

Platanoid infructescences *Friisicarpus kubaensis* sp. nov. and leaves *Ettingshausenia kubaensis* sp. nov. from the Albian-Cenomanian of Chulym-Yenisei depression, Russia

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ABSTRACT

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New species of an infructescence of *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova and leaves of *Ettingshausenia kubaensis* N. Maslova & Sokolova, sp. nov. are described from the Albian-Cenomanian of Chulym-Yenisei depression, Russia. Similar epidermal characteristics and joint co-occurrence of the described infructescences and leaves imply that the leaves and infructescences belong to the same plant.

Key-words—*Friisicarpus*, *Ettingshausenia*, Cretaceous, Leaf fossils, Infructescence, Pollen.

चुलीम-येनिसी अवनमन, रूस के एल्बीअन-सेनोमेनिअन से प्राप्त प्लेटानॉइड इन्फ्रक्टैकेसेन्सेस *फ्राईसाइकार्पस कुबेन्सिस* जाति नवम एवं *ईटिंगशॉसेनिया कुबेन्सिस* जाति नवम पत्तियाँ

नटालिया पी. मास्लोवा, मारिआ वी. टेक्लेवा, एलेक्जेंड्रा बी. सोकोलोवा, एनाटॉली बी. ब्रॉशकिन एवं नटालिया वी. गॉर्डेन्को

सारांश

चुलीम-येनिसी अवनमन, रूस के एल्बीअन-सेनोमेनिअन से प्राप्त *फ्राईसाइकार्पस कुबेन्सिस* एन. मास्लोवा, टेक्लेवा व सोकोलोवा की एक इन्फ्रक्टैकेसेन्सेस नवीन जाति तथा *ईटिंगशॉसेनिया कुबेन्सिस* एन. मास्लोवा व सोकोलोवा की पत्तियाँ, जाति नवम वर्णित की गई हैं। वर्णित इन्फ्रक्टैकेसेन्सेस के अधिचर्म अभिलक्षणन व संयुक्त सह-प्राप्ति एवं पत्तियाँ इंगित करती हैं कि पत्तियाँ और इन्फ्रक्टैकेसेन्सेस उसी वनस्पति की हैं।

संकेत-शब्द—*फ्राईसाइकार्पस*, *ईटिंगशॉसेनिया*, चाकमय, पत्ती जीवाश्म, इन्फ्रक्टैकेसेन्सेस, पराग।

INTRODUCTION

To date, palaeobotanical studies have achieved considerable success in revealing the geological history of the Platanaceae, whose members have played a significant role in the Cretaceous and Early Cenozoic floras of the Northern Hemisphere. The modern family is monotypic, however, having

appeared in the Early Cretaceous (the earliest findings are dated to the Albian, Friis *et al.*, 1988; Crane *et al.*, 1993; Pedersen *et al.*, 1994), it showed a considerable diversity of genera as early as the Late Cretaceous-Paleogene. Fossil members of the Platanaceae are known both as leaf and reproductive remains.

The genus *Friisicarpus* N. Maslova & Herman, 2006 is characterized by capitate infructescences, comprised of 50 to 100 closely packed pentamerous flowers with a prominent undifferentiated perianth. The generic name *Platanocarpus* was proposed by Friis *et al.* (1988) for pistillate heads from the Albian deposits of Maryland, U.S.A., Santonian-Campanian deposits of North Carolina, U.S.A. and Scania, Sweden. The name turned out to be a homonym of the genus *Platanocarpus* Jarmolenko (Jarmolenko, 1935). Having discussed the problem with Prof. Friis, N. Maslova and Herman (2006) proposed a new generic name *Friisicarpus* that replaces *Platanocarpus* Friis, Crane & Pedersen, 1988 according to the International Code of Botanical Nomenclature (Greuter *et al.*, 2000).

The earliest record of *Friisicarpus*, *F. brookensis* (Crane *et al.*) N. Maslova & Herman, 2006, was dated to the Early to Middle Albian (Crane *et al.*, 1993) and the latest *F. carolinensis* (Friis, Crane & Pedersen) N. Maslova & Herman, 2006, was found in the Santonian-Campanian deposits (Friis *et al.*, 1988).

Four species of *Friisicarpus* have been so far described: *F. brookensis* (U.S.A., North Virginia, Early-Middle Albian; Crane *et al.*, 1993), *F. marylandensis* (Friis, Crane & Pedersen)

N. Maslova & Herman, 2006 (U.S.A., Maryland, Late Albian; Friis *et al.*, 1988), *F. elkneckensis* (Pedersen, Friis, Crane & Drinnan) N. Maslova & Herman, 2006 (U.S.A., northeast Maryland, Late Albian; Crane *et al.*, 1993) and *F. carolinensis* (U.S.A., North Carolina, Santonian-Campanian; Friis *et al.*, 1988). Infructescences from the Santonian-Campanian of Scania, Sweden (Friis *et al.*, 1988), Cenomanian of Western Siberia, Russia (N. Maslova & Herman, 2006) and Albian-Cenomanian of Kansas, North America (Wang, 2008) were attributed to *Friisicarpus* sp.

Infructescences from the Kubaevo Locality show excellent anatomical preservation. This allowed us to describe them as a new species *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova. *Platanus*-like leaves were found in association with the infructescences. Most finds of reproductive structures referred to *Friisicarpus* were not associated with leaf morphotypes. The exceptions are *F. brookensis* associated with leaves of cf. *Sapindopsis variabilis* Fontaine, 1889 (Crane *et al.*, 1993) and *Friisicarpus* sp. occurring with leaves of a typical *Platanus* L., 1754 morphotype (N. Maslova & Herman, 2006). In our opinion the

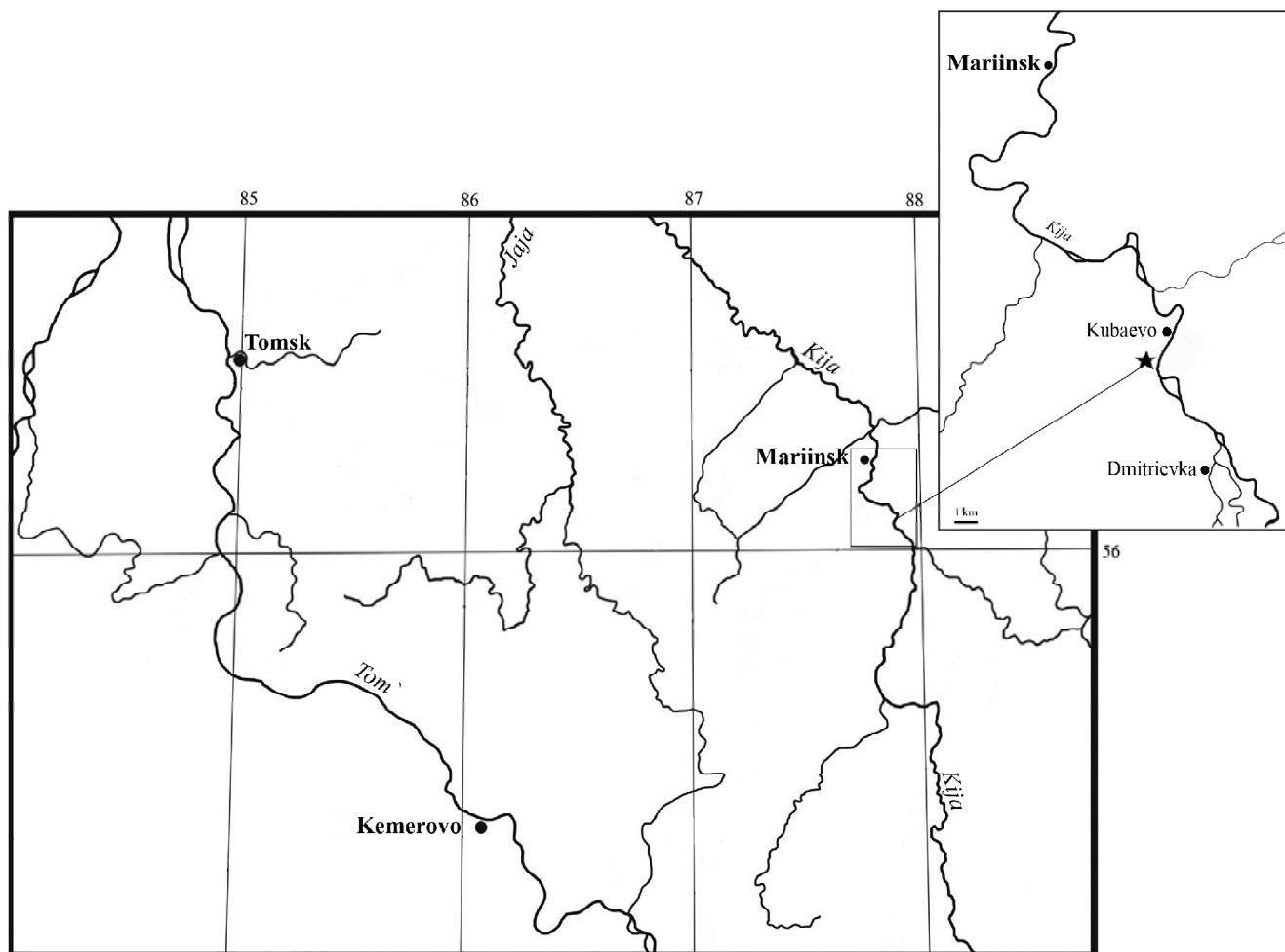


Fig. 1—Schematic map of the locality Kubaevo.

infructescences of *F. kubaensis* sp. nov. and leaves of platanaceous appearance, described here as *Ettingshausenia kubaensis* N. Maslova & Sokolova could well have belonged to the same plant species because of their similar epidermal structure.

Newly found infructescences of the genus *Friisicarpus* increase our knowledge of the diversity of reproductive structures of early Platanaceae representatives. Association of these infructescences and leaves of platanaceous appearance provides another example of this type of leaf occurring together with fundamentally different reproductive structures referred to the Platanaceae.

MATERIAL AND METHODS

The material studied comes from continental Cretaceous deposits of the Kubaevy Locality which is situated on the left bank of the Kiya River, 7 km to the north of the village Dmitrievka (near the village of Kubaevy, Mariinsk District, Kemerovo Region; 56°04'30" N, 87°52'21" E, Fig. 1). The Cretaceous deposits up to 6 m thick exposed stretching for approximately 400 m along the riverbank are represented by a compound alluvial complex composed of grey-coloured terrigenous sediments. The section of the Kubaevy Locality was published earlier (Golovneva & Shchepetov, 2010 and references, therein). Some of the present authors (Broushkin, Gordenko and Sokolova) studied Cretaceous deposits of the locality during the field seasons of 2006–2009; special attention was paid to tracing of individual layers due to their considerable lateral variability. Following is the brief description of the section; detailed geology of the locality will be considered elsewhere.

The rocks exposed above the river level (Fig. 2):

Light grey to nearly white sandy clays (I; Roman numerals on the Fig. 2) are mostly massive, at places with root traces

and signs of pedogenic alteration. The clays contain numerous, predominantly sandy small channel fills, usually with accumulations of coarse plant debris and large lignified wood fragments. Well-preserved plant macroremains occur in clays (collection point A). Freshwater bivalves were also found. Visible thickness of this unit is up to 3.5 m.

In the northern (downstream) part of the outcrop, the clays (I) are overlain by light-grey, medium to coarse-grained channel sandstones (II). The contact of the sandstones with clays (I) is erosive; in their lower part the sandstones are coarser-grained, cross-bedded, containing lenses of gravelites, at places with accumulations of pebbles and large wood fragments. Upward, the sandstones are thinning, in their upper part clayey admixture appears, wavy lamination is predominant. The sandstones (II) wedge out to the south. The thickness of the unit is up to 2.2 m.

Further to the south, the clays (I) are overlain by a lens of pale-lilac-grey clays (III). The horizontal lamination of the clays appears more distinct because of the presence of numerous well-preserved leaf remains (collection point B). In their lower part, the clays are interbedded with medium-to coarse-grained sands. The unit is up to 1.5 m thick.

A clay-sand heterolithic unit (IV) is at the top of the section. In different parts of the outcrop, the unit lies on the sandstones (II), which in places pass into it by gradual transition, on clays (III) or directly on clays (I). The unit is composed of thin, often rhythmical alternation of clay and sand layers, with horizontal ("varved") and wavy lamination. Individual layers contain abundant fine plant detritus. The thickness of the unit varies from 0.4 m in the northern part of the outcrop to 2.7 m in the south. The unit is unconformably overlain by Quaternary conglomerates.

In most recent papers (Chlonova, 1976; Golovneva & Shchepetov, 2010), Cretaceous deposits of the Kubaevy Locality are regarded as comprising two heterochronous

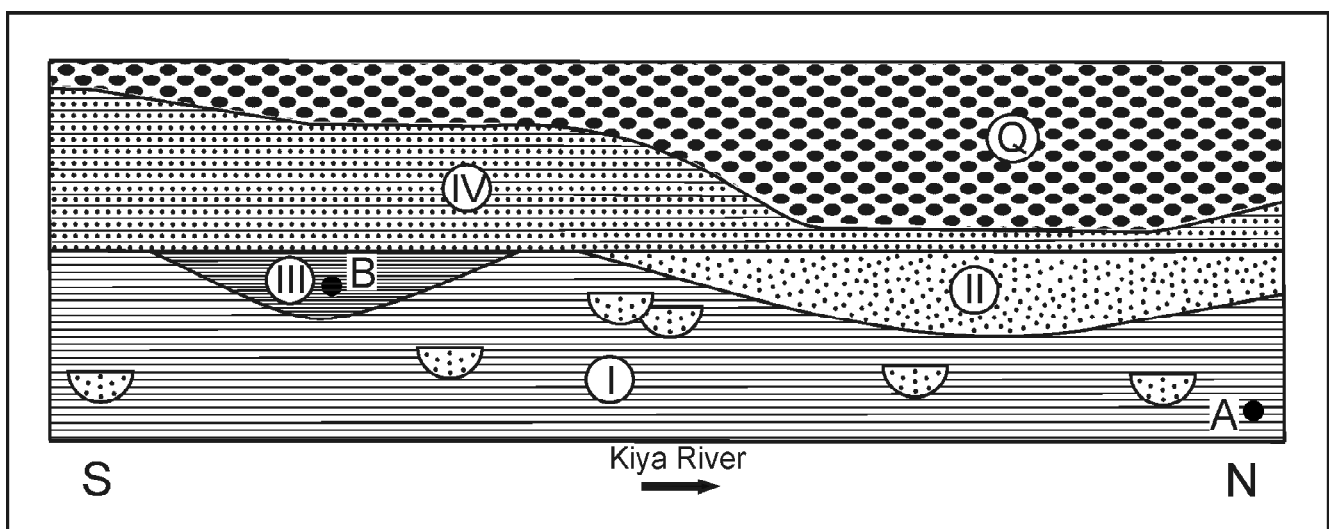


Fig. 2—Generalized drawing of Cretaceous deposits of the Kubaevy locality. A, B—collecting points of plant remains; units designated by Roman numerals. See text for further explanation.

formations, on the basis of supposed disconformity above the sandy clays (I) and/or palynological data and data on plant macroremains. The lower part of the section (sandy clays I) is attributed to the Kiya Formation, and the upper part (all the overlying deposits) to the Simonovo Formation, which were dated to the Albian-Cenomanian and Cenomanian-Turonian (Chlonova, 1976) or Albian and Cenomanian (Golovneva & Shchepetov, 2010) correspondingly.

