was shown for *Krassilovianthus* differing from all capitate inflorescences which are macromorphologically similar to the Platanaceae (Maslova *et al.*, 2012). This genus which combines features of both Platanaceae and Hamamelidaceae, has dimerous flowers with bisporangiate stamens.

The arrangement of pollen sacs in the stamen was not determined for *Kundurianthus* gen. nov. The stamens are supposedly tetrasporangiate as is characteristic for modern *Platanus* and most extinct Platanaceae and related taxa. Stamens of *Platanus* consist of a very short filament and elongated tetrasporangiate anthers with a well-developed connective and having an apical extension. In *Kundurianthus* gen. nov. a stamen filament is not observe; anthers are sessile and maceration results in disintegrating individual pollen sacs of different sizes and shapes. The connective cuticle is thin; and there is no apical extension of the connective. The apical extension of the connective also lacking in Paleocene *Chemurnautia* N. Maslova, 2002 (Maslova, 2002) and only weakly developed in *Platanites* (Crane *et al.*, 1988). Most fossil Platanaceae have more or less developed connectives transitioning to triangular conical apical extension of the connective. The apical extension of the connective can be expressed to a variable degree, from weakly developed (*Aquia*; Crane *et al.*, 1993) to rather massive and differently shaped: conical in *Platananthus synandrus* Manchester, 1986 (Manchester, 1986) and *P. speirsae* (Pigg & Stockey, 1991), triangular in *P. scanicus* (Friis *et al.,* 1988), flattened in *P. hueberi* Friis, Crane & Pedersen (Friis *et al.,* 1988) or peltate in *P. potomacensis* Friis, Crane & Pedersen (Friis *et al.*, 1988).

A characteristic feature of *Kundurianthus* gen. nov. is rather low density of pollen grains in the anthers. The cuticle of pollen sacs is very thin and mostly is not preserved after maceration. The pollen mass in the sac is heterogeneous, with spaces in between; besides, some pollen grains are arranged rather loosely that make pollen sacs easily break up into fragments. In our opinion the pollen sacs are characterized by loosely arranged pollen rather than they have already dispersed much of the pollen. The pollen density in the sac is usually very high in modern *Platanus* and related fossil species.

Fruitlets in Kundurianthus gen. nov. inflorescences—Developed fruitlets sporadically occur in *Kundurianthus* gen. nov. heads. Heads with several fruitlets were observed (Pl. 7.4) or with one fruitlet exceeding the diameter of the head (Pl. 6.1, 2, 4, 5, 7, 10, 11). In the majority of inflorescences fruitlets were not observed. They are either invisible on the impressions or absent in the head or probably too small to be revealed on the material of such preservation.

Functionally unisexual flowers of modern *Platanus* and of some fossil platanoids show rudiments of structures of the opposite sex: undeveloped stamens (staminodia) in pistillate flowers and rudimentary pistils in staminate ones. Herein these rudimentary structures are extremely tiny and inconspicuous to the naked eye. So, pistillate flowers of *P. racemosa* have staminodia (Boothroyd, 1930; Floyd *et al.*, 1999) and in some pistillate flowers of *P. occidentalis* rudimentary or functional stamens occur (Schwarzwalder & Dilcher, 1981). Staminodia in pistillate flowers and stamen appendages, which are interpreted as staminodia, in staminate flowers were observed for *Platanus* sp. (e.g., Magallón-Puebla *et al.*, 1997). Von Balthazar & Schönenberger (2009) have not observed rudimentary pistils in staminate flowers of *P. hispanica* while such structures were earlier described for *P. occidentalis* (e.g., Bretzler, 1924; Boothroyd, 1930, and others).

While *Platanus* generally has unisexual heads, joint occurrences of both female and male flowers in the inflorescence are known (e.g., for *P. racemosa,* Floyd *et al.*, 1999).

