



Research paper

Krassilovianthus gen. nov., a new staminate inflorescence with similarities to Platanaceae and Hamamelidaceae from the Cenomanian–Turonian of western Kazakhstan

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ABSTRACT

Staminate inflorescences from Cenomanian–Turonian deposits of the Sarbay locality of western Kazakhstan are described as *Krassilovianthus* gen. nov. The new genus is characterized by the unique structure of the flower, which is unknown in similar platanoid heads. Flowers of *Krassilovianthus* gen. nov. possess a perianth that is considerably longer than its two stamens. The stamens are bisporangiate and dithecate, with small tricolporate pollen grains. Platanoid reproductive organs and leaves found at the Sarbay locality are considered.

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1. Introduction

Palaeobotanical studies dealing with fossil capitate inflorescences and infructescences have revealed that they are similar in general morphology, but show considerable variability in their microstructure (Manchester, 1986; Crane et al., 1988; Friis et al., 1988; Pigg and Stockey, 1991; Crepet et al., 1992; Crane et al., 1993; Pedersen et al., 1994; Krassilov and Shilin, 1995; Crepet and Nixon, 1996; Magallón-Puebla et al., 1997; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a,b; Zhou et al., 2001; Maslova, 2002; Maslova and Kodrul, 2003; Maslova and Herman, 2004; Maslova et al., 2005; Maslova and Herman, 2006; Mindell et al., 2006; Maslova et al., 2007; Tschan et al., 2008; Wang, 2008; Maslova, 2009; Wang et al., 2011). These heads exhibit characters of extant Platanaceae and Hamamelidaceae; moreover, some of them combine characters of the two families. Maslova (2010) developed a new system for fossil platanoids and hamamelids, which includes both extinct families and those that have survived until the present. We believe that members of extinct families (Bogutchanthaceae, Sarbaicarpaceae and Kasicarpaceae) co-existed in the Cretaceous with the earliest members of the extant families Platanaceae and Hamamelidaceae.

Takhtajan (1966, 1987) and Cronquist (1981) considered Platanaceae and Hamamelidaceae within the order Hamamelidales. Recent molecular phylogenies abolished the order Hamamelidales and placed Platanaceae and Hamamelidaceae within the orders Proteales and Saxifragales respectively (APG, 2003 and others). Here, we are not discussing contradictions between traditional and molecular systems, since it is out of the scope of the present paper. We think that the traditional concept is in better agreement with available palaeobotanical data, which suggest relations between the two families (e.g., Maslova, 2010 and cited therein). *Krassilovianthus* gen. nov. shows features characteristic for both Platanaceae and Hamamelidaceae, and we think it should be considered within the order Hamamelidales sensu Takhtajan (1987) and Cronquist (1981). By showing an eclectic combination of platanaceous and hamamelidaceous characters, *Krassilovianthus* gen. nov. extends our knowledge on diversity of fossil capitate reproductive structures. Due to its unique combination of characters we describe *Krassilovianthus* gen. nov. without referring it to any family until additional palaeobotanical data become available.

2. Material and methods

Structurally preserved inflorescences come from grey clays of the Sarbay locality, near Rudnyi city (western Kazakhstan). Fossil plants were collected and partly identified by Shilin (1986), who considered the age of the locality to be Cenomanian–Turonian based on the floristic analysis. The age has been also supported by palynological data (Levina

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et al., 1990). Shilin recognized *Asplenium dicksonianum* Heer, *Gleichenia* sp., *Sphenopteris* sp., *Sequoia heterophylla* Velenovsky, *Cedrus* sp., *Platanus pseudoguillelmae* Krassilov, *P. cuneiformis* Krassilov, *Dalbergites simplex* (Newberry) Seward and *Ilex* sp. Frumin and Friis (1996, 1999) reported members of the Ranunculales, Urticales, Rosales, Myrtales, Celastrales, Platanaceae, Illiciaceae and Magnoliaceae from the flora.

Four inflorescences were studied. Photos of the inflorescences were taken using a Leica M165 stereomicroscope equipped with a Leica DFC420 digital camera. The general morphology of the inflorescences was studied by a CamScan scanning electron microscope (SEM) after cleaning flowers with hydrofluoric acid. Some fragments of the inflorescences were macerated with Schulze's solution and alkali and then observed with a CamScan SEM.

For anatomical examination the inflorescences were cleaned with hydrofluoric acid, then gradually dehydrated and embedded in Kulzer's Technovit 2100 (2-hydroxyethyl methacrylate) as described in Igersheim and Cichocki (1996). The embedded material was serially sectioned at 6–10 µm with a rotary microtome. Sections were mounted unstained in BioMount mounting medium. Sections were examined under a Carl Zeiss Axioplan-2 bright field light photomicroscope (LM). Digital photomicrographs of sections were taken using a Leica DFC420 camera.

Individual pollen grains and fragments of microsporangia were studied and photographed with the same LM and CamScan SEM at Borissiak Paleontological Institute (PIN) and CamScan and JSM SEMs and Jeol 100 B and Jeol 1011 transmission electron microscopes (TEMs) at Lomonosov Moscow State University. Standard methods for TEM studies were followed after Meyer-Melikyan et al. (2004). Ultrathin sections were made with an LKB Ultratome V and stained after Reynolds (1963).

Collections # 417, 419 are housed at the Institute of Botany and Plant Introduction of the Committee of Science and Education of the Republic of Kazakhstan, Almaty, Kazakhstan.

3. Systematic descriptions

Phylum Magnoliophyta

Order and Family Incertae Sedis

Genus *Krassilovianthus* N. Maslova, Tekleva et Remizowa, gen. nov.

Etimology: in honour of the palaeobotanist Professor Valentin Krassilov.

Type species: *Krassilovianthus sarbaensis* N. Maslova, Tekleva et Remizowa, gen. et sp. nov.

Diagnosis: Sessile staminate heads with numerous flowers per head. Flower with a well-developed perianth, exceeding stamen length. Androecium consists of two sessile stamens. Anthers bisporangiate and

dithecate. Pollen sacs narrow, elongated. Connective indistinguishable