Our data do not support the presence of the disconformity above the sandy clays (I). Gravelites, which were considered by Golovneva and Shchepetov (2010) as the "basal member" of the Simonovo Formation, as well as indications of erosion in the base of the upper part of the section, are observed only in some places where they were caused by local current activity. Also, our data question the presumed difference in age between the lower and upper parts of the section. New palynological data (Smirnova, Lomonosov Moscow State University, pers. comm.) date both parts of the section to the Albian-Cenomanian. According to Golovneva and Shchepetov (2010), all known plant macroremains of the locality came from the upper part of the section, which they correlated with the Simonovo Formation. We found abundant macroflora in the lower part of the section (Fig. 2, collection point A), which was correlated by our predecessors with the Kiya Formation. This flora is similar to the flora of the upper part and corresponds in its composition to the Kubaev floristic assemblage and not to Serta floristic assemblage as was thought by Golovneva and Shchepetov (2010).

Thus, to date there are no reasons to regard the Cretaceous deposits of Kubaev Locality as two different formations. We consider them as a single complex, palynologically dated to the Albian-Cenomanian. The correspondence between these deposits and the Kiya or Simonovo formations is still an open question.

Leaf remains of *Ettingshausenia kubaensis* N. Maslova & Sokolova, sp. nov. were found in sandy clays (I), collection point A, and pale-lilac-grey clays (III), collection point B; heads of the new species occur only in sandy clays (I), collection point A. Golovneva (2004) reported from light-lilacish-grey clays (III), collection point B, leaf remains of the following supposedly platanaceous plant remains: *Araliopsoides kiensis* (Baikovskaya) Golovneva, *Platanophyllum simonovskiense* (Lebedev) Golovneva, *Sapindopsis kryshstofovichii* (Lebedev) Golovneva and *S. janschirii* (Vachrameev) Golovneva.

After preparation of the reproductive structures, photographs were taken using a Nikon Coolpix 8700 Digital Camera. A head was transferred on varnish film by dissolving the sediment in fluoric acid and then macerated with Schulze solution and alkali. Sediment was removed from detached flowers by fluoric acid, after that the flowers were mounted on Scanning Electron Microscope (SEM) stubs. Floral elements were macerated by concentrated nitric acid and alkali and studied under a CamScan SEM. The epidermal morphology of the leaves and infructescences were studied in cuticle specimens and incrustations under an Axioplan 2 (Zeiss) Light Microscope (LM) equipped with a Leica DFC420 Digital Camera and CamScan SEM.

Pollen grains were studied and photographed with a CamScan SEM (Borissiak Paleontological Institute RAS (PIN RAS)) and CamScan and JSM SEMs (Moscow State University). Pollen grains adhered to the fruitlet surface of *Friisicarpus kubaensis* sp. nov. were removed from a SEM stub after SEM study, stained with osmium tetroxide and uranyl acetate and prepared for TEM according to Meyer-Melikian *et al.* (2004). Ultrathin sections were made by a LKB Ultratome V, some sections were stained with lead citrate. Stained and unstained sections were studied with a Jeol 100 B and Jeol 1011 TEMs (Moscow State University).

The fossil plants were collected in 2006-2007 summer field trips by research workers of the laboratory of Palaeobotany, PIN RAS (Broushkin, Gordenko, Karasev, Krassilov and Sokolova), Laboratory of Arthropods, PIN RAS (Shmakov & Yan) and Laboratory of Palaeobotany, Institute of Biology and Soil Sciences, Far East Branch of Russian Academy of Sciences (Shuklina). Collection 5167 is housed at PIN RAS.

SYSTEMATICS

Family—PLATANACEAE Lestiboudois, 1826

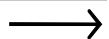
Genus—FRIISICARPUS N. Maslova & Herman, 2006

Type Species—*Friisicarpus marylandensis* (Friis, Crane & Pederson) N. Maslova & Herman, 2006

Friisicarpus kubaensis N. Maslova, Tekleva & Sokolova sp. nov.

(Pl. 1, Pl. 2.1, 3-8, Pl. 3.1, 3-6, Pls. 4-9)

PLATE 1



Morphology of infructescences of *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova sp. nov., scale bar 2 mm (1-7), 1 mm (8-11), 1-11-collecting point A.

1. Specimen 5167/527.
2. Specimen 5167/542.
3. Specimen 5167/577.
4. Specimen 5167/511.
5. Specimen 5167/588.
6. Holotype 5167/562.

7. Specimen 5167/558.
8. Holotype 5167/562, enlargement of 6.
9. Specimen 5167/505.
10. Specimen 5167/576.
11. Specimen 5167/596.

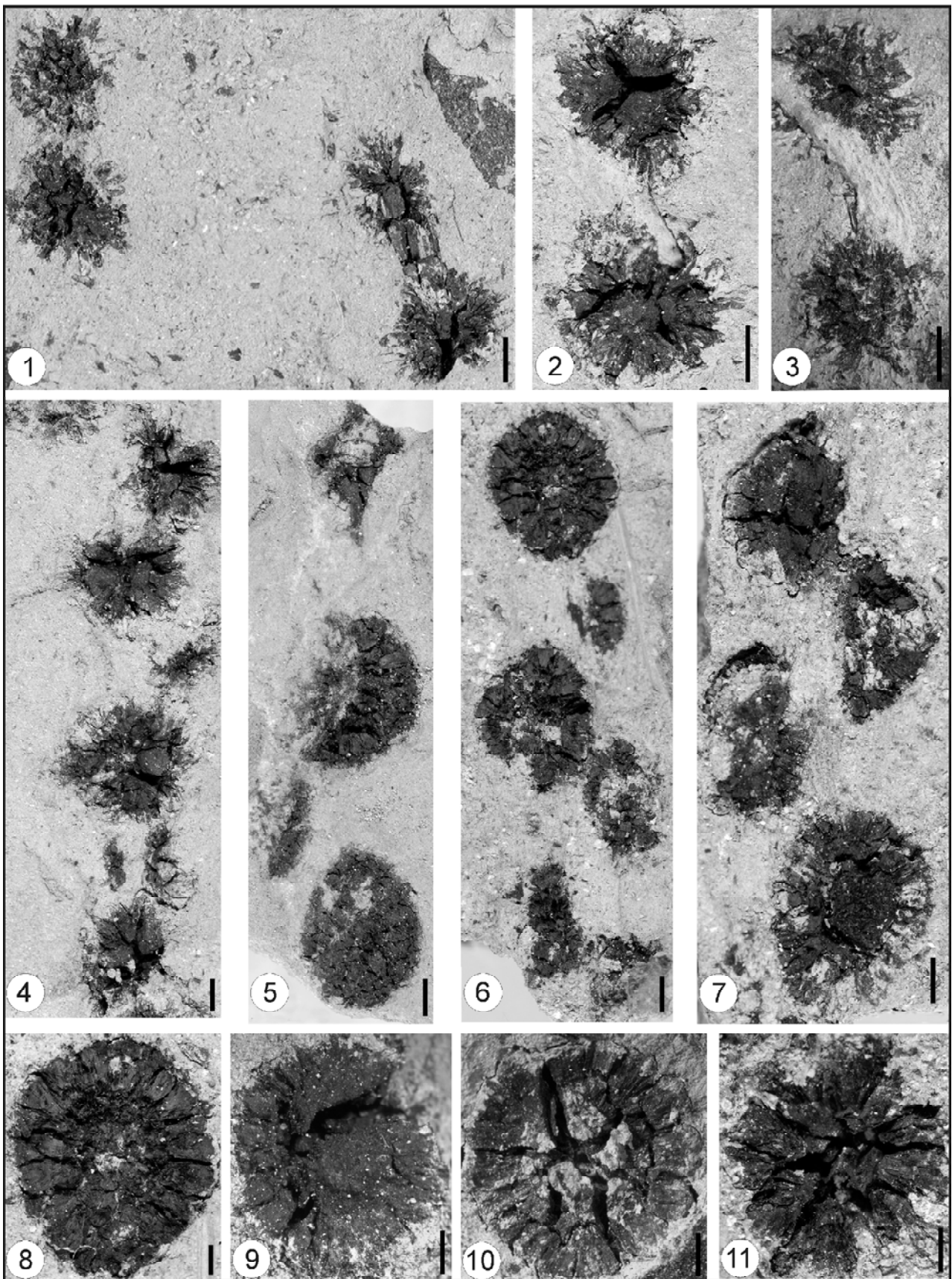


PLATE 1

Diagnosis—Compound infructescence with a longitudinally striate axis and several sessile heads, each with more than 60 (up to 100) fruits; fruits enclosed in a well-developed perianth, covering more than half of fruit length, perianth elements linear, parallel-margined, free from fruit base, fruits pentamerous; ventral suture of fruitlet is often open, widening at the bilobate apex having triangular conical expansion and short stylodium; epidermal cells of fruitlets longitudinally elongated at base, square or rhomboid centrally and apically while some bear median papillae and globose trichomes, abundant anomocytic stomata and trichome bases present at fruitlets apices; seed solitary with a well-developed endosperm, probably, developed from an orthotropous ovule, epidermal cells of seed vary from nearly square to rectangular or polygonal, some of them bear median papillae, cells with strongly sinuous anticlinal walls and finely striate periclinal walls form a sub-epidermal layer; endosperm well-developed.

Description—A compound infructescence consists of a longitudinally striate axis up to 2 mm in diameter bearing several alternating sessile heads (Pl. 1.1-7). The heads vary from 3 to 8 mm in diameter. Spheroidal heads (Pl. 1.9-11) occur with others that are slightly flattened and oval in plan (Pl. 1.5-7). The most complete specimen enumerates six heads on the axis.

The longitudinal striation of the axis is emphasized by distinct cuticular folds (Pl. 2.1). Ordinary epidermal cells of the axis are longitudinally elongated and vary from 10-15 μm to 20-30 μm in size. Their outer periclinal walls are convex, finely and densely striate parallel to the long axis of the cell (Pl. 2.5, 6). The infructescence axis is covered with numerous, irregularly situated trichomes, being more abundant on the terminal slender parts of the axis (Pl. 2.5). There are three types of trichomes. Trichomes of the first type are formed on only one epidermal cell with their bases barrel-shaped oval in plan view, strongly cutinized, 10-15 μm in diameter (Pl. 2.5). The trichomes apices are elongated, often broken, at least 25-30 μm long. Trichomes of the second type appear at the contact of two or more cells and have a cutinized oval base and capitate apical part (Pl. 2.7, 8). Trichomes of the third type have rounded cutinized bases up to 10 μm in diameter and are surrounded by eight to ten epidermal cells about 8 μm in diameter, smaller than most ordinary epidermal cells with straight anticlinal walls (Pl. 3.1). In addition to the trichomes, lenticel-like structures occur in the epidermis of the infructescence axis. They are lenticular structures from 30 to 60 μm long and 30-35 μm wide

with a central stoma from 20 x 30 μm to 30 x 60 μm in size (Pl. 3.3-5). Parenchyma cells of the axis are rectangular, 46-60 μm long and 30-40 μm wide with straight anticlinal walls; periclinal walls bear small rounded pits (Pl. 3.6).

The head consists of a globose core, 1-2 mm in diameter and radially attached, closely packed fruits (Pl. 1.8; Pl. 4.1). Abscised fruits leave rounded scars which are clearly marked by preserved fragments of perianth elements (Pl. 4.3).

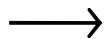
The number of fruits in a head exceeds 60 (up to 100) and are nearly identical in size within the same head. Among different specimens the length of an individual fruit varies from 1200 to 2000 μm ; the width, from 400 to 750 μm .

Fruits are enclosed in a well-developed perianth, covering more than half of a fruit length (Pl. 4.1); the perianth elements are linear with nearly parallel margins, free from the very fruit base (Pl. 4.6) and are arranged in two or three rows (Pl. 4.3). The outer elements of the perianth (Pl. 4.7) are more cutinized than the inner elements (Pl. 4.8). Epidermal cells of perianth elements are longitudinally elongated, up to 40 μm long and 10 μm wide.

The fruits are pentamerous (Pl. 4.2-4) and narrow triangular in plan. The fruitlets are uniformly developed; rarely an underdeveloped carpel might occur which is shorter, narrower (about 350 μm), and with an almost undeveloped apical part (Pl. 6.3). The apices of normally developed fruitlets are wide and bear bilobate and triangular conical expansions (Pl. 4.4, 5). The fruitlets have short stylodes (Pl. 4.4; Pl. 6.4, 5). In mature heads the ventral suture of the fruitlet is often open (Pl. 6.4, 5); the seeds are freely dispersed.

Epidermal cells at the fruitlet base are longitudinally elongated (Pl. 5.1), with straight thickened anticlinal walls. In the central part of the fruitlet, cells are more or less square or rhomboid, 10-20 μm in size, and with straight thickened anticlinal walls (Pl. 5.2), some of them bearing median papillae (Pl. 5.4). Rounded trichomes with a cutinized base occur in the fruitlet epidermis (Pl. 6.1, 2). Trichome bases (Pl. 5.5, 6, 8) and abundant anomocytic stomata (Pl. 5.3, 5-8) are also seen in the fruitlet apices. The stomata are rounded (10 x 11 μm) and broadly oval (16 x 11 μm). The guard cells of most stomata rise above the level of the epidermis surface forming a distinct ring with numerous radiating, small, parallel cuticular folds which are perpendicular to the long axis of the stoma (Pl. 5.7). Trichome bases are oval (Pl. 5.5, 8) and vary in size from 12 x 7 μm to 9 x 5 μm .

PLATE 2



Axis epidermis of infructescence of *Früisicarpus kubaensis* N. Maslova, Tekleva & Sokolova sp. nov. (1, 3-8) and *Platanus acerifolia* Willd. (2), 1, 3-8-collecting point A.