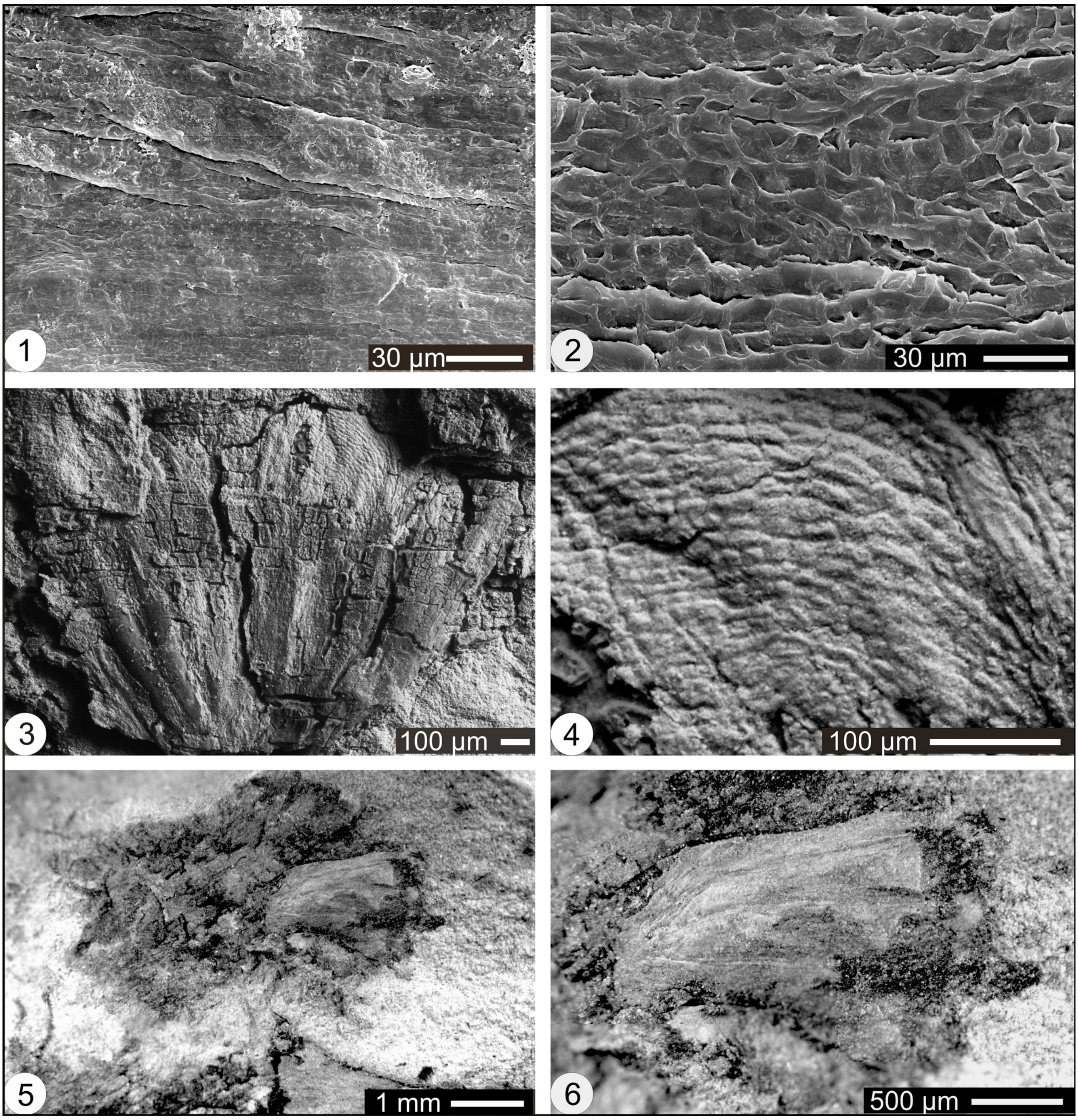

PLATE 9

Morphological and epidermal characters of *Kundurianthus mirabilis* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov., (1 - 4) - SEM.

1. Specimen BIN 1538/383a, outer surface of the cuticle of inflorescence axis.
2. Specimen GIN 4867-K16/3-88, epidermis of inflorescence axis, internal view.
3. Specimen BIN 1538/369, inflorescence fragment, individual stamens are visible.
4. Specimen BIN 1538/369, enlargement of fig. 3, epidermis of apical part of a stamen.
5. Specimen BIN 1538/383a, head with a prominent flower.
6. Specimen BIN 1538/383a, enlargement of fig. 5, flower, borders of pollen sacs are visible.

Schwarzwalder and Dilcher (1981) suggested an idea of bisexual ancestors of the Platanaceae but it did not find any support from fossil records. As it was mentioned above, there is a proliferation of the tissue between stamens in male flowers in a number of findings. Such a proliferation observed in the centre of a staminate flower of *Quadriplatanus* and also in *Platanus neptuni* was interpreted as rudimentary carpels (Friis, 1985). Staminate flowers of *Gynoplatananthus* (Mindell *et al.*, 2006) have five (rarely four) carpels without any style and ovules and are interpreted as rudimentary carpels.

One large fruitlet was observed in some *Kundurianthus* gen. nov. heads and heads with several fruitlets occur. It is indistinct whether these fruitlets are part of a bisexual flower or *Kundurianthus* gen. nov. heads include both staminate and pistillate flowers. Unfortunately, preservation of the fossil material precludes us from clear conclusion. Fruitlets in *Kundurianthus* gen. nov. inflorescences show great similarity to those from mature infructescences of *Kunduricarpus* gen. nov. in their body shape and style development, but differ in greater sizes. The maximum length of the fruitlet body reaches 4 mm, the maximum width-3 mm, while for *Kunduricarpus* gen. nov. they are 2·6 mm and 1·2 mm respectively.

Modern genera *Liquidambar* and *Altingia* have rudimentary carpels in staminate capitate inflorescences (Bogle, 1986). According to Wisniewski and Bogle (1982) there is one circle of 5-9 stamens with usually two aborted carpels in the centre in the staminate flower of *Liquidambar*.

Pollen grains—Pollen grains of *Kundurianthus* gen. nov. are of a common platanoid type: small, tricolpate or tricolporate, finely reticulate, semitectate, columellate. They show most similarity to the Late Cretaceous-Paleocene species such as *Platanus quedlinburgensis* Pacltová emend Tschan, Denk & von Balthazar, 2008 (Tschan *et al.*, 2008), *Platananthus synandrus* (Manchester, 1986), and *Platananthus spersae* Pigg & Stockey, 1991 (Pigg & Stockey, 1991) in the exine sculpturing. The studied pollen grains also show a rim of fused ectexine elements along the colpus margin, this was observed in several extinct platanoids, e.g. in *Platananthus scanicus*, *P. speirsae*, *P. synandrus*, as well as in *Archaranthus*. A number of modern Hamamelidaceae species also have colpi bordered by a somewhat similar rim (“margo”) but unlike the species under study it is usually accompanied by coarsely or medium-sized lumina and by a central zone of granular membrane sculpturing common for the Hamamelidaceae (Bogle & Philbrick, 1980, etc). The studied species reveals unusual for platanoids ultrastructure (the innermost layer of the exine), this can be partly explained by preservation, but still it distinguishes *Kundurianthus* gen. nov. from all previously known species of the group. *Kundurianthus* gen. nov. appears to have smooth aperture membrane that is also uncommon for the Platanaceae as a whole, among modern species being known for *Platanus kerrii* only (Denk & Tekleva, 2006). As for fossil platanoid taxa, while most of them are characterized by a granular aperture membrane, for others the preservation state prevents from clear interpretation of the membrane sculpturing details. *Kundurianthus* gen. nov. has most likely tricolporate pollen grains with unclear ora, such an aperture type is known for a number of the fossil Platanaceae (e.g., Krassilov & Shilin, 1995; Maslova & Tekleva, 2012). The footlayer and endexine are indistinguishable and this innermost layer (conventionally indicated here as nexine) differs in thickness throughout the pollen grain that also distinguishes the species from all known fossil Platanaceae and Hamamelidaceae pollen.