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| <p>1. Specimen 5167/527, axis cuticle, longitudinal folds and cutinized trichome base, SEM.</p> <p>2. Modern species, herbarium collected by authors for comparison, axis cuticle, longitudinal folds, trichome base and lenticel, SEM.</p> <p>3. Specimen 5167/527, axis cuticle, trichome bases, on the left elongated trichome with a broken tip, SEM.</p> | <p>4. Specimen 5167/602, rounded cutinized trichome, SEM.</p> <p>5. Specimen 5167/602, surface of terminal axis region with numerous trichome bases, SEM.</p> <p>6. Specimen 5167/577, surface of axis with rounded cutinized trichomes, SEM.</p> <p>7, 8. Specimen 5167/557, axis cuticle, trichome bases at the contact of two and more cells, LM.</p> |
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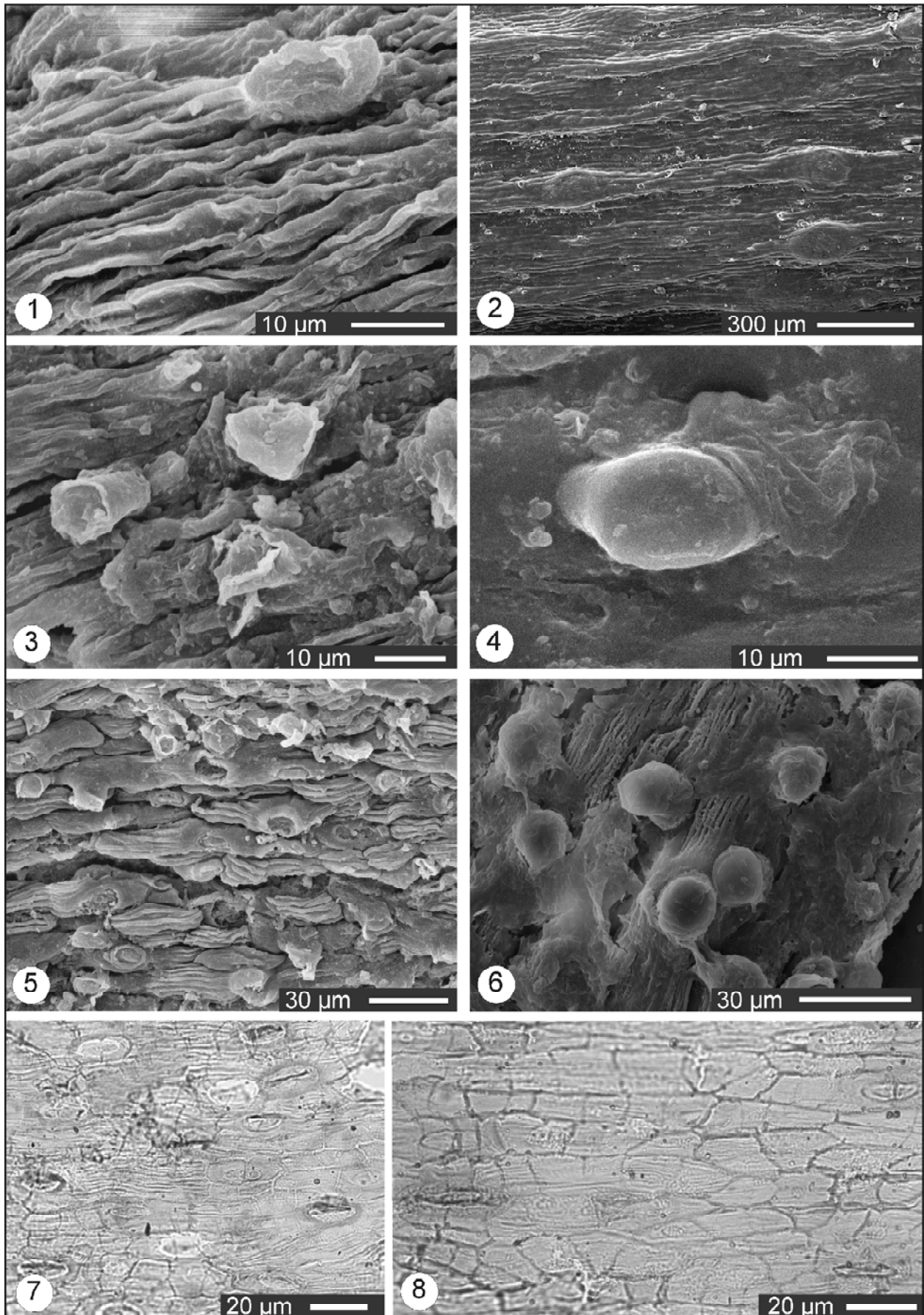


PLATE 2

Each fruitlet bears a solitary seed (Pl. 6.4-9) which completely fills the fruitlet cavity. The micropile is located on the same axis as the funiculus, the seed probably develops from an orthotropous ovule. Within the species seeds vary in size from 1900 to 1070 μm long and from 720 to 360 μm wide.

The outer layer of the spermoderm consists of cells varying from nearly square to rectangular or polygonal; the anticlinal walls are straight (Pl. 7.2-4; Pl. 8.4). These epidermal cells diminish from the median area towards the periphery of the seed. On the periphery they are exceptionally elongated, rectangular, occasionally with inclined walls (Pl. 7.3). The cellular structure disappears on the outer surface of the cuticle after maceration but median papillae are clearly visible (Pl. 7.1, 6). Papillae are rare on some seeds (Pl. 7.1) but frequently occur on others (Pl. 7.5). Papillae vary from small rounded (Pl. 7.7), often folded (Pl. 7.8) to elongated (Pl. 7.6). They are from 10 to 25 μm in height. Their rounded or oval bases 6 to 12 μm in diameter are evident on the inner cuticular surface (Pl. 7.2).

There is a layer of cells with strongly sinuous anticlinal walls and finely striate periclinal walls under the epidermis (Pl. 8.7). The endosperm is well-developed and occupies the whole seed cavity (Pl. 8.2), consisting of more or less isodiametric cells, 8-15 μm in diameter (Pl. 8.8).

Pollen grains were found on the fruitlet surface. They are small, prolate, elliptic from the equatorial view and rounded trilobate from polar view, tricolpate, finely reticulate, semitectate, the polar axis is 13.2 (11.1-16.3) μm and the equatorial diameter is 10.2 (8.0-12.7) μm (Pl. 9.1-3). The colpi are 8.7 (5.8-12.5) μm long, the mesocolpium length is 6.0 (4.3-7.9) μm (Pl. 9.1-2); the distance between apocolpia extremities is 4.5 (2.3-6.6) μm (Pl. 9.3). The exine sculpturing is uniform throughout the pollen surface, no change in the reticulum pattern was detected at the transition from non-aperture to aperture regions. The lumina of the reticulum are rounded-pentagonal or hexagonal, sometimes oblong or slit-like. The aperture membrane is granular (Pl. 9.5, 7).

The ectexine is less electron dense than the endexine (Pl. 9.4, 8). The ectexine in the non-aperture region is 0.9 (0.72-1.18) μm thick, the tectum is 0.29 (0.19-0.43) μm , the columellae are 0.25 (0.13-0.29) μm high and 0.16 (0.11-0.21) μm in width, and the foot layer is 0.34 (0.19-0.65) μm thick. The endexine in the non-aperture region is 0.09 (0.06-0.13) μm thick, granular, the granular structure is especially noticeable in the inner part of the endexine (Pl. 9.4, 8). Towards the apertures the ectexine

gradually reduces in thickness, whereas the endexine thickens up to 0.8 μm (Pl. 9.4, 6). Orbicules occur, about 0.6 μm in diameter with a hollow core of about 0.35 μm in diameter.

Etymology—After the locality Kubaev.

Holotype—PIN RAS 5167/562 (Pl. 1.6, 8).

Locality—Western Siberia, Kiya River, near the village of Kubaev.

Age—Albian-Cenomanian.

Comparison & Remarks—Unlike other known species of the genus, *F. kubaensis* sp. nov. is characterized by the presence of stomata and trichomes on the apical parts of fruitlets; trichomes and epidermal cells with median papillae in the central part of fruitlet; seed epidermal cells, variable in shape and size and often bearing median papillae; and nearly isodiametric cells of the second spermoderm layer with sinuous anticlinal walls. A developed endosperm was described for the first time in *Friisicarpus*.

Several leaf genera were assigned to the Platanaceae in the Kubaev flora: *Araliopsoides* Berry, 1911, *Sapindopsis* Fontaine and leaves of plane tree appearance which Lebedev (1954) previously assigned to *Platanus* while Golovneva (2004) referred them to the genus *Platanophyllum* Fontaine, 1889. However, these findings originate exceptionally from the upper part of the section, while infructescences of *Friisicarpus kubaensis* sp. nov. were found in the lower part of the section in association with only platanoid leaves *Ettingshausenia kubaensis* sp. nov. We suppose that these leaves and infructescences belonged to the same plant based on the similarity between their cuticular-epidermal characters.

Class—MAGNOLIOPSIDA

Group—PLATANOFOLIA Krassilov, 1979

Genus—ETTINGSHAUSENIA Stiehler, 1857

Type Species—*Ettingshausenia cuneifolia* (Bronn) Stiehler, 1857

Ettingshausenia kubaensis N. Maslova & Sokolova sp. nov.

(Pl. 10-13)

PLATE 3



Axis anatomy of infructescence of *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova sp. nov. (1, 3-6) and *Platanus acerifolia* Willd. (2, 7), SEM, 1, 3-6-collecting point A.

- | | |
|---|---|
| <p>1. Specimen 5167/532, axis cuticle from inner side, rounded trichome base surrounded by numerous small cells.</p> <p>2. Modern species, herbarium collected by authors for comparison, axis cuticle, lenticel.</p> <p>3-5. Specimen 5167/532, axis cuticle from inner side, cutinized stomata.</p> | <p>6. Specimen 5167/527, cells of parenchyma of infructescence axis.</p> <p>7. Modern species, herbarium collected by authors for comparison, cells of parenchyma of infructescence axis.</p> |
|---|---|

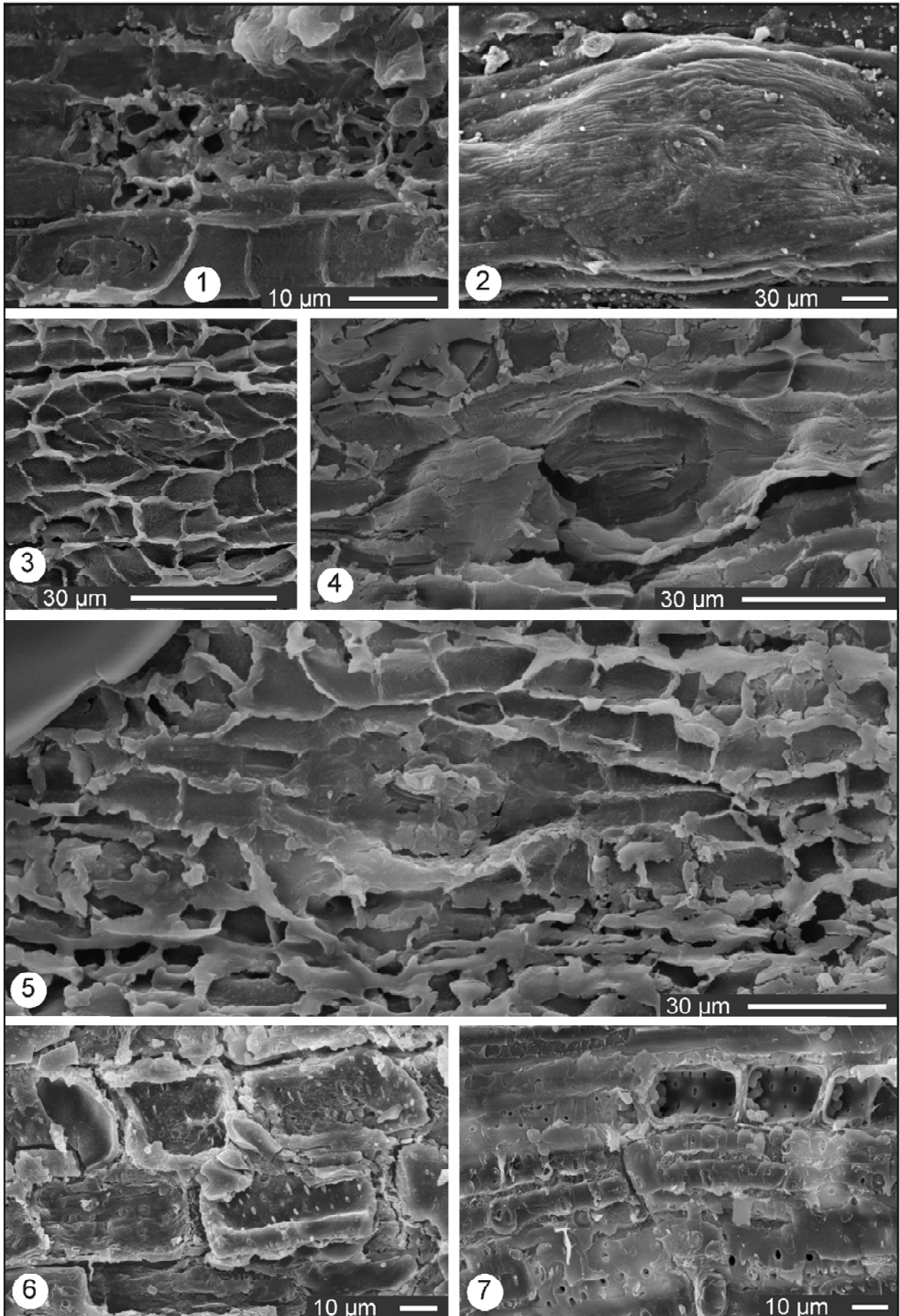


PLATE 3

Diagnosis—Leaves simple, entire, with or without small lateral lobes, leaf lamina rhomboid with acuminate apex and widely wedge-shaped, decurrent base, margin toothed, sinuses between the lobes toothed, teeth small, triangular, concave-concave or convex-concave with small apical glands, venation actinodromous or palynactinodromous, up to four pairs of variously developed infrabasal veins present, tertiary veins alternating and percurrent; epidermis of upper surface of leaf lamina near midrib consists of cells with more or less straight anticlinal walls, whereas, those of marginal part of lamina mostly sinuous, epidermal cells usually show sinuous anticlinal walls, sometimes straight anticlinal walls, trichomes bases rounded, strongly cutinized, developed on contact of six to ten ordinary epidermal cells; bases 10–20 μm in diameter, surrounded by distinct radiating cuticular folds; epidermal cells of lower leaf surface elongated, isodiametric with distinctly sinuous anticlinal walls, trichomes and stomata present, stomata anomocytic, irregularly oriented, widely oval or rounded with six to ten subsidiary cells; trichomes of two types, abundant, evenly distributed on leaf surface and near veins, trichomes occurring on veins with strongly cutinized barrel-shaped bases about 15 μm in diameter and elongated apices, elsewhere, trichomes domelike, up to 10 μm in diameter, often surrounded by stomata.

Description—Leaves are simple, entire (Pl. 10.1–7; Pl. 11.1–8) with a rhomboid lamina, an acuminate apex and a wide wedge-shaped, decurrent base. The leaf margin bears teeth which are small, triangular, concave-concave or convex-concave, and have small apical glands (Pl. 11.2). Venation is palmate-pinnate with basal veins which are opposite and may be virtually identical in thickness to the adjacent pair of secondary veins which have one or two acroscopical and up to six basicopical branches. There are up to three pairs of variously developed infrabasal veins. The tertiary veins are alternating and percurrent (Pl. 10.7).

Leaves are hypostomatic with a noticeably thick, finely folded, cuticle on the upper surface. Distinct, radially disposed, cuticular folds diverge from the trichome bases (Pl. 12.1, 2). Ordinary epidermal cells of the upper leaf surface are elongated or isodiametric, 10–20 μm wide and 20–40 μm long (Pl. 13.1, 3, 5) with their anticlinal walls varying from nearly straight to strongly sinuous whereas, cells confined to trichome bases have straight anticlinal walls (Pl. 12.3, 4). The epidermis of the central part of the leaf lamina, close to the midrib, is mostly

composed by cells with almost straight anticlinal walls (Pl. 13.1). The anticlinal walls of epidermal cells of the leaf margin are mostly sinuous (Pl. 13.5) while those of the median part of the lamina are characterized by a mixture of wall types varying from more or less sinuous to those with straight walls (Pl. 13.3). In the costal zone the cells are tetragonal, stretched along the vein axis or nearly square with straight anticlinal walls and arranged in distinct longitudinal rows (Pl. 13.7). The rounded trichome bases are strongly cutinized and developed at the contact of several ordinary epidermal cells with a distribution of about 1–2 per 100 μm^2 . They are from 10 to 20 μm in diameter, surrounded by distinct radiating cuticular folds (Pl. 12.1, 2) and have massive cuticular thickenings which are from the inner cuticular surface. The radial anticlinal walls of adjoining cells are also cutinized (Pl. 12.3, 4; Pl. 13.8).

The cuticle of the lower leaf surface is thin, with fine folds, oriented along the long axis of ordinary epidermal cells (Pl. 13.2, 6) which are elongated or isodiametric, 10–30 μm wide, 20–50 μm long with distinct sinuous anticlinal walls of the cells (Pl. 13.6). The ordinary epidermal cells of the lower leaf surface are similar in shape to those of the upper leaf surface, but their anticlinal walls are sinuous to a greater degree.

The epidermis of the lower leaf surface bears stomata and trichomes (Pl. 12.7, 8). The stomata are irregularly oriented, widely oval or rounded, 25 x 20 μm to 10 x 20 μm in size and are anomocytic and up to four stomata per 100 μm^2 of the surface. There are five or six subsidiary cells. Guard cells of the stomata rise above the level of the epidermal surface, forming a distinct ring. Their outer stomatal apertures are elliptic with the inner ones fusiform.

Trichomes are abundant, up to 8 per 100 μm^2 of the surface, more or less regularly distributed over the leaf surface and near veins (Pl. 12.7, 8). Two types occur. Those of the first type, mostly confined to leaf veins (Pl. 12.6), are partially preserved, with strongly cutinized barrel-shaped bases about 15 μm in diameter and elongated but broken apices. The second type are domelike, up to 10 μm in diameter, covering other areas of the leaf and often surrounding stomata (Pl. 12.7, 8).

Etymology—After the locality Kubaevo.

Holotype—PIN RAS, 5167/10 (Pl. 10.6).

Locality—Western Siberia, Kiya River, near the village of Kubaevo.

Age—Albian-Cenomanian.

PLATE 4

Morphological and epidermal characters of *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova sp. nov., SEM, 1–8—collecting point A. →

- | | |
|--|---|
| 1. Specimen 5167/576, fragmentary infructescence, fruits surrounded by perianth elements. | 5. Holotype 5167/562, apices of two fruitlets. |
| 2. Specimen 5167/576, two fruits. | 6. Specimen 5167/576, fruit base, note that perianth elements are free from the base. |
| 3. Specimen 5167/576, trace from removed fruit, note remnants of several perianth circles. | 7. Specimen 5167/576, epidermis of outer perianth elements. |
| 4. Specimen 5167/576, apical part of pentamerous fruit. | 8. Specimen 5167/576, epidermis of inner perianth elements. |

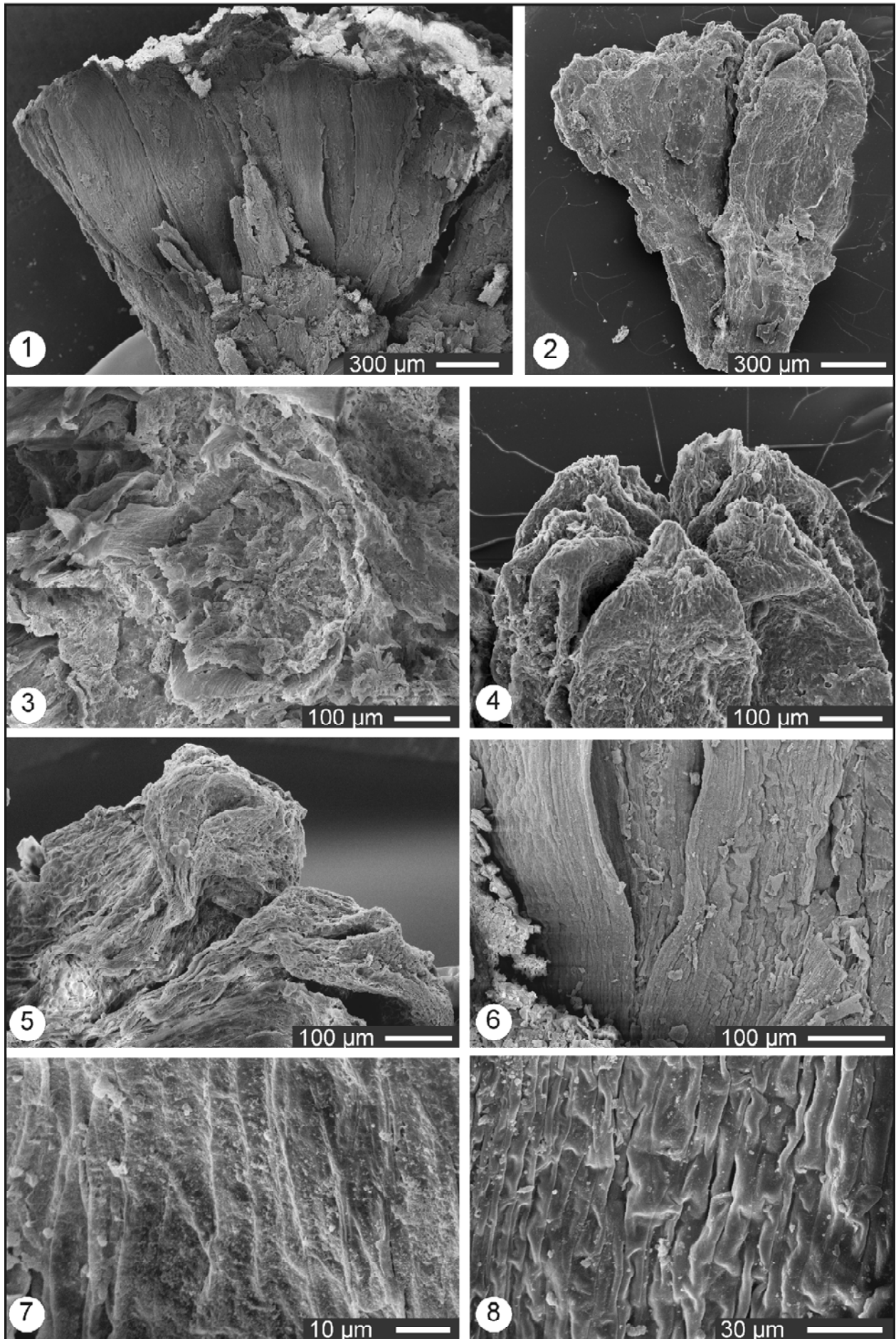


PLATE 4

Comparison & Remarks—*E. louravetlanica* (Herman & Shchepetov) Herman & Moiseeva, 2010 from the Cenomanian of Ugol'naya Bay region, Northeastern Russia (Moiseeva, 2010) and *E. cuneifolia* (Bronn) Stiehler, 1857 from the Cenomanian of Czech Republic (Kvacek & Váchová, 2006) are the most similar species of the genus, to judge by the general leaf morphology. *E. kubaensis* sp. nov. is characterized by distinct alternating and percurrent type of tertiary venation, while *E. louravetlanica* differs in its orthogonal-reticulate tertiary venation. Additionally, both leaf lamina and leaf base are asymmetrical in *E. louravetlanica*. The new species differs from *E. cuneifolia* in somewhat smaller length/width ratio of the leaf lamina and in epidermal structure. It is very peculiar in its cuticular-epidermal characters in that the anticlinal walls of ordinary epidermal cells are sinuous in various degrees within the leaf lamina, and trichomes are numerous and variable in the epidermis of the lower leaf surface. The cuticular-epidermal characters of the leaves under study correspond to those of the associated infructescences *Friisicarpus kubaensis* sp. nov. and we suppose that the leaves and infructescences were produced by the same plant species.

Lebedev (1954) described similar macromorphologic leaves of *Platanus newberryana* Heer, 1867 and *P. simanovskiensis* Lebedev, 1954 from more or less contemporaneous deposits of the Chulym-Yenisei depression (at the Chulym and Bol'shoi Kass rivers). Some morphotypes of *Pseudoprotophyllum* Hollick, 1930 (Lebedev, 1954) are also indistinguishable in macromorphology from *Platanus* species from Lebedev (1954). The differences found by Lebedev (1954) fit into the variability range of leaf laminae of plane tree appearance. Considering that there are no data on cuticular-epidermal structure of the leaves studied by Lebedev (1954), we do not include these leaves in the synonymy of *E. kubaensis* sp. nov.

DISCUSSION

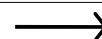
Infructescence architecture—The compound infructescence of *Friisicarpus kubaensis* sp. nov. is a rather massive axis bearing numerous sessile heads. The axis is longitudinally striate, as observed in reflected light and its epidermis bears trichomes which are irregularly distributed, being more abundant on thin terminal parts. Trichomes on the epidermis of inflorescence and infructescence axes are described in modern *Platanus* and some Proteaceae (Carpenter *et al.*, 2005) and were shown for fossil *Bogutchanthus* N.

Maslova, Kodrul & Tekleva, 2007 (N. Maslova *et al.*, 2007) and *Sarbaicarpa* N. Maslova, 2009 (N. Maslova, 2009), the two latter taxa combine characters of the Platanaceae and Hamamelidaceae. *Friisicarpus kubaensis* sp. nov. is characterized by a maximal number of trichomes per axis surface. Trichomes, which are present at the contact of two and more cells, are also typical of modern *Platanus* (Carpenter *et al.*, 2005). Lenticular structures of *Friisicarpus kubaensis* sp. nov. are comparable to lenticels in *Platanus* (Pl. 2.2; Pl. 3.2). In modern *Platanus* such structures are formed by growth of periderm cells directly under stomata. The epidermal cells in the lenticular region are usually smaller while the stomata under which lenticels are formed are larger than other stomata. Unlike *Platanus*, *Friisicarpus kubaensis* sp. nov. lacks normally developed lenticels. However, on the axis there are larger stomata than on the fruitlets and smaller, more abundant, epidermal cells surrounding stomata, which causes these lenticel-like structures to simulate the lenticels of modern *Platanus*. Such structures can be evolutionary predecessors of lenticels of the modern plane tree. Unfortunately, it was impossible to trace the growth of the periderm in *F. kubaensis* sp. nov. to pursue the matter further. The function of trichomes of *F. kubaensis* sp. nov. is still unclear. Those with elongated apices might have protected plants from extra transpiration and those with capitate apices might have performed a secretory function. The parenchyma cells of *F. kubaensis* sp. nov. axis are similar in shape and pore structure to those of modern *Platanus* (Pl. 3.7), but larger.

Heads of modern *Platanus* and majority of fossil platanaceous genera consist of a relatively massive central core with radially attached flowers, compressed in various degrees. In modern *Platanus*, the borders between individual flowers are indistinguishable because the flowers lack a developed perianth and are closely packed. In the fossil Platanaceae, particularly in species of *Friisicarpus*, the perianth is well-developed and often consists of several whorls of perianth elements and therefore the borders between flowers are rather distinct.

The fruit number per infructescence differs among the Platanaceae taxa. *Quadriplatanus* Magallón-Puebla, Herendeen & Crane, 1997 (Magallón-Puebla *et al.*, 1997) has about 40 flowers in the head, *Macginicarpa* Manchester, 1986 (Manchester, 1986) infructescence includes up to 60 fruits. Heads of *F. kubaensis* sp. nov. contain more than 60 (up to 100) fruits. Other species of *Friisicarpus* differ in fruit number per head—about 100 fruits for *F. marylandensis* and *F.*

PLATE 5



Epidermal characters in *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova sp. nov., holotype 5167/562, SEM, 1-8-collecting point A.

- | | | | |
|----|---|----|--|
| 1. | Epidermis of fruitlet base. | 6. | Epidermis of fruitlet apex, stomata of different shape and trichome bases. |
| 2. | Epidermis of central part of fruitlet. | 7. | Stoma in epidermis of fruitlet apex. |
| 3. | Epidermis of fruitlet apex. | 8. | Epidermis of fruitlet apex, stomata and a rounded cutinized trichome base. |
| 4. | Epidermis of central part of fruitlet, papillae. | | |
| 5. | Epidermis of fruitlet apex, stomata and broken trichomes. | | |

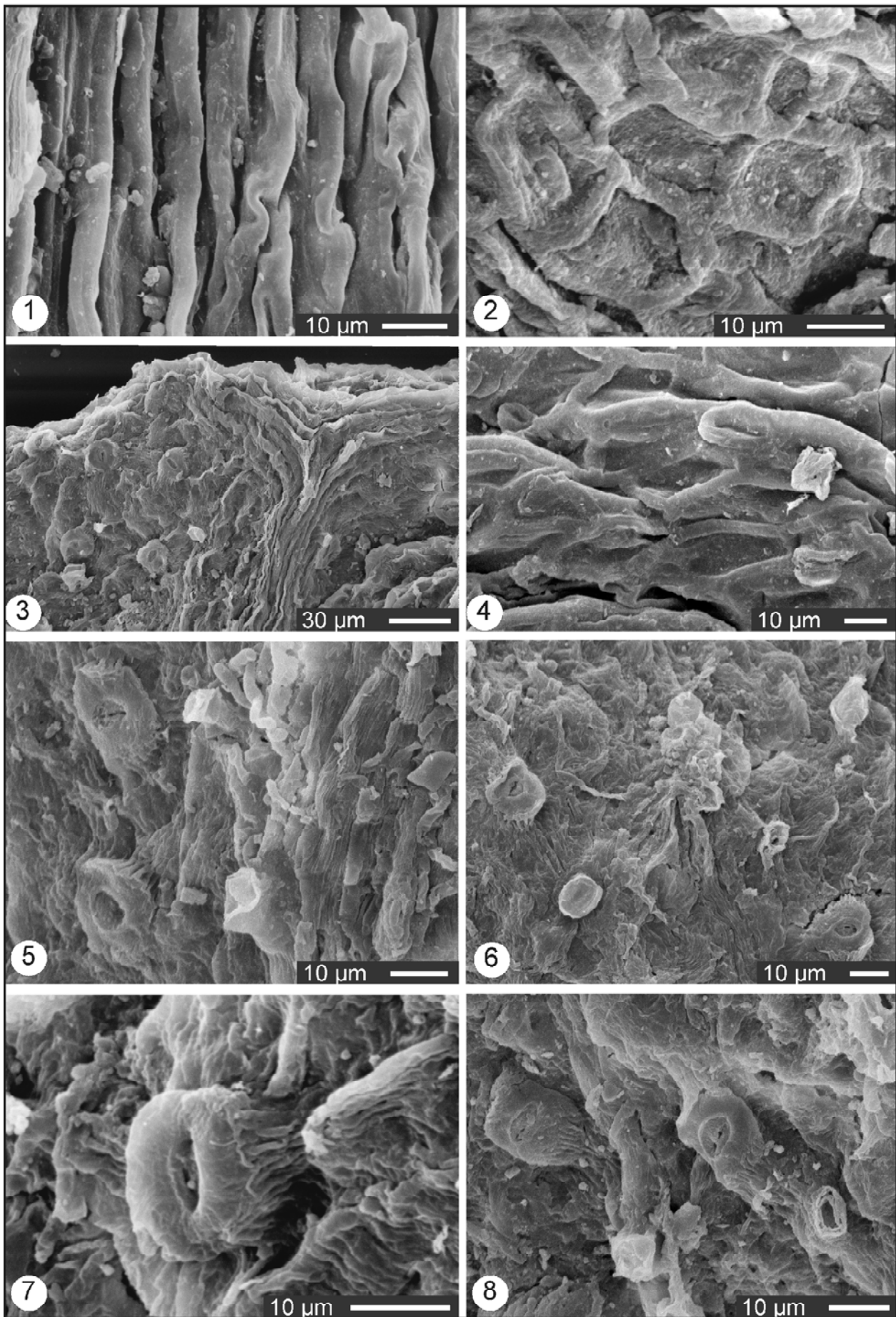


PLATE 5

carolinensis (Friis *et al.*, 1988), more than 50 for *F. brookensis* (Crane *et al.*, 1993) and about 50 flowers were described for *Friisicarpus* sp. (N. Maslova & Herman, 2006). For *F. elkneckensis* the flower number per inflorescence is unknown (Crane *et al.*, 1993).