Relationships of Kunduricarpus gen. nov. infructescences and staminate inflorescences of Kundurianthus gen. nov.—Possible attribution of fossil organs to the same plant can be supported by the presence of common characteristic features and also when the findings were discovered from the same plant-bearing beds with no other appropriate and similar organs present. There are a number of reproductive and vegetative organs found in association at various localities around the northern hemisphere (Manchester, 1986; Crane *et al.*, 1988; Pigg & Stockey, 1991; Crane *et al.*, 1993; Maslova, 1997, 2002; Kvaček & Manchester, 2004; Maslova & Herman, 2006; Tschan *et al.*, 2008; Maslova *et al.*, 2011, and others).

Kunduricarpus gen. nov. infructescences and *Kundurianthus* gen. nov. inflorescences co-occurred in almost all orictocoenoses of the Kundur plant-bearing horizons and have some features in common. They share a general architecture of reproductive organs (heads), unique structure of the axis epidermis, differing from other platanaceous genera in cell shape and arrangement and lack of trichomes. Both genera are characterized by nonsimultaneous maturation of the elements (fruitlets in *Kunduricarpus* gen. nov. and stamens in *Kunduri-*

PLATE 10

Morphological and epidermal characters of *Kundurianthus mirabilis* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov., (1-12) - SEM, (13, 14) - LM.

→

1. Holotype GIN 4867-K16/6-39, cuticle of a pollen sac.
2. Holotype GIN 4867-K16/6-39, fragment of a pollen sac, note a low density of pollen grains in a sac.
3. Specimen BIN 1538/369, apical part of a stamen with four pollen sacs.
4. Holotype GIN 4867-K16/6-39, flower.
5. Specimen BIN 1538/372, theca, two pollen sacs.
6. Holotype GIN 4867-K16/6-39, differently shaped and sized pollen sacs.
7. Specimen BIN 1538/369, pollen sac.

8-11. Holotype GIN 4867-K16/6-39, pollen sacs.

12. Holotype GIN 4867-K16/6-39, loosely arranged pollen in a pollen sac.
13. Specimen BIN 1538/372, apical part of a pollen sac with loosely arranged pollen.
14. Specimen BIN 1538/372, enlargement of fig. 13, pollen sac with loosely arranged pollen.

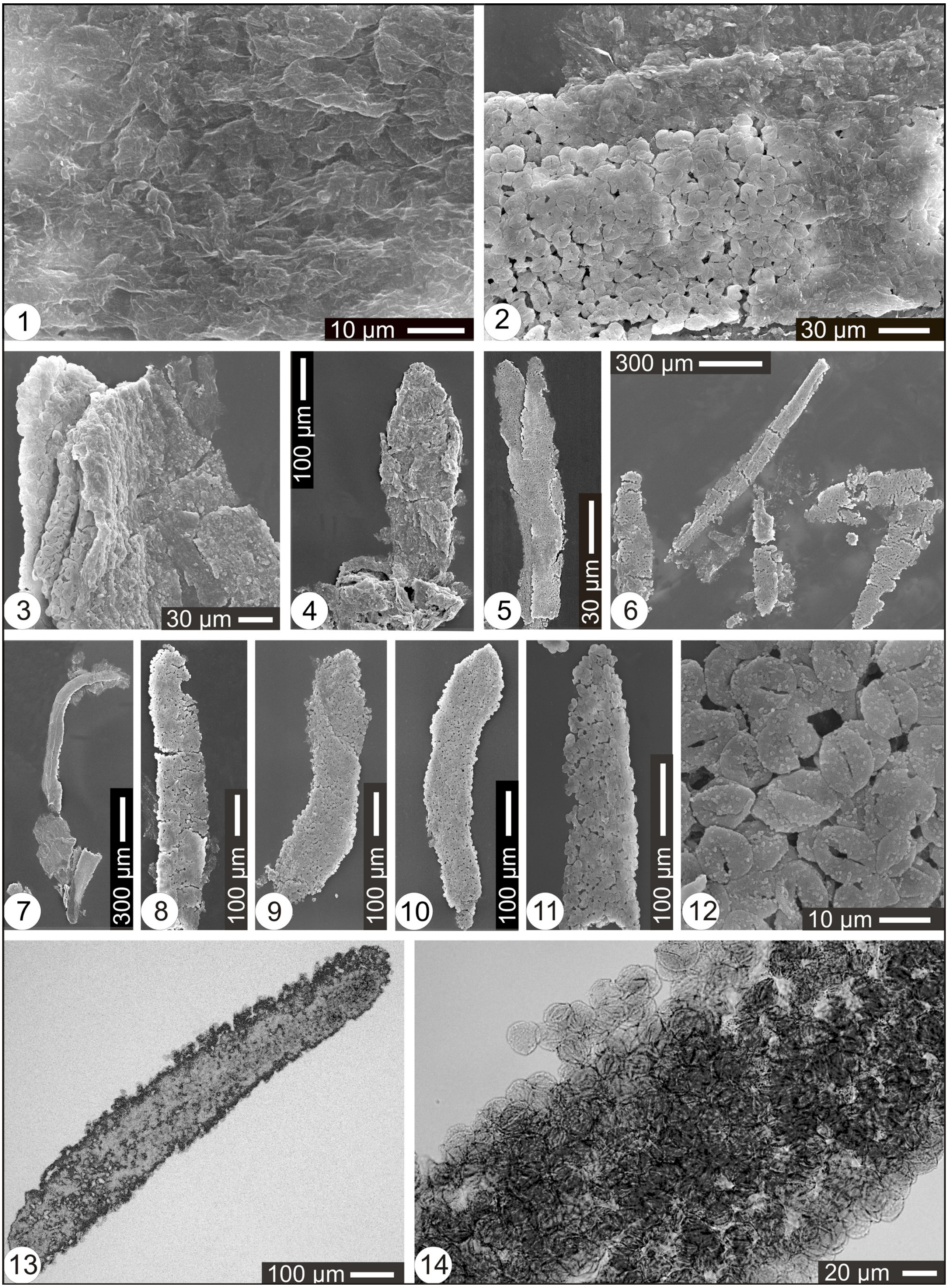
1
10 µm
2
30 µm
3
30 µm
4
100 µm
5
30 µm
6
300 µm
7
300 µm
8
100 µm
9
100 µm
10
100 µm
11
100 µm
12
10 µm
13
100 µm
14
20 µm