Perianth—The perianth of *F. kubaensis* sp. nov. extends for more than half of the flower and its elements are disposed in several (most probably two or three) whorls with the outer ones slightly shorter than inner, thicker and more cutinized. The perianth elements are free from the base, linear with nearly parallel margins and are membranous. Similar narrow, linear perianth elements were noted in the Santonian-Campanian *Friisicarpus* sp. (Friis *et al.*, 1988), but their length is unknown. Among known *Friisicarpus* species the new species is most similar to *F. brookensis* and *F. elkneckensis* in perianth development. The new species has linear perianth elements while *F. brookensis* and *F. elkneckensis* are characterized by spatulate ones, which are wider in their central part. The perianth of *F. carolinensis* extends for one third of the fruit length and its elements are shorter and wider.

Gynoecium—Modern *Platanus* is characterized by an apocarpous gynoecium with a variable number of carpels (five to eight, more rarely three to nine) in two or three whorls with relatively developed stylodes. Extinct Platanaceae differ in their carpel number within the flower with *Friisicarpus* and

Macginicarpa being pentamerous whereas, *Quadriplatanus* is tetramerous.

All *Friisicarpus* species possess narrowly triangular carpels. The differences in the species are: the presence or absence of a stylodium, the degree of development of carpel apices and epidermal features of the carpel wall. *F. kubaensis* sp. nov. has a short stylodium which is only known in *Friisicarpus* sp. from the Santonian-Campanian deposits of Sweden (Friis *et al.*, 1988). Among other fossil Platanaceae, pentamerous infructescences of *Macginicarpa* have well-developed stylodes (Manchester, 1986).

The new species shows most similarity with *Friisicarpus elkneckensis*, *Friisicarpus* sp. from the Cenomanian of Western Siberia (N. Maslova & Herman, 2006) and *Friisicarpus* sp. 2 from the Albian-Cenomanian of Kansas, North America (Wang, 2008) in shape of an apical expansion of the carpel, but *F. kubaensis* sp. nov. differs in the presence of stomata and trichomes in the epidermis of the apical expansion. Only for *F. carolinensis* the epidermal features of the carpel wall structure were described (Friis *et al.*, 1988). The ordinary epidermal cells are longitudinally elongated with straight anticlinal walls and form distinct longitudinal rows. The epidermal structure shows much variation in the fruitlet wall in *F. kubaensis* sp. nov. At the base of the fruitlets the epidermal cells are longitudinally elongated and have straight anticlinal walls as was also

PLATE 6

Morphological and epidermal characters of *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova sp. nov., SEM, 1-9-collecting point A. →

- | | | | |
|----|---|-------|---|
| 1. | Holotype 5167/562, globose trichome in fruitlet epidermis. | 4, 5. | Specimen 5167/539, fruitlet with open ventral suture, seed. |
| 2. | Holotype 5167/562, globose cutinized trichome base in fruitlet epidermis. | 6, 7. | Specimen 5167/539, seeds. |
| 3. | Specimen 5167/602, underdeveloped carpel. | 8, 9. | Holotype 5167/562, seeds. |

PLATE 7

Epidermal characters of *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova sp. nov., SEM, 1-8-collecting point A. →

- | | | | |
|-------|---|----|--|
| 1. | Specimen 5167/539, outer surface of seed cuticle, papillae. | 5. | Specimen 5167/576, outer surface of seed cuticle with numerous partly broken papillae. |
| 2, 4. | Specimen 5167/539, inner surface of seed cuticle, epidermal cells of different shape and papilla bases of different diameter. | 6. | Holotype 5167/562, outer surface of seed cuticle, rounded and elongated papillae. |
| 3. | Holotype 5167/562, inner surface of seed cuticle, epidermal cells of different shape, in the peripheral region of seed cells are elongated, in central part they are polygonal. | 7. | Specimen 5167/576, rounded papilla. |
| | | 8. | Specimen 5167/576, contorted papilla of larger diameter. |

PLATE 8

Seed anatomy of *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova sp. nov., SEM, 1-8-collecting point A. →

- | | | | |
|----|--|----|---|
| 1. | Specimen 5167/539, fruitlet with open ventral suture, solitary seed with partly removed epidermis; second layer of spermoderm which is formed of cells with sinuous anticlinal walls is visible under epidermis. | 4. | Specimen 5167/576, fragment of outer (above) and inner (below) surface of seed cuticle. |
| 2. | Specimen 5167/539, longitudinal section of fruitlet, solitary seed fills the entire fruitlet cavity. | 5. | Specimen 5167/576, micropylar part of seed with partly withdrawn cuticle. |
| 3. | Specimen 5167/576, seed cuticle after maceration, epidermal cells of different shape. | 6. | Specimen 5167/576, epidermal cells of central part of seed. |
| | | 7. | Specimen 5167/576, cells of second spermoderm layer with sinuous anticlinal walls. |
| | | 8. | Specimen 5167/576, cells of endosperm. |