PLATE 10

anthus gen. nov.), and have excessively developed elements which exceed other fruitlets and stamens. *Kunduricarpus* gen. nov. fruits and *Kundurianthus* gen. nov. flowers lack a perianth and trichomes in the epidermis, individual flowers are separated by a distinct ring of a proliferated tissue, which is most pronounced in mature heads. The body shape and style type of the fruitlet occasionally presented in *Kundurianthus* gen. nov. are identical to those in *Kunduricarpus* gen. nov. fruits. Besides, pollen grains found on the fruitlets and inflorescences axes of *Kunduricarpus* gen. nov. are identical to those of *Kundurianthus* gen. nov. On this basis we consider that these reproductive structures belong to the same plant.

Leaves—Several morphotypes of platanoid leaves were found in association with the capitate reproductive structures. Leaves which were previously referred to the new species of the genus *Celastrinites* Saporta, 1865, *C. kundurensis* Golovneva, Sun & Bugdaeva, 2008 (Golovneva *et al.*, 2008), dominate in the Kundur locality. Leaves of this morphotype occur in almost all orictocoenoses, confined to different facies: channel, overbank/floodplain, and oxbow lake ones. The leaves are characterized by a complex of morphological features which vary greatly and are typical for the Platanaceae as well as for several Hamamelidaceae genera.

Leaves of another morphotype were assigned to the new combination *Arthollia tschernyschewii* (Konst.) Golovneva, Sun & Bugdaeva, 2008 (Golovneva *et al.*, 2008). These leaves and several other morphotypes of platanoid leaves from the Kundur locality are more rarely represented in the orictocoenoses than leaves of the first morphotype (referred to *Celastrinites*). A detailed study and an analysis of platanoid leaves found in association with capitate reproductive structures *Kunduricarpus* gen. nov. and *Kundurianthus* gen. nov. will be published in a separate paper.

Possible relationship of the reproductive capitate structures and leaves of the defined morphotypes was not detected. We only can state a co-occurence of the studied reproductive structures and leaves referred to *Celastrinites kundurensis* in all known orictocoenoses of the Kundur locality. An association of the reproductive structures and platanoid leaves of other morphotypes was observed only in some plant-bearing beds.

CONCLUSIONS

Capitate reproductive organs assigned to *Kunduricarpus* gen. nov. and *Kundurianthus* gen. nov. of the Platanaceae are described from the Campanian of Amur Region, Russia. *Kunduricarpus* gen. nov. infructescences are referred to the Platanaceae on the basis of the capitate type of the infructescence, lack of the perianth in mature fruits and trichomes in the fruitlet epidermis, characteristic fruitlet form with developed style, and a solitary seed in the fruitlet. *Kunduricarpus* gen. nov. differs from the modern genus *Platanus* in the lesser number of fruits per head, in the epidermal structure of the infructescence axis. The infructescence axis of *Kunduricarpus* lacks trichomes and has differently shaped cells, which are not arranged in longitudinal rows. Besides there is no bundle of hairs in the fruitlet base of *Kunduricarpus* gen. nov. Another distinguishing feature is a proliferation of an interfruit tissue in mature heads that is also characteristic for capitate infructescences of *Liquidambar* and *Altingia*. *Kunduricarpus* gen. nov. infructescences share several features with modern *Liquidambar orientalis*: wide, relatively smooth surface between adjacent fruits and epidermal structure of the fruitlet (differently shaped cells including extended ones with oblique ends).

Staminate inflorescences of *Kundurianthus* gen. nov. were referred to the Platanaceae based on capitate inflorescences, absence of the perianth, sessile anthers, differently sized pollen sacs within the stamen, structures of the opposite sex in the inflorescence, tricolpate/tricolporate finely reticulate pollen grains. *Kundurianthus* gen. nov. differs from modern *Platanus* in the lesser number of flowers in the inflorescence, a unique epidermal structure of the inflorescence axis, absence of the apical extension of the connective and developed fibrous subepidermal layer in anthers, and in developing a large fruitlet (or several fruitlets) which exceeds the inflorescence diameter in size. Also in contrast to *Platanus* the studied species is char-

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PLATE 11

Pollen morphology and ultrastructure of *Kundurianthus mirabilis* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov. (1-5, 7, 8, 10-13, 15, 16), LM, SEM, TEM and pollen adhered to *Kunduricarpus longistylium* Kodrul, N. Maslova, Tekleva & Golovneva gen. *et* sp. nov. (6, 9, 14), SEM.

→

1. Holotype GIN 4867-K16/6-39, pollen in polar and equatorial views, LM, scale 10 µm.
2. Specimen BIN 1538/369, pollen mass, LM, scale 10 µm.
3. Specimen BIN 1538/369, broken pollen, note inner surface and ultrastructure of the exine, scale 1 µm.
4. Holotype GIN 4867-K16/6-39, equatorial view, SEM, scale 3 µm.
5. Specimen BIN 1538/369, polar view, SEM, scale 3 µm.
6. Specimen GIN 4867-K16/6-18b, equatorial view, SEM, scale 5 µm.
7. Holotype GIN 4867-K16/6-39, part of the pollen, note a smooth aperture membrane and rim along colpus margin (arrow), SEM, scale 3 µm.
8. Specimen BIN 1538/369, equatorial view, note a rim along colpus margin (arrow), SEM, scale 3 µm.
9. Specimen GIN 4867-K16/6-61, equatorial view, SEM, scale 5 µm.
10. Holotype GIN 4867-K16/6-39, section through the whole pollen grain, TEM, scale 2 µm.
11. Holotype GIN 4867-K16/6-39, aperture region, note a supposed os, TEM, scale 0·67 µm.

12, 13. Specimen BIN 1538/369, sections through the whole pollen grain, TEM, scale 0·67 µm.

14. Specimen GIN 4867-K16/6-61, pollen in polar and equatorial views, note a rim along colpus margin (arrows), SEM, scale 5 µm.
15. Holotype GIN 4867-K16/6-39, non-aperture region of exine, TEM, scale 1 µm.
16. Specimen BIN 1538/369, aperture region, TEM, scale 0·67 µm.

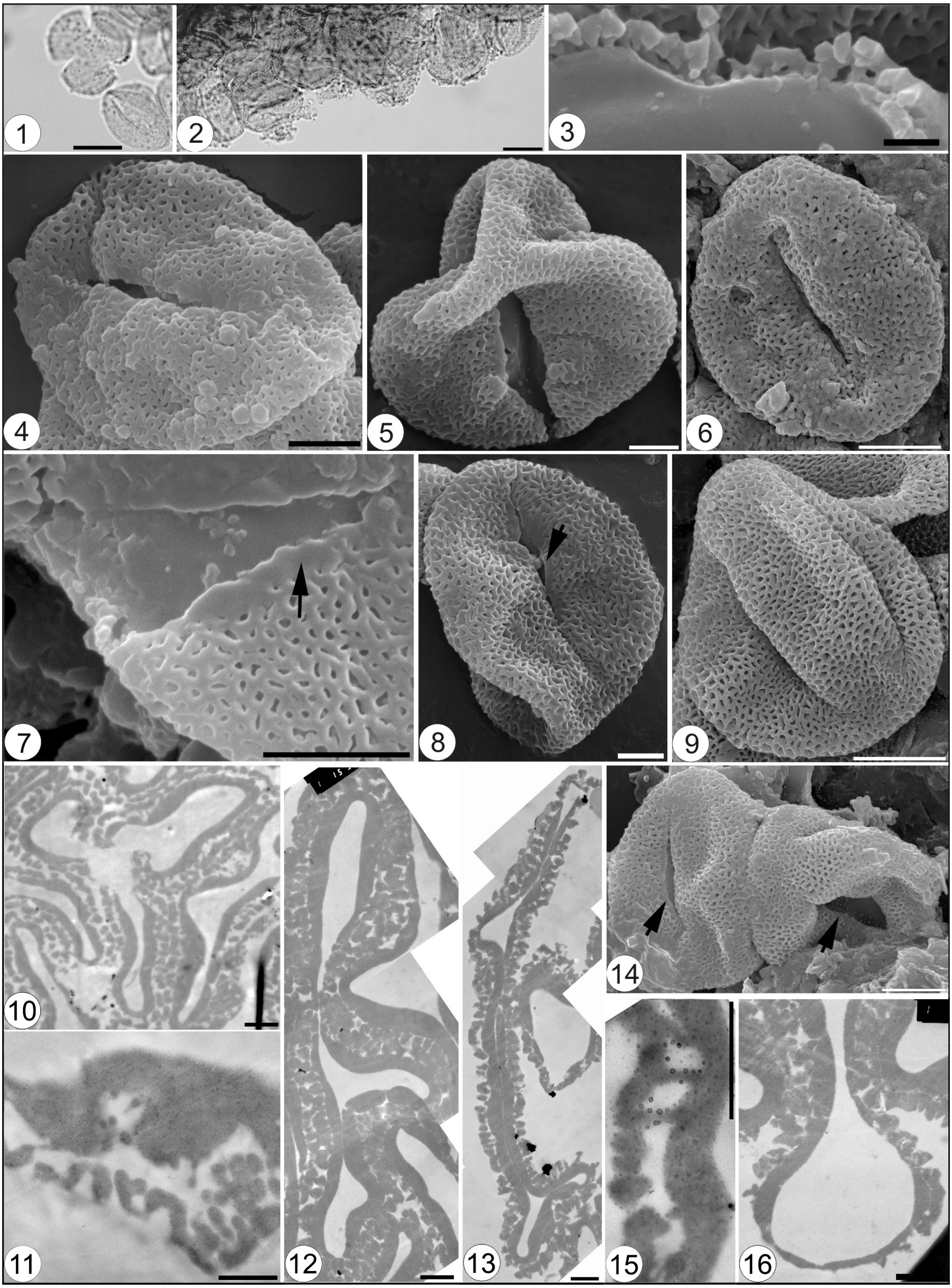

PLATE 11

acterized by a loose structure of pollen sacs with low density of pollen grains, in the presence of a sporopollenin rim near the aperture margin and probably smooth aperture membrane, as well as in the sporoderm ultrastructure, especially, in uneven thickness of the foot layer throughout the pollen grain. The presence of the structure of an opposite sex in capitate inflorescences was shown for the modern *Platanus* as well as for the genera *Liquidambar* and *Altingia* but such structures were always characterized by rather small size.

The similarity of *Kunduricarpus* gen. nov. and *Kundurianthus* gen. nov. includes unique Platanaceae axis structure, absence of hairs, identical body shape and style of mature fruitlets. Pollen grains from *Kundurianthus* gen. nov. and those adhered to fruitlets and infructescence axes of *Kunduricarpus* gen. nov. are extremely similar in their morphology. This implies that these reproductive organs belong to the same plant.

However, it is impossible to conclude whether associated platanoid leaves of a definite morphotype also belong to the same plant as there is no data on their epidermal features.

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REFERENCES

Bogle AL 1986. The floral morphology and vascular anatomy of the Hamamelidaceae: subfamily Liquidambaroideae. Annals of the Missouri Botanical Garden 73: 325-347.

Bogle AL & Philbrick CT 1980. A generic atlas of hamamelidaceous pollen. Contributions from the Gray Herbarium of Harvard University 210: 29-103.