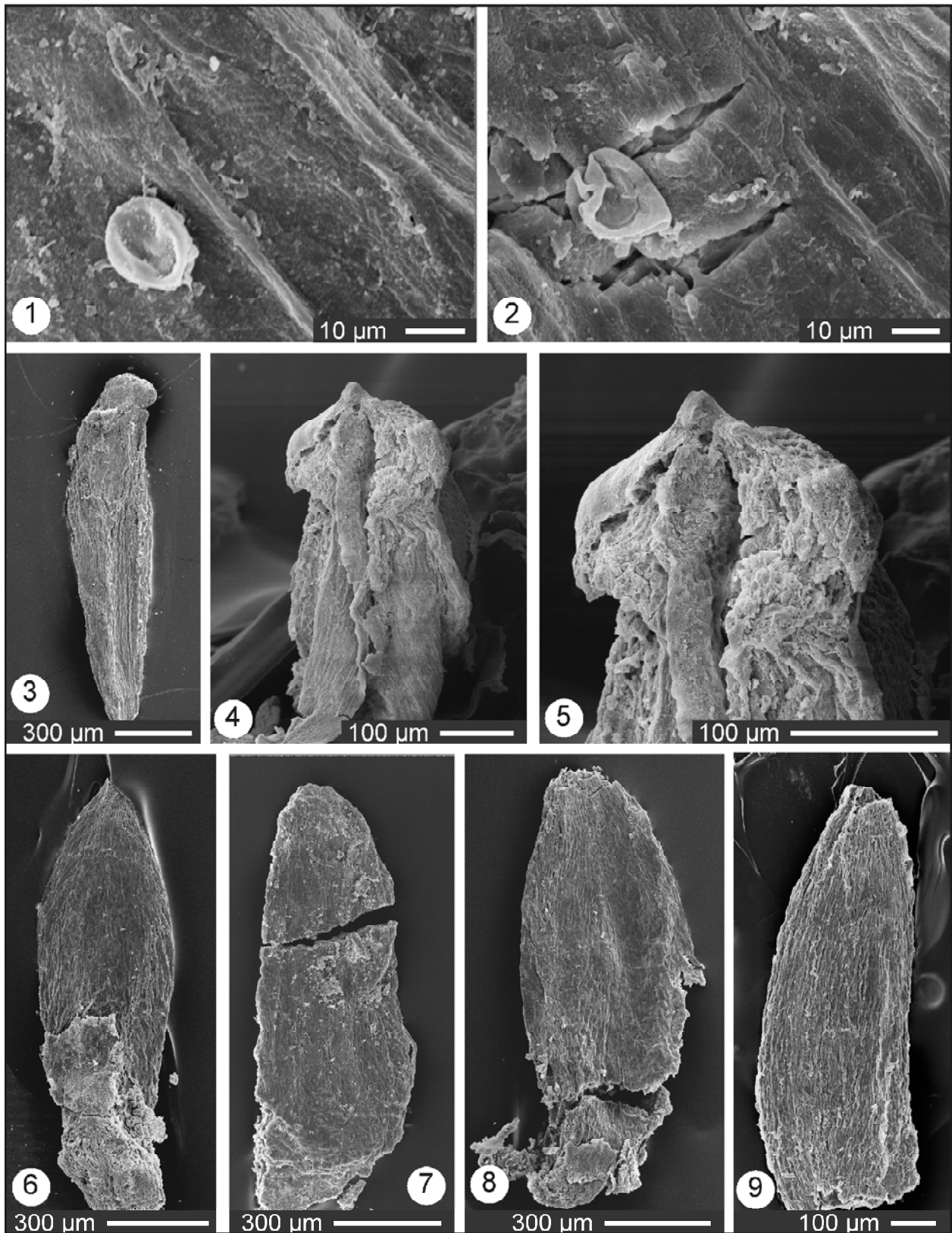


PLATE 6

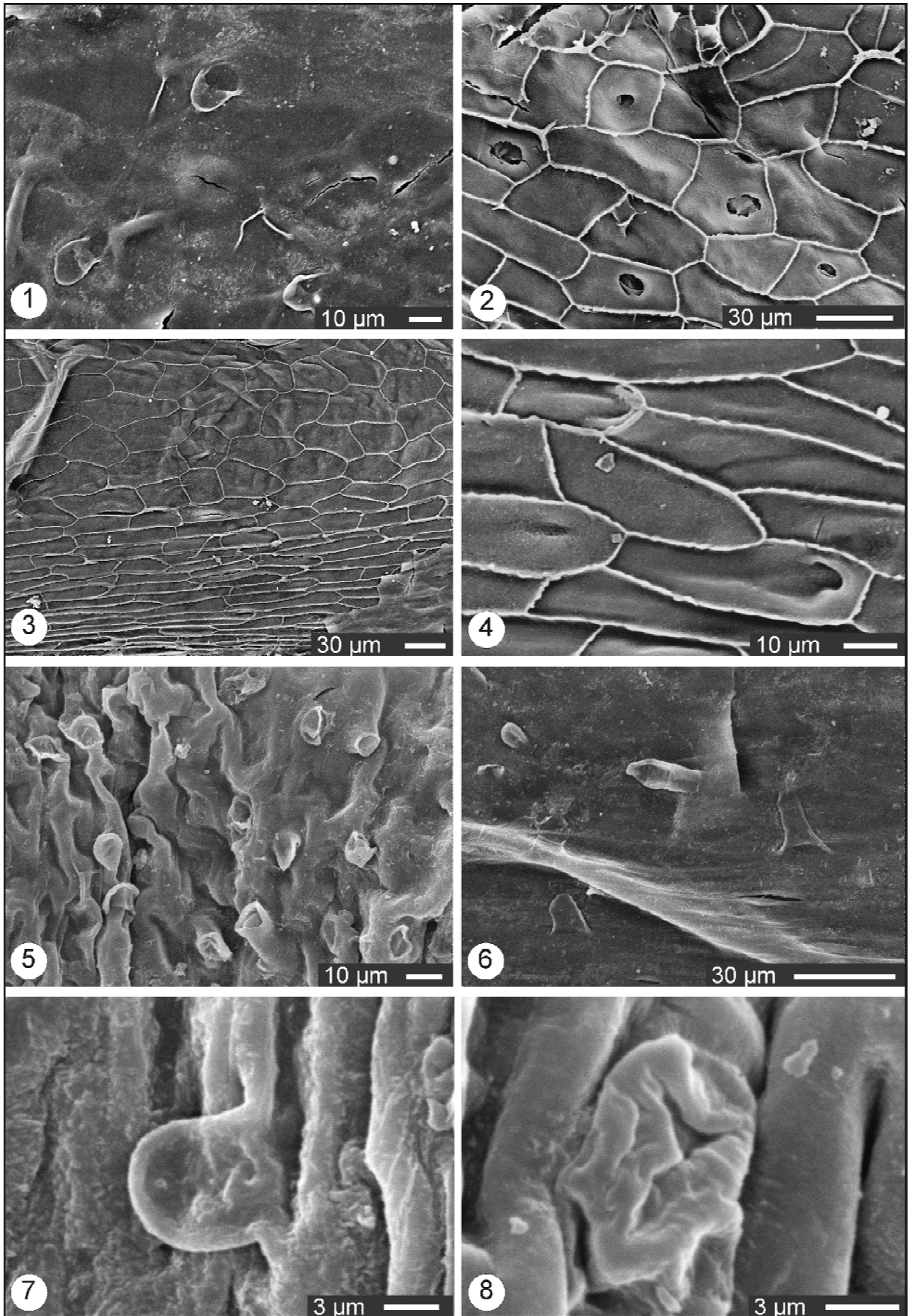


PLATE 7

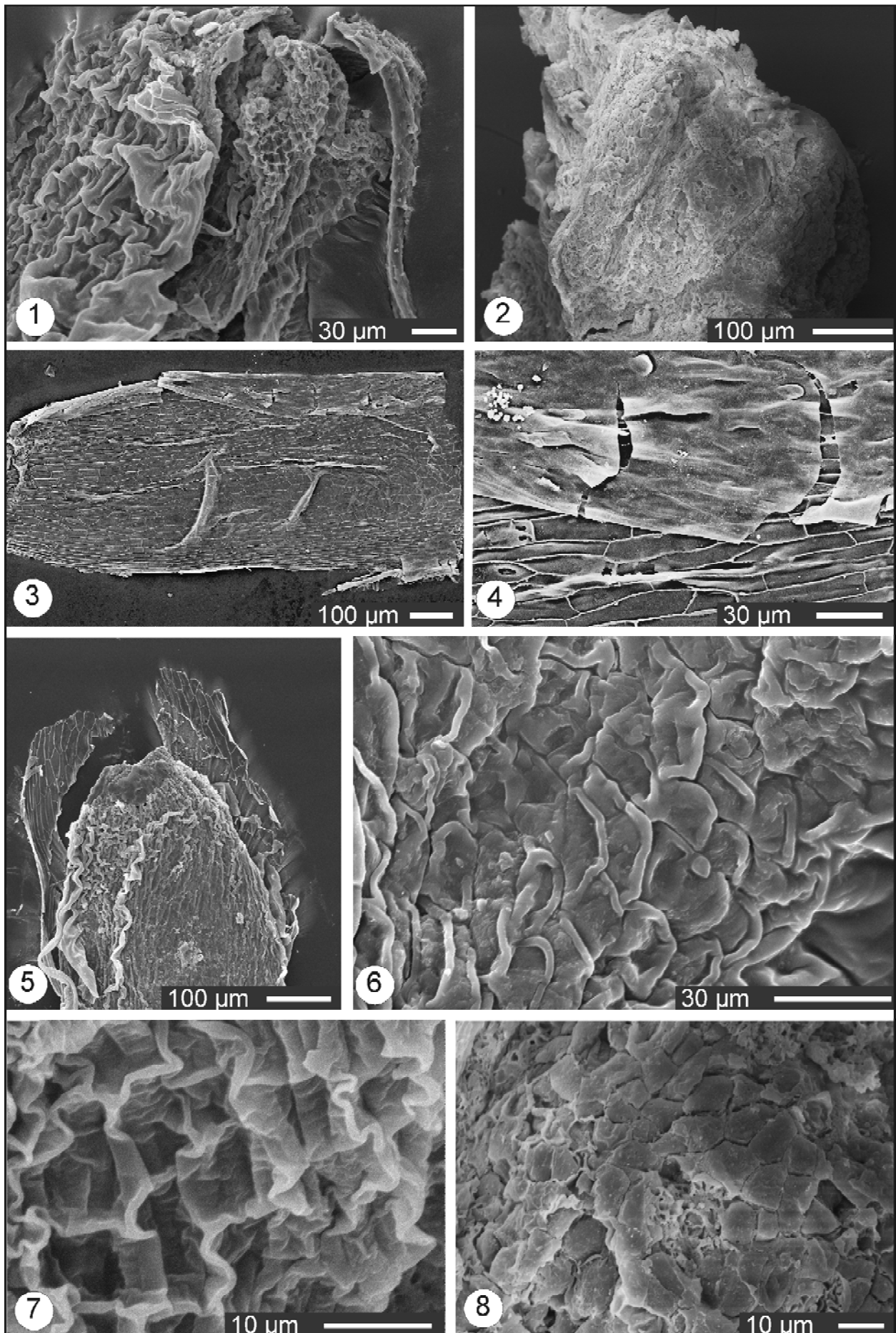


PLATE 8

observed in *F. carolinensis* (Friis *et al.*, 1988). In the central part of the fruitlet epidermal cells are more or less square or rhomboid, with straight, thickened anticlinal walls, some of which bear median papillae. In this part of the fruitlet there are domelike, perhaps glandular, trichomes with round cutinized bases. Such peltate glands on carpel walls are known for *Quadriplatanus georgianus* Magallón-Puebla, Herendeen & Crane, 1997 (Magallón-Puebla *et al.*, 1997) assigned to the Platanaceae and for *Sarbaicarpa* which combines features of the Platanaceae and Hamamelidaceae (N. Maslova, 2009). There are abundant anomocytic stomata and oval or rounded trichome bases in the apices of the fruits. The presence of these distinguishes *Friisicarpus kubaensis* sp. nov. from other members of the genus as well as from other known fossil genera of the Platanaceae. Stomata in the epidermis of fruit apices are also described in *Kasicarpa* N. Maslova, Golovneva & Tekleva, 2005 (N. Maslova *et al.*, 2005), infructescences which are similar in macromorphology to the Platanaceae but differ in the monomerous gynoecium and mosaic combination of the Platanaceae and Hamamelidaceae features.

In the Platanaceae taxa, the presence of stomata and trichomes was shown for stamen epidermis. Thus, hairy connectives occur in *Platananthus hueberi* Friis *et al.* 1988 (Friis *et al.*, 1988), *P. synandrus* Manchester, 1986 (Manchester, 1986), *Platanus neptuni* (Ettingshausen) Bužek *et al.* 2004 (Kvacek & Manchester, 2004), *Aquia brookensis* Crane *et al.* 1993 (Crane *et al.*, 1993), *Archaranthus krassilovii* N. Maslova & Kodrul, 2003 (N. Maslova & Kodrul, 2003) and *Macginistemon mikaneides* (MacGinitie) Manchester, 1986 (Manchester, 1986). Stomata on extension of connectives were observed only for *Aquia brookensis*, *Quadriplatanus georgianus* (Magallón-Puebla *et al.*, 1997) and dispersed platanoid stamens from the Santonian-Campanian deposits of Sweden (Friis *et al.*, 1988).

Dehiscence of mature fruitlets along the ventral suture was previously shown for *Friisicarpus carolinensis* and for the Santonian-Campanian *Friisicarpus* sp. (Friis *et al.*, 1988). Mature fruitlets of *F. kubaensis* sp. nov. dehisced along the ventral suture and seeds could have dispersed more or less freely. Modern plane trees have indehiscent fruitlets.

Trichomes on the fruitlet surface appeared for the first time for the genus *Friisicarpus*, other species of the genus lack these. The carpels of *Platanus* are covered with hairs to varying extents.

Seed—The fruitlet of *Friisicarpus kubaensis* sp. nov. contains a solitary seed which is closely in contact to the walls and occupies almost the entire space. Probably, the seed develops from an orthotropous ovule, as micropylar area and funiculus are situated on the same axis.

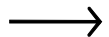
In the Platanaceae, orthotropous ovules occur in modern *Platanus* and fossil *Macginicarpa*, but not in *Quadriplatanus georgianus* (Magallón-Puebla *et al.*, 1997). The preservation of the material did not reveal much of the ovule morphology: the adaxial side of the ovule has a longitudinal narrow median flap of tissue resembling a narrow wing. The absence of a micropyle in the region of the ovule opposite its attachment point indicates that the ovule is not orthotropous.

The structure of the spermoderm outer layer in *Friisicarpus kubaensis* sp. nov. is unique for this genus. The seed wall structure of *F. carolinensis* and *F. brookensis* has already been published (Friis *et al.*, 1988) where it was found that in *F. carolinensis* there were two layers of spermoderm cells, an outer layer of polygonal isodiametric cells with straight walls and an inner layer of elongated cells with straight walls. The outer spermoderm layer of *F. brookensis* consists of elongated cells with straight anticlinal walls. Epidermal cells in *F. kubaensis* sp. nov. vary from almost square to rectangular or polygonal and have straight anticlinal walls. The median part of the seed and in the peripheral region the shape of epidermal cells differs. Some bear small, rounded, or elongated papillae which are unknown in other species of *Friisicarpus* as well as other genera of the Platanaceae. There are domelike cells with a small apical pore in the epidermis of modern plane tree which secrete mucous which assist with water retention (Sravnitel'naja anatomija semjan, 1991). *Kasicarpa* from the Turonian is similar to *Platanus* in the epidermal structure of the seed. There is a possibility that the epidermal cells of the seed of *F. kubaensis* sp. nov. that bear median papillae evolved into domelike epidermal cells of the seed of modern *Platanus*.

There is a layer of cells with strongly sinuous anticlinal walls and finely striate periclinal walls under the epidermis in *Friisicarpus kubaensis* sp. nov., in contrast to *F. carolinensis* where this layer consists of elongated cells with straight anticlinal walls.

In the absence of developmental data, we tentatively describe the nutritional tissue of the seed as endosperm (rather than perisperm) by analogy with modern *Platanus* (Sravnitel'naja anatomija semjan, 1991; Floyd *et al.*, 1999). The

PLATE 9



Morphology and ultrastructure of pollen adhered to *Friisicarpus kubaensis* N. Maslova, Tekleva & Sokolova sp. nov., SEM, TEM, 1-8-collecting point A.

1. Two pollen grains adhered to fruitlet surface, SEM, scale bar 3 μm .
2. Pollen from equatorial view, SEM, scale bar 3 μm .
3. Pollen from polar view, SEM, scale bar 3 μm .
4. Section throughout the whole pollen, arrows indicate aperture regions, TEM, scale bar 1.25 μm .
5. Part of pollen showing aperture region, SEM, scale bar 1 μm .
6. Transition from non-aperture to aperture region in sporoderm, t-tectum, c-columella, fl-foot layer, end-endexine, TEM, scale bar 0.5 μm .
7. Part of pollen showing colpus margin, SEM, scale bar 5 μm .
8. Non-aperture region of sporoderm, t-tectum, c-columella, fl-foot layer, end-endexine, TEM, scale bar 1 μm .

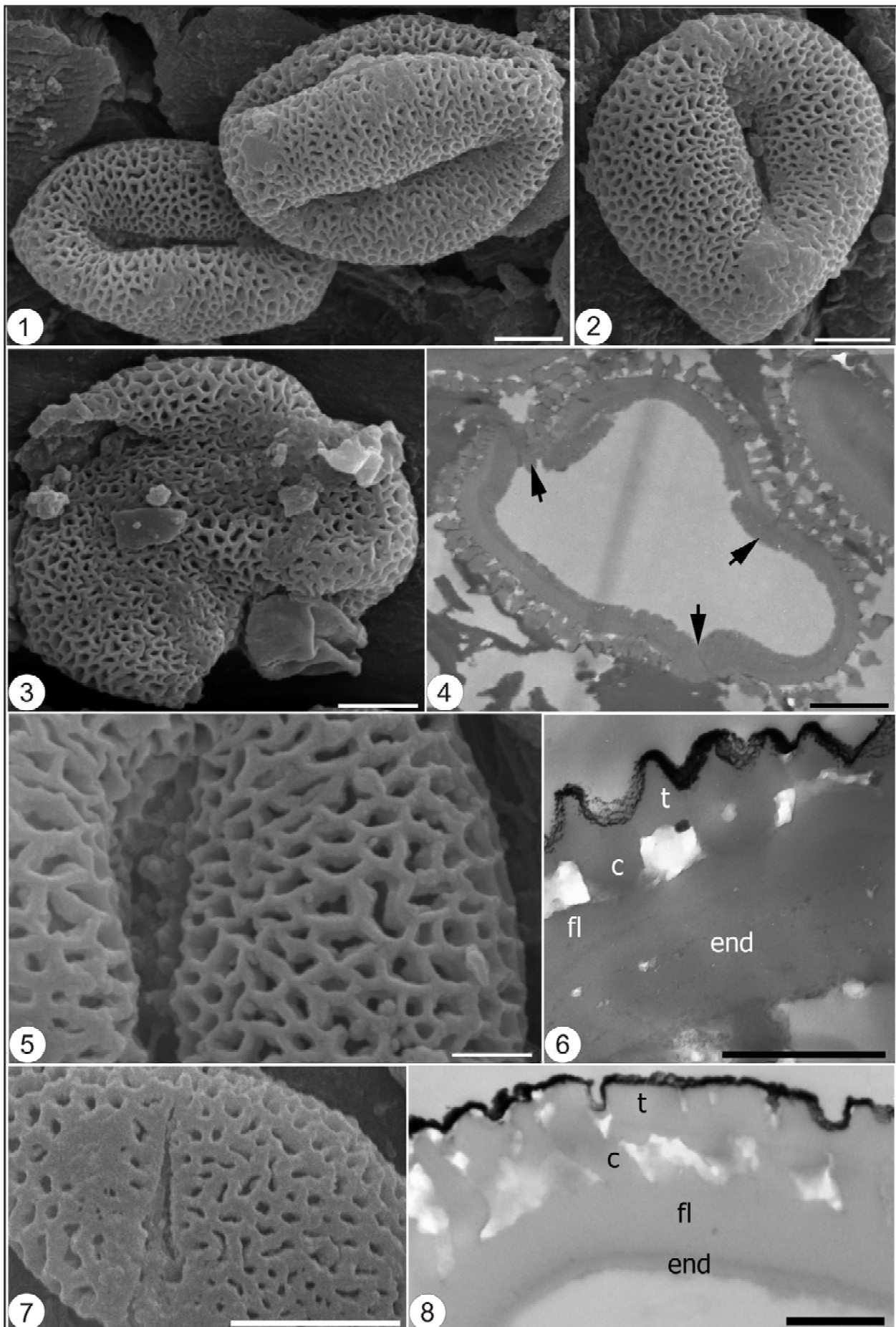


PLATE 9

endosperm of *F. kubaensis* sp. nov. is well developed, consists of more or less isodiametric cells occupying the entire seed. There is no information on the presence of a developed endosperm in other species of *Friisicarpus* as well as in the seeds of other genera of fossil Platanaceae. In modern *Platanus* endosperm is almost completely assimilated by a growing embryo leaving a thin peripheral layer in mature seeds (Poddubnaya-Arnoldi, 1982). Among fossil genera, *Sarbaicarpa* combines platanaceous and hamamelidaceous features, has seeds with a well-developed endosperm and variable shape of epidermal cells. In contrast to *F. kubaensis* sp. nov., *Sarbaicarpa* has an anatropous ovule and there are also numerous specific differences in the structure of the infructescences and individual fruits.

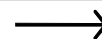
Pollen grains—Pollen of modern and fossil Platanaceae is rather uniform. It is small, tricolpate with a granular aperture membrane, reticulate sculpture, semitectate columellate ectexine and granular endexine (Tekleva, 2007). Among modern species *Platanus kerrii* Gagnepain, 1939 is distinct in its smaller pollen size, smooth aperture membrane and unusual reticulum pattern (Denk & Tekleva, 2006). Among fossil species, there are several taxa also with unusual pollen features. For example, *Aquia brookensis* has foveolate-reticulate pollen and *Platananthus hueberi* has coarsely reticulate pollen which are types unknown in other platanoids. A number of fossil taxa (*Archaranthus* (N. Maslova & Kodrul, 2003), *Platananthus scanicus* Friis, Crane & Pedersen (Friis *et al.*, 1988), *P. speirsae* Pigg & Stockey (Pigg & Stockey, 1991), *P. synandrus* (Manchester, 1986), *Bogutchanthus* (N. Maslova *et al.*, 2007)) have a sporopollenin rim along the aperture region. A narrow row of smaller lumina can be observed along the aperture margin in *Platananthus hueberi*; the lumina size decreases gradually towards the apertures in *Hamatia* Pedersen *et al.*, 1994 (Pedersen *et al.*, 1994). For *Hamatia* and *Sarbaya* tricolporate pollen was reported (Pedersen *et al.*, 1994; Krassilov & Shilin, 1995). The occurrence of tricolporoidate pollen was also observed in a few samples of several modern species (Tekleva & N. Maslova, in press). The endexine is mostly two-layered, either differing in structure only in the aperture region (*Aquia*, *Hamatia*, *Platananthus potomacensis*, *P. hueberi*, *P. scanicus*) or also in electron density throughout the pollen (*Archaranthus*, *Chemurnautia* N. Maslova, 2002, *Bogutchanthus*, *Platanus quedlinburgensis*) Pacltova emend. Tschan *et al.*, 2008 (Tschan *et al.*, 2008).