Boothroyd LE 1930. The morphology and anatomy of the inflorescence and flower of the Platanaceae. American Journal of Botany 17: 678-693.

Boulter MC & Kvaček Z 1989. The Palaeocene flora of the Isle of Mull. Special Paper in Palaeontology 42: 1-149.

Bretzler E 1924. Beitrage zur Kenntniss der Gattung *Platanus*. Botanisches Archiv 7: 388-417.

Bugdaeva EV, Markevich VS, Sorokin AP & Bolotsky YL 2001. Glava 2. Stratigrafiya. *In:* Bugdaeva EV (Editor)-Flora i dinosavry na granitse mela i paleogena Bureinskogo basseyna: 25-43. Dalnauka,Vladivostok (in Russian with English summary).

Carpenter RJ, Hill RS & Jordan GJ 2005. Leaf cuticular morphology links Platanaceae and Proteaceae. International Journal of Plant Sciences 166: 843-855.

Chang HT 1962. *Semiliquidambar,* novum Hamamelidacearum genus sinicum. Sunyatsen University Bulletin of Natural Science 1: 34-44.

Crane PR 1989. Paleobotanical evidence on the early radiation of nonmagnoliid Dicotyledons. Plant Systematics and Evolution 162: 165-191.

Crane PR, Manchester SR & Dilcher DL 1988. Morphology and phylogenetic significance of the angiosperm *Platanites hybridicus* from the Palaeocene of Scotland. Palaeontology 31: 503-517.

Crane PR, Pedersen KR, Friis EM & Drinnan AN 1993. Early Cretaceous (Early to Middle Albian) platanoid inflorescences associated with *Sapindopsis* leaves from the Potomac Group of Eastern North America. Systematic Botany 18: 328-344.

Crepet WL, Nixon KC, Friis EM & Freudenstein JV 1992. Oldest fossil flowers of hamamelidaceous affinity from the Late Cretaceous of New Jersey. Proceedings National Academy Sciences USA 89: 8986-8989.

Denk T & Tekleva MV 2006. Comparative pollen morphology and ultrastructure of *Platanus*: Implications for phylogeny and evaluation of the fossil record. Grana 45: 195-221.

Douglas AW& Stevenson DW 1998. The reproductive architecture of Platanaceae: evolutionary transformations based on fossil and extant evidence. American Journal of Botany 85 (Suppl.): 7.

Drinnan AN, Crane PR & Hoot SB 1994. Patterns of floral evolution in the early diversification of nonmagnoliid dicotyledons (Eudicots). Plant Systematics and Evolution 8: 93-122.

Endress PK 1989. A suprageneric taxonomic classification of the Hamamelidaceae. Taxon 38: 371-376.

Endress PK 1990. Patterns of floral construction in ontogeny and phylogeny. Biological Journal of the Linnean Society 39: 153-175.

Ernst WR 1963. The genera of Hamamelidaceae and Platanaceae in the southeastern United States. Journal Arnold Arboretum of Harvard University 44: 193-210.

Floyd SK, Lerner VT & Friedman WE 1999. A developmental and evolutionary analysis of embryology in Platanus (Platanaceae), a basal eudicot. American Journal of Botany 86: 1523-1537.

Forbes E 1851. Note on the fossil leaves represented in plates II, III, and IV. Quarterly Journal of the Geological Society 7: 103.

Friis EM 1985. Angiosperm fruits and seeds from the Middle Miocene of Jutland (Denmark). Det Kongelige Danske Videnskaberne Selskab Biologiske Skrifter 24: 1-165.

Friis EM, Crane PR & Pedersen KR 1988. Reproductive structures of Cretaceous Platanaceae. Det Kongelige Danske Videnskaberne Selskab Biologiske Skrifter 31: 1-55.

Gagnepain F 1939. Un genre nouveau de Butomacees *et* quelques especes nouvelles d'Indo-Chine. Bulletin de la Société Bowtanique de France 86: 300-303.

Golovneva LB, Bugdaeva EV, Sun G, Akhmetiev AM & Kodrul TM 2004. Systematic composition and age of floristic assemblages from the Kundur and Taipinglinchang formations. *In*: Proceedings of the 3rd Symposium on Cretaceous Biota and K/T boundary in Heilongjiang River area, Sun G, Sun YW, Akhmetiev MA & Ashraf RA (Editors), Jilin University, Chanchun, 23-26.

Golovneva LB, Sun G & Bugdaeva EV 2008. Campanian flora of the Bureya River Basin (Late Cretaceous of the Amur Region). Paleontological Journal 42: 554-567.

Herman AB, Akhmetiev MA, Kodrul TM, Moiseeva MG & Yakovleva AI 2009. Flora development in Northeastern Asia and Northern Alaska during the Cretaceous-Paleogene transitional epoch. Stratigraphy and Geological Correlation 17: 79-97.

Hesse M 1978. Entwicklungsgeschichte und ultrastruktur yon pollenkitt und exine bei nahe verwandtcn entomophilen und anemophilen angiospermensippen: Ranunculaceae, Hamamelidaceae, Platanaceae und Fagaceae. Plant Systematics and Evolution 130: 13-42.

Ickert-Bond SM, Pigg KB & Wen Jun 2005. Comparative infructescence morphology in *Liquidambar* (Altingiaceae) and its evolutionary significance. American Journal of Botany 92: 1234-1255.

Ickert-Bond SM, Pigg KB & Wen Jun 2007. Comparative infructescence morphology in *Altingia* (Altingiaceae) and discordance between morphological and molecular phylogenies. American Journal of Botany 94: 1094-1115.

Knobloch E & Mai DH 1986. Monographie der Früchte und Samen in der Kreide von Mitteleuropa. Edice Rozpravy Ustredniho ustavu geologickeho. Geological Survey Prague 47: 1-219.

Krassilov VA 1973. Upper Cretaceous staminate heads with pollen grains. Palaeontology 16: 41-44.