Friis *et al.* (1988) noted that pollen grains of more ancient platanaceous taxa are characterized by smaller sizes. The study of pollen grains adhered to *F. kubaensis* sp. nov. generally confirms this trend, being comparable in size or slightly larger than known Albian species (*Aquia*, *Platananthus potomacensis*, *Hamatia*) and smaller than less ancient taxa (*Sarbaya*, *Quadriplatanus*, etc). Pollen grains adhered to the fruitlets of *F. kubaensis* sp. nov. do not have a sporopollenin rim along colpus margin; pollen grains are characterized by a finely reticulate sculpture and a typically platanaceous endexine. Exine sculpturing of the studied species is similar to that of *Friisicarpus* sp. 1 and sp. 3 (Wang, 2008), *Sarbaya*, *Archaranthus*, *Chemurnautia*, *Platanus neptuni* (Ettingshausen) Bužek *et al.*, 1967 (Friis, 1985; Kvacek & Manchester, 2004), *P. quedlinburgensis*, pollen grains from pollen organs associated with *Platanites hebridicus* Forbes, 1851 (Crane *et al.*, 1988) and modern species of *Platanus*. The analysis of modern and fossil pollen revealed a difference in the ratio of exine layers thickness in platanaceous species. The ratio of the columellae thickness to sexine is 0.3–0.4 in modern species and varies from 0.2 to 0.7 in fossil taxa. The portion of the foot layer in ectexine thickness is smaller in modern species: usually about 0.2–0.3 in modern taxa and 0.4–0.5 in fossil taxa (Denk & Tekleva, 2006). In the studied pollen, the ratio of the columellae to sexine is about 0.46, the portion of the foot layer in the ectexine is 0.37–0.38 as in most fossil species.

Comparison of the pollen adhered to the fruitlets of *F. kubaensis* sp. nov. with known platanaceous species from the Albian and Cenomanian showed that the pollen under study is very similar to those of *Friisicarpus* sp. 1 and sp. 3 (Wang, 2008), the size range is close to Albian *Aquia*, *Platananthus potomacensis* and *Hamatia*, while the exine sculpturing demonstrates a closer resemblance to less ancient taxa (*Sarbaya*, *Archaranthus*, *Chemurnautia*, *Platanus neptuni*, *P. quedlinburgensis*) and modern species of *Platanus*.

Leaves of *Ettingshausenia kubaensis* sp. nov., associated with infructescences of *Friisicarpus kubaensis* sp. nov.—Previous studies showed that in the early evolutionary stages the platanaceous plants were considerably variable in the structure of male reproductive structures, while their female structures were more conservative. Interestingly, the same morphotype of *Friisicarpus* infructescences co-occurred in Cretaceous deposits with staminate inflorescences of *Hamatia*

PLATE 10



Leaf morphology of *Ettingshausenia kubaensis* N. Maslova & Sokolova sp. nov., scale bar 1 cm, 1, 3–7-collection point A, fig. 2-collecting point B.

- | | |
|---|--|
| 1. Specimen 5167/65, fragment of leaf <i>Ettingshausenia kubaensis</i> N. Maslova & Sokolova sp. nov. and infructescence of <i>Friisicarpus kubaensis</i> N. Maslova, Tekleva & Sokolova sp. nov. | 5. Specimen 5167/534, fragment of leaf <i>Ettingshausenia kubaensis</i> N. Maslova & Sokolova sp. nov. and infructescence of <i>Friisicarpus kubaensis</i> N. Maslova, Tekleva & Sokolova sp. nov. |
| 2. Specimen 5167/810. | 6. Holotype 5167/10 and infructescence fragment of <i>Friisicarpus kubaensis</i> N. Maslova, Tekleva & Sokolova sp. nov. |
| 3. Specimen 5167/36. | 7. Specimen 5167/111. |
| 4. Specimen 5167/41. | |

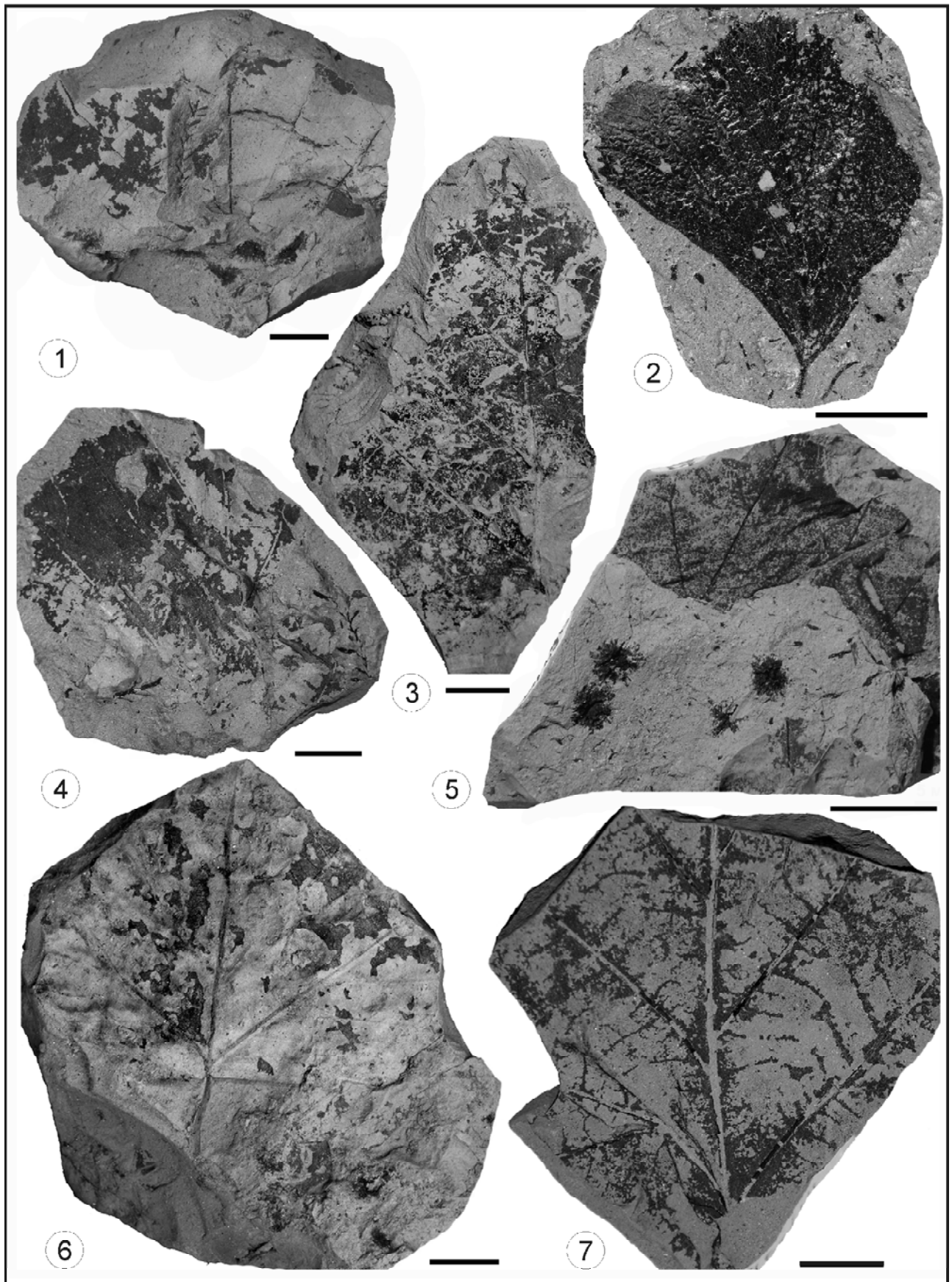


PLATE 10

(Pedersen *et al.*, 1994), *Aquia* (Crane *et al.*, 1993) and *Platananthus* (Friis *et al.*, 1988).

The infructescences of *Friisicarpus* were probably associated with several leaf types. Crane *et al.* (1993) described an association of infructescences of *Friisicarpus brookensis* with leaves of cf. *Sapindopsis variabilis*. The affinity of *Sapindopsis* leaves, *Friisicarpus* infructescences and *Aquia* staminate inflorescences to the same plant species was based on the similar epidermal characters of these fossils, however, only the finely striate cuticle was mentioned as such a character (Crane *et al.*, 1993, Figs 44-46). The absence of any other platanaceous leaves in this locality and co-occurrence of heads and *Sapindopsis* leaves in other floras of the Potomac Group (e.g., West Brouthers flora; Huang & Dilcher, 1987) were claimed as additional support for the association.

Sapindopsis is characterized by pinnate, compound and pinnatifid leaves and for a long time has been considered close to the subclass Rosidae, though some authors have suggested that it could belong to the Platanaceae (Hickey & Doyle, 1977; Crane, 1989). Possible affinities of *Sapindopsis* to the Platanaceae were enhanced by Upchurch (1984), who studied the epidermal morphology of the genus from the Cretaceous of the Potomac Group. He showed that ordinary epidermal cells of the lower leaf surface of *Sapindopsis* are irregularly tetragonal or polygonal, isodiametric or elongated, with almost straight anticlinal walls; stomata are widely oval, slightly sunken, and with four to six (rarely eight) subsidiary cells of various sizes and shapes. The same author placed the stomata of the genus into three groups: paracytic, laterocytic or cyclocytic. Among characters similar to the Platanaceae several features were considered, namely the finely folded cuticle surface, stomata surrounded by cuticle folds, which are perpendicular to their long axis, and the presence of trichomes. Complex trichomes interpreted as secretory cells by Upchurch (1984) and hemispherical glands which are slightly larger than stomata were also described for the genus. The trichomes are developed at the contact of several radially arranged cells and are globose, or flattened and occasionally with cutinized, irregular protuberances and at their bases there are thickened cuticular rings.

Recently a detailed study of epidermal characters of modern *Platanus* species allowed them to be distinguished by their specific features and shed doubt on the assignation of *Sapindopsis* to the Platanaceae (Carpenter *et al.*, 2005).

Leaves of *Sapindopsis* are highly variable as to their margins and outlines (Fontaine, 1889; Hickey & Doyle, 1977). Pinnately compound and pinnately lobate morphotypes with


entire or toothed margins occur. Such leaf types are not characteristic of modern plane tree, though among fossil platanoids such leaf types are known from the Cretaceous (*Erlingdorffia* Johnson, 1996) and Lower Paleogene (*Platanites*, Crane *et al.*, 1988). Some morphotypes with pinnately compound leaves have trilobate terminal leaflets resembling typical leaves of *Platanus* (Hickey & Doyle, 1977). Leaflets of *Sapindopsis* are characterized by an unusual venation in which connivent secondary veins form irregular broken loops and tertiary veins form a complex of meshes unequal in outline and size. Such a venation differs from the opposite percurrent type which is characteristic of the Platanaceae.

Krassilov and Volynets (2008) believe that trilobed leaflets of compound leaves typically occur in the Ranunculaceae rather than in the Platanaceae. Infructescences of *Friisicarpus brookensis*, described by Crane *et al.* (1993) in association with leaves of *Sapindopsis*, are also more probably ranunculoid than platanoid ones according to Krassilov and Volynets (2008). We think that *Friisicarpus brookensis* is a typical representative of the genus *Friisicarpus*, which has characteristic features of the Platanaceae.

This analysis shows that we should be more cautious hypothesizing about the assignment of these leaves and heads to the same plant species. A final solution must wait until much more palaeobotanical evidence is available.

In this study a contemporaneous occurrence of *Friisicarpus kubaensis* sp. nov. and *Platanus*-like leaves, described as *Ettingshausenia kubaensis* sp. nov., is documented. In the locality Kubaev, Golovneva (2004) also lists *Araliopsoides kiensis*, *Sapindopsis kryshstofovichii* and *Platanophyllum simonovskiense* in the Platanaceae. However, these morphotypes only occur in the upper part of the section while infructescences of *Friisicarpus kubaensis* sp. nov. occur in the lower part. Leaves of *Ettingshausenia kubaensis* sp. nov. occur in the lower and upper parts of the section, but similar epidermal characters of both leaves and infructescences can be used as additional evidence that contemporaneity indicates their affinity to the same plant species. We identified leaf remains from the lower and upper parts of the section as belonging to *E. kubaensis* sp. nov. based on their identical morphology and epidermal characters. It should be noted, that leaves of *E. kubaensis* sp. nov. from the upper part of the section are better preserved compared to those from the lower part where leaves are more fragmented. The only leaves of platanoid type in the lower part of the section are those of *E. kubaensis* sp. nov.

PLATE 11

Leaf morphology of *Ettingshausenia kubaensis* N. Maslova & Sokolova sp. nov., scale bar 1 cm, 1-7-collecting point A. 