Krassilov V & Kodrul T 2009. Reproductive structures associated with *Cobbania*, a floating monocot from the Late Cretaceous of the Amur Region, Russian Far East. Acta Palaeobotanica 49: 233-251.

Krassilov VA, Kodrul TM & Maslova NP 2010. Plant systematics and differentiation of species over Trans-Beringian land connections including a newly recognized cupressaceous conifer *Ditaxocladus* Guo & Sun. Bulletin of Geosciences 85: 95-110.

Krassilov VA & Shilin PV 1995. New platanoid staminate heads from the Mid-Cretaceous of Kazakhstan. Review of Palaeobotany and Palynology 85: 207-211.

Kvaček Z & Manchester SR 2004. Vegetative and reproductive structures of the extinct *Platanus neptuni* from the Tertiary of Europe and relationships within the Platanaceae. Plant Systematics and Evolution 244: 1-29.

Lestiboudois T 1826. Botanographie Elementaire, ou, Principes de Botanique, D´Anatomie *et* de Physiologie. Roret, Paris, and Vanackere, Lille. 559 p.

Linnaeus C 1754. Genera plantarum: eorumque characteres naturales secundum numerum, figuram, situm, *et* proportionem omnium fructificationis partium. Impensis Laurentii Salvii, Stockholm, 500 p.

Magallón-Puebla S, Herendeen PS & Crane PR 1997. *Quadriplatanus georgianus* gen. *et* sp. nov.: staminate and pistillate platanaceous flowers from the Late Cretaceous (Coniacian-Santonian) of Georgia, U.S.A. International Journal Plant Science 158: 373-394.

Magallón-Puebla S, Crane PR & Herendeen PS 1999. Phylogenetic pattern, diversity and diversification of eudicots. Annals of the Missouri Botanical Garden 86: 297-372.

Manchester SR 1986. Vegetation and reproductive morphology of an extinct plane tree (Platanaceae) from the Eocene of Western North America. Botanical Gazette 147: 200-226.

Manchester SR 1994. Fruits and seeds of the Middle Eocene Nut Beds flora, Clarno Formation, Oregon. Palaeontographica Americana 58: 1-205.

Markevich VS, Golovneva LB & Bugdaeva EV 2005a. Stratigrafiya i flora kundurskoy svity (verkhniy mel, Priamur'e). *In:* Arkadiev VV & Prozorovsky VA (Editors)—Melovaya sistema Rossii: problem stratigrafii i paleogeografii: 160-176. St. Petersburg State University, St. Petersburg (in Russian).

Markevich VS, Golovneva LB & Bugdaeva EV 2005b. Floristicheskaya kharakteristika santon-kampanskikh otlozheniy Zeysko-Bureinskogo basseyna (Priamur'e). *In*: Sovremennye problem paleofloristiki, paleogeografii i fitogeografii. Trudy mezhdunarodnoy paleobotanicheskoy konferentsii, Akhmetiev MA & Herman AB (Editors), GEOS, Moscow, 198-206 (in Russian).

Maslova NP 1997. The genus *Platanus* L. (Platanaceae Dumortier) in the Paleocene of the Kamchatka Peninsula. Paleontological Journal 31: 203-208.

Maslova NP 2002. A new Early Paleogene plant of the family Platanaceae (based on leaves and inflorescences). Paleontological Journal 2: 207-218.

Maslova NP 2008. Association of reproductive organs of platanoids (Angiospermae): significance for systematics and phylogeny. Paleontological Journal 42: 1393-1404.

Maslova NP 2009. A new taxon of infructescence *Sarbaicarpa* gen. nov. (Hamamelidales) from the Cenomanian-Turonian of the Western Kazakstan. Paleontological Journal 43: 1281-1297.

Maslova NP 2010 Systematics of fossil platanoids and hamamelids. Paleontological Journal 44: 1379-1466.

Maslova NP & Golovneva LB 2000. *Lindacarpa* gen. *et* sp. nov., a new infructescence of the Hamamelidaceae from the Upper Cretaceous of Eastern Siberia. Paleontological Journal 34: 462-468.

Maslova NP, Golovneva LB & Tekleva MV 2005. Infructescences of *Kasicarpa* gen. nov. (Hamamelidales) from the Late Cretaceous (Turonian) of the Chulym-Enisey depression, western Siberia, Russia. Acta Palaeobotanica 45: 121-137.

Maslova NP & Herman AB 2004. New finds of fossil hamamelids and data on the phylogenetic relationships between the Platanaceae and Hamamelidaceae. Paleontological Journal 5: 563-575.

Maslova NP & Herman AB 2006. Infructescences of *Friisicarpus* nom. nov. (Platanaceae) and associated foliage of the platanoid type from the Cenomanian of Western Siberia. Paleontological Journal 1: 109-113.

Maslova NP & Kodrul TM 2003. New platanaceous inflorescence *Archaranthus* gen. nov. from the Maastrichtian-Paleocene of the Amur Region. Paleontological Journal 1: 92-100.

Maslova NP, Kodrul TM & Tekleva MV 2007. A new staminate inflorescence of *Bogutchanthus* gen. nov. (Hamamelidales) from the Paleocene Beds of the Amur Region, Russia. Paleontological Journal 5: 564-579.

Maslova NP & Krassilov VA 1997. New hamamelid infructescences from the Palaeocene of Western Kamchatka, Russia. Review of Palaeobotany and Palynology 97: 67-78.

Maslova NP & Krassilov VA 2002. A new genus of Platanaceae from the Paleocene of the Amur Region. Paleontological Journal 1: 106-110.

Maslova NP & Tekleva MV 2012. Infructescences of *Friisicarpus sarbaensis* sp. nov. (Platanaceae) from the Cenomanian-Turonian of Western Kazakhstan. Paleontological Journal 46: 433-443.

Maslova NP, Tekleva MV, Sokolova AB, Broushkin AV & Gordenko NV 2011. Infructescences of *Friisicarpus kubaensis* sp. nov. and leaves of *Ettingshausenia kubaensis* sp. nov. from the Albian-Cenomanian of Chulym-Yenisei depression, Russia. Palaeobotanist 60: 209-236.