- | | | | |
|----|---|----|--------------------|
| 1. | Specimen 5167/859. | 4. | Specimen 5167/807. |
| 2. | Specimen 5167/859, enlargement of 1, venation near leaf margin and teeth. | 5. | Specimen 5167/825. |
| 3. | Specimen 5167/516. | 6. | Specimen 5167/600. |
| | | 7. | Specimen 5167/522. |

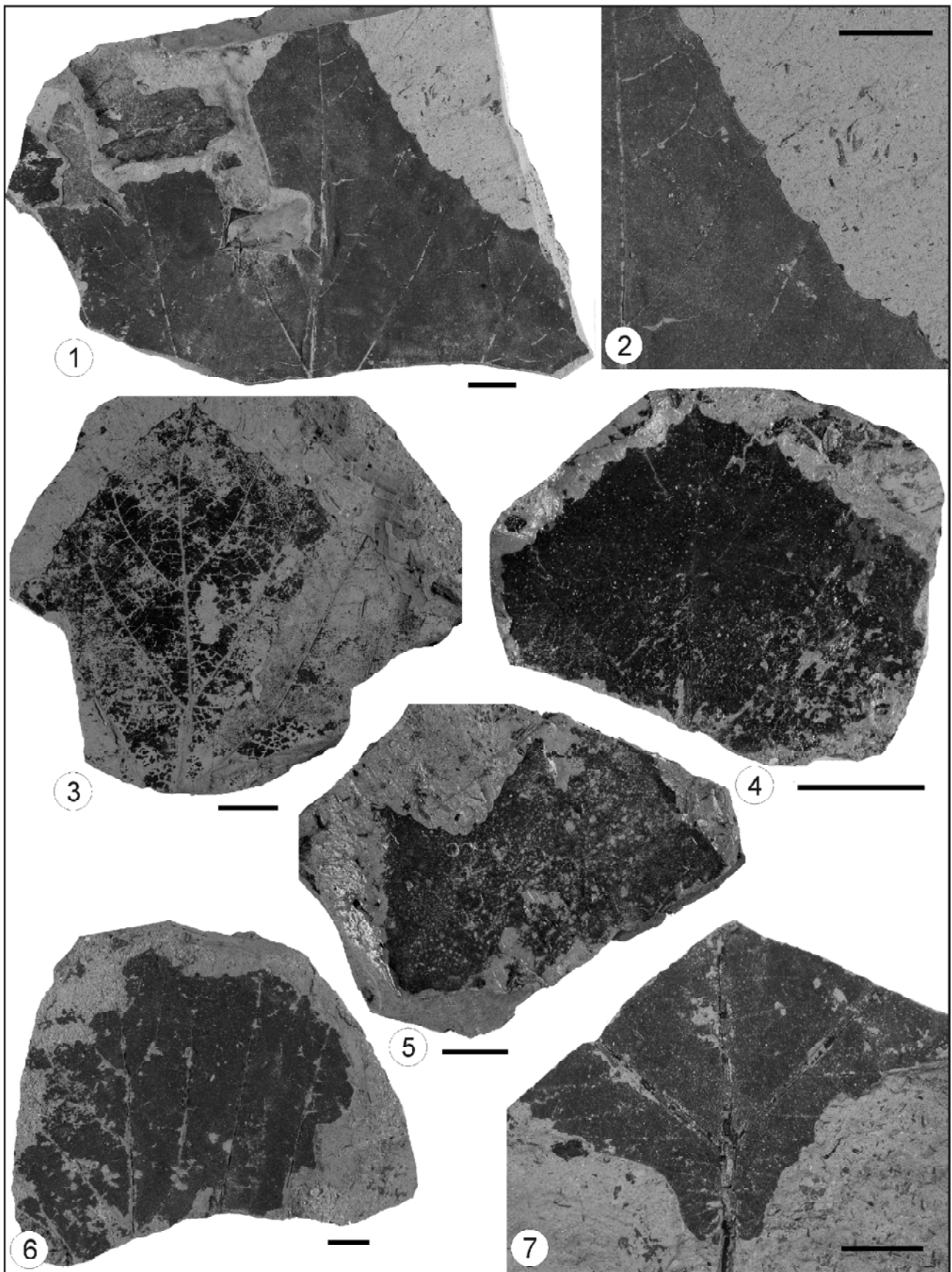


PLATE 11

This is the second find of *Friisicarpus* associating with leaves of similar morphotype in more or less contemporaneous deposits. Earlier N. Maslova and Herman (2006) reported inflorescences of *Friisicarpus* sp. associating with leaves of typical *Platanus* morphotypes from the Cenomanian of Siberia. These inflorescences were represented by imprints as cavities in the rock, duplicating the external sculpture of the head. The heads are about 5 mm in diameter and consist of about 50 pentamerous flowers devoid of stylodes. The carpel apex is more or less uniform, ribbed, without stomata and trichomes, bearing bilobate, triangular, conical expansion. Boundaries between individual *Friisicarpus* sp. flowers are distinct, suggesting that the perianth was rather well-developed and reaches carpel apex. Although these inflorescences and leaves were not found in organic connection, they occur on the same piece of rock very close to each other and show features characteristic of the Platanaceae, suggesting that they belonged to the same plant (N. Maslova & Herman, 2006).

Leaves of a typical modern *Platanus* (subgenus *Platanus*) morphotype were common in the Cretaceous floras of Northern Hemisphere. First finds are dated to the Early Cretaceous. Since the end of the 19th century such leaves are usually determined as *Platanus* in palaeobotanical studies. There is an obvious similarity of such morphotypes with leaves of modern *Platanus* which for a long time had given grounds that the genus appeared early in the palaeontological record. However, several studies discovered that in the past leaves of a typical plane tree appearance might have been associated with reproductive structures different from those of *Platanus* (Krassilov, 1976; N. Maslova & Herman, 2004, 2006; N. Maslova *et al.*, 2005; N. Maslova, 2009). These finds showed that most Cretaceous species of *Platanus* described on the basis of leaf remains should be revised (N. Maslova & Herman, 2004; N. Maslova *et al.*, 2005). Krassilov (1979) proposed to describe dispersed leaf remains of Cretaceous angiosperms using names of a morphological leaf classification, based on observed characters of leaf morphology. N. Maslova *et al.* (2005) propose not to use epidermal characters, which are in any case often unavailable for Cretaceous and Early Paleogene leaves with a typical plane tree appearance, but to use the generic name *Ettingshausenia* Stiehler with type species *E. cuneifolia*. More information on the classification of Cretaceous dispersed

angiosperm leaves in a morphological system is presented in N. Maslova (2010).

Leaves of *Ettingshausenia kubaensis* sp. nov., associated with infructescences of *Friisicarpus kubaensis* sp. nov., are characterized by the possession of typical modern plane tree morphological characters. Cuticle-epidermal characters of *E. kubaensis* sp. nov. are comparable with those of the Platanaceae and we consider that belonging of the infructescences and leaves to the same plant species can be demonstrated by the similarity in their epidermal structure. Both the leaf epidermis and fruitlet epidermis bear anomocytic stomata, the guard cells of which are raised above the general epidermal surface, forming a distinct ring with numerous cuticle folds radiating from them. Two types of trichomes occur with the first mostly near to the veins and with rather strongly cutinized barrel-like bases and elongated apices. Similar structures were observed on the infructescence axes of *Friisicarpus kubaensis* sp. nov. Those of the second type are abundant, domelike and are the most common of all the trichomes, often surrounding stomata. These are similar to those occurring in the epidermis of median and apical parts of fruitlets and on the axes of *F. kubaensis* sp. nov. because of the shape of the apices, considerable cutinized bases with a massive cuticular ring on the inner side of the cuticle and in the number (up to 10) of epidermal cells which surround them.

The function of the trichomes in the epidermis of *E. kubaensis* sp. nov. and *F. kubaensis* sp. nov. is still unclear. Elongated ones might provide mechanical support, for example, or minimize dehydration whereas globular, capitate trichomes can be glandular.

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PLATE 12



Epidermal characters of *Ettingshausenia kubaensis* N. Maslova & Sokolova sp. nov., SEM, 1-4-collection point A, 5-8-collecting point B.

- | | | | |
|----|--|----|---|
| 1. | Specimen 5167/41, cutinized trichome base with radiating folds in epidermis of upper leaf surface, view from outer surface of cuticle. | 5. | Specimen 5167/600, cuticle of upper leaf surface, trichome bases. |
| 2. | Specimen 5167/41, globose trichome with radiating folds in epidermis of outer leaf surface, view from outer surface of cuticle. | 6. | Specimen 5167/522, incrustation of lower leaf surface near vein. |
| 3. | Specimen 5167/10, strongly cutinized trichome base at contact of ten epidermal cells, view from inner surface of cuticle. | 7. | Specimen 5167/522, incrustation of lower leaf surface, stomata and numerous bases of trichomes. |
| 4. | Specimen 5167/10, strongly cutinized trichome base at con- | 8. | Specimen 5167/600, incrustation of lower leaf surface, stomata and numerous bases of trichomes. |

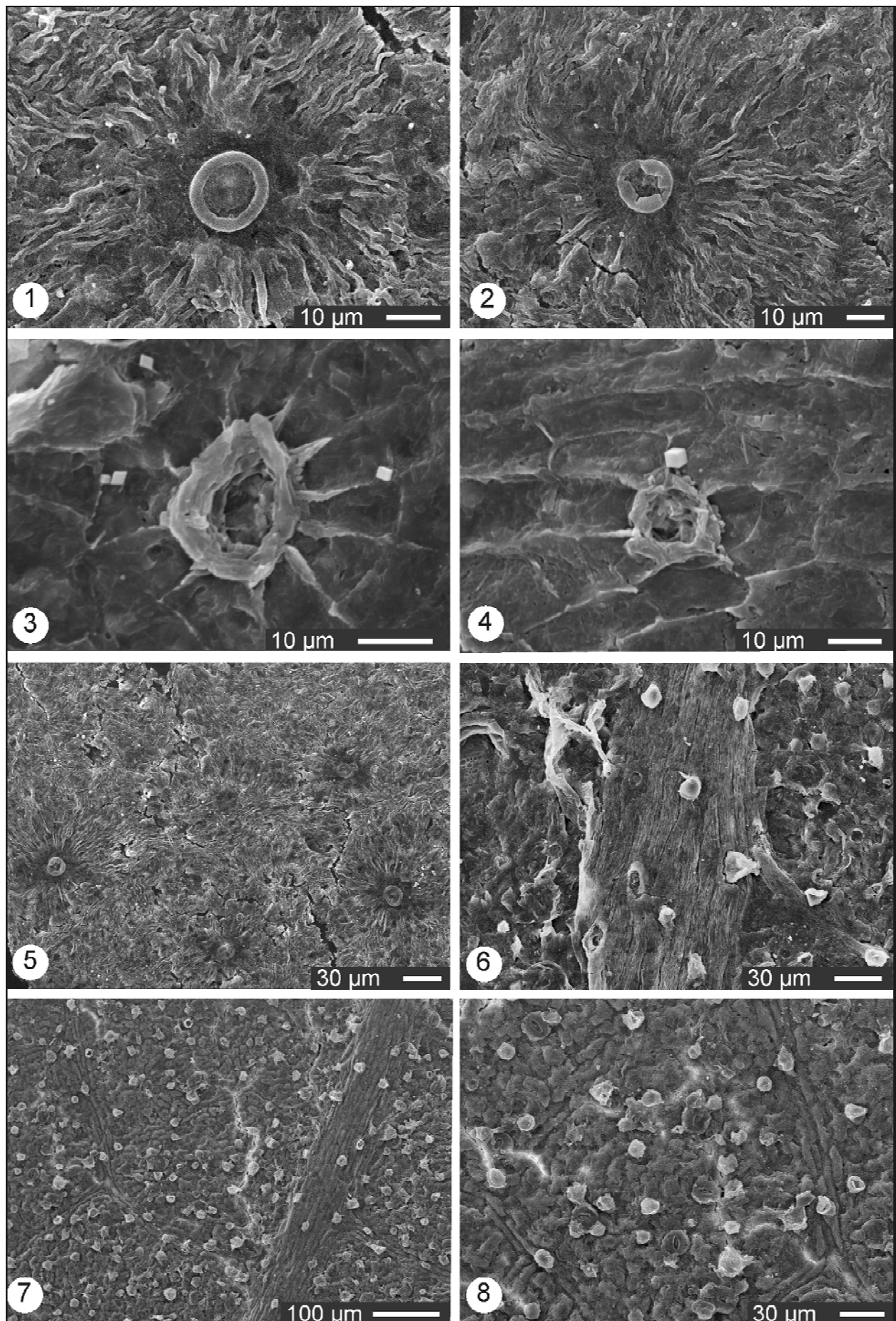


PLATE 12

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PLATE 13



Epidermal characters of *Ettingshausenia kubaensis* N. Maslova & Sokolova sp. nov., SEM, 1-5, 7-collection point A, 6, 8-collecting point B.

1. Specimen 5167/10, epidermal cells of upper leaf surface near midrib.
- 2, 4. Specimen 5167/10, cuticle of lower leaf surface, stomata and trichome bases.
3. Specimen 5167/10, epidermal cells of upper leaf surface in the central region of leaf lamina.
5. Specimen 5167/10, epidermal cells of upper leaf surface near margin.
6. Specimen 5167/807, epidermal cells of lower leaf surface with sinuous anticlinal and finely striate periclinal walls.
7. Specimen 5167/10, epidermal cells of costal zone, view from inside.
8. Specimen 5167/807, strongly cutinized trichome base, view from inner cuticle side.

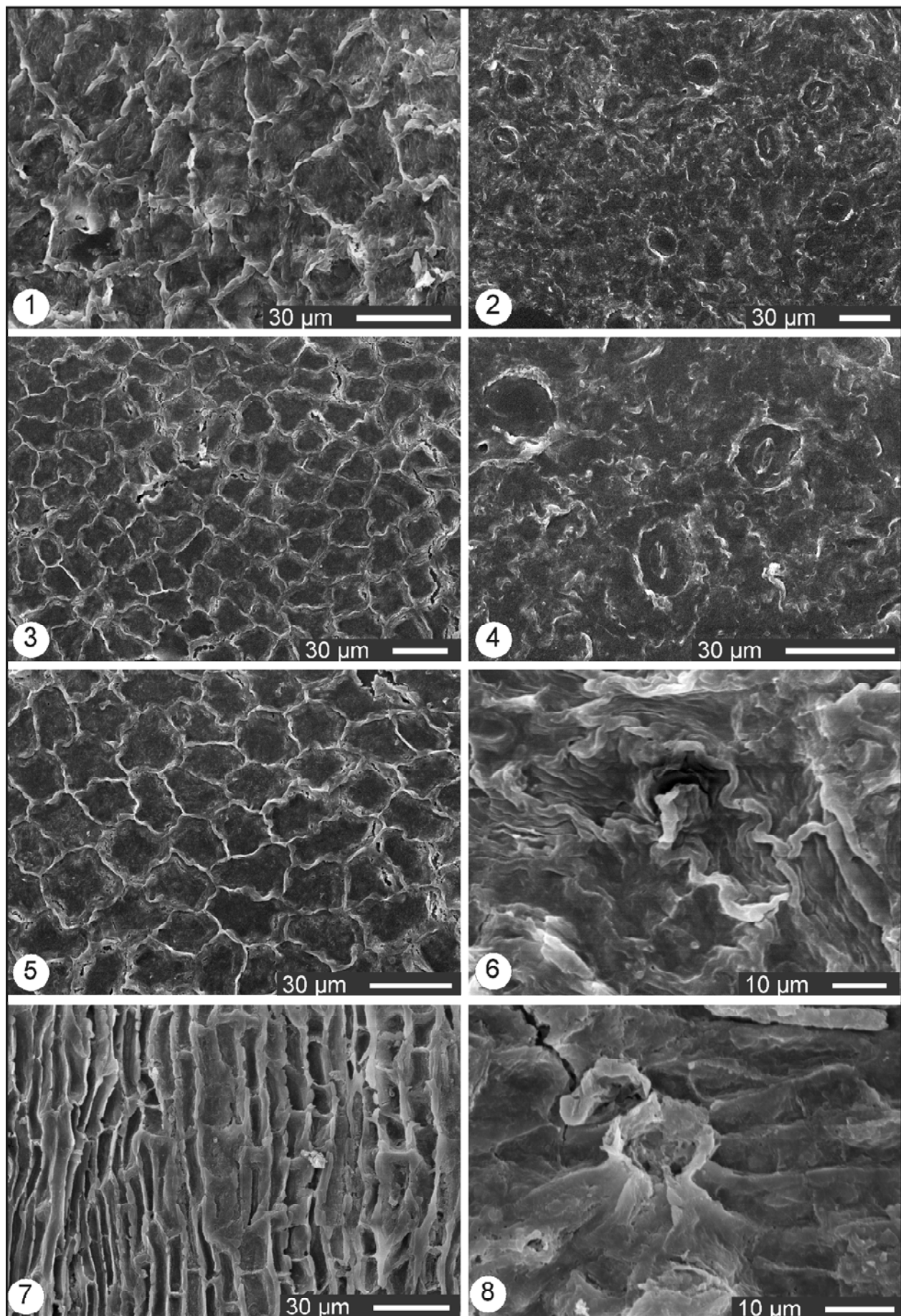


PLATE 13

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