Maslova NP, Tekleva MV & Remizowa MV 2012. *Krassilovianthus* gen. nov., a new staminate inflorescence with similarities to Platanaceae and Hamamelidaceae from the Cenomanian-Turonian of western Kazakhstan. Review of Palaeobotany and Palynology 180: 1-14.

Meyer-Melikyan NR, Bovina IYu, Kosenko YaV, Polevova SV, Severova EE, Tekleva MV & Tokarev PI 2004. Atlas of morphology of Asterales (Asteraceae). Palynomorphology and the development of sporoderm in members of the family Asteraceae. KMK, Moscow, 236 p (in Russian).

Mindell RA, Stockey RA & Beardt G 2006. Anatomically preserved staminate inflorescences of *Gynoplatananthus oysterbayensis* gen. *et* sp. nov. (Platanaceae) and assotiated pistillate fructifications from the Eocene of Vancouver Island, British Columbia. International Journal of Plant Sciences 167: 591-600.

Nixon KC & Poole JM 2003. Revision of the Mexican and Guatemalan species of *Platanus* (Platanaceae). Lundellia 6: 103-137.

Nuttall T 1842. The North American Sylva; or, A description of the forest trees of the United States, Canada, and Nova Scotia, considered particularly with respect to their use in the arts, and their introduction into commerce; to which is added a description of the most useful of the European forest trees. J. Dobson, Philadelphia, USA, 136 p.

Pedersen KR, Friis EM, Crane PR & Drinnan AN 1994. Reproductive structures of an extinct platanoid from the Early Cretaceous (Latest Albian) of eastern North America. Review of Palaeobotany and Palynology 80: 291-303.

Pigg KB & Stockey RA 1991. Platanaceous plants from the Paleocene of Alberta, Canada. Review of Palaeobotany and Palynology 70: 125-146.

Pigg KB, Ickert-Bond SM & Jun Wen 2004. Anatomically preserved *Liquidambar* (Altingiaceae) from the Middle Miocene of Yakima Canyon, Washington State, USA, and its biogeographic implications. American Journal of Botany 91: 499-509.

Reynolds ES 1963. The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. The Journal of Cell Biology 17: 208-212.

Schwarzwalder RN & Dilcher DL 1981. Bisexuality in the pistillate inflorescences of *Platanus occidentalis* L. Proceedings of the Indiana Academy of Science 90: 89-90.

Sun G, Akhmetiev MA, Dong ZM, Ashraf AR, Sun YW, Bugdaeva E, Dilcher DL, Golovneva L, Harding I, Johnson KR, Kezina T, Kodrul T, Lu JS, Markevich VS, Nishida H, Okada H, Park SO, Sun CL, Xiong XZ, Xing YL & Zhou ZL 2002. In search of the Cretaceous-Tertiary boundary in Heilongjiang River area of China. Journal of Geoscientific Research in Northeast Asia 5: 105-113.

Sun G, Akhmetiev M, Ashraf AR, Sun YW, Dong ZM, Bugdaeva E, Markevich V, Kezina T, Kodrul T, Johnson K, Nishida H, Okada H, Sun CL, Suzuki S, Dilcher DL, Lu JS, Luo KL, Bolotsky Yu, Hicks J, Yang HX, Harding I & Quan C 2004. Recent advance in the research of Cretaceous-Tertiary boundary in Jiayin of Heilongjiang, China. *In*: Proceedings of the 3rd Symposium on Cretaceous Biota and K/T boundary in Heilongjiang River area, Sun G, Sun YW, Akhmetiev MA & Ashraf RA (Editors)—Jilin

University, Chanchun: 1-6.

Sun G, Akhmetiev MA, Golovneva L, Bugdaeva E, Quan C, Kodrul TM, Nishida H, Sun YW, Sun CL, Johnson K & Dilcher DL 2007. Late Cretaceous plants from Jiayin along Heilongjiang River, Northeast China. Courier Forschungsinstitut Senckenberg 258: 75-83.

Sun G, Akhmetiev M, Markevich V, Ashraf AR, Bugdaeva E, Godefroit P, Bolotsky Yu, Dong ZM, Golovneva L, Yang HX, Sun CL, Sun YW, Quan C, Kodrul T, Kezina T, Johnson K, Nishida H, Dilcher DL, Harding I & Chen YJ 2011. Late Cretaceous biota and the Cretaceous-Paleogene (K-Pg) boundary in Jiayin of Heilongjiang, China. Global Geology 4: 115-143.

Tschan GF, Denk T & Von Balthazar M 2008. *Credneria* and *Platanus* (Platanaceae) from the Late Cretaceous (Santonian) of Quedlinburg, Germany. Review of Palaeobotany and Palynology 152: 211-236.

Van Itterbeeck J, Bolotsky Y, Bultynck P & Godefroit P 2005. Stratigraphy, sedimentology and ecology of the dinosaur-bearing Kundur section (Zeya-Bureya Basin, Amur Region, Far Eastern Russia). Geological Magazine 142: 735-750.

von Balthazar M & Schönenberger J 2009. Floral structure and organization in Platanaceae. International Journal of Plant Sciences 170: 210-255.

Velenovský J 1882. Die Flora der böhmischen Kreideformation. Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients. Alfred Hölder, Wien. 159 p.

Wang X 2008. Mesofossils with platanaceous affinity from the Dakota Formation (Cretaceous) in Kansas, USA. Palaeoworld 17: 246-255.

Wang H, Dilcher DL, Schwarzwalder RN & Kvaček J 2011. Vegetative and reproductive morphology of an extinct Early Cretaceous member of Platanaceae from the Braun's Ranch locality, Kansas, U.S.A. International Journal of Plant Sciences 172: 139-157.

Wisniewski M & Bogle AL 1982. The ontogeny of the inflorescence and flower of *Liquidambar styraciflua* L. (Hamamelidaceae). American Journal of Botany 69: 1612-1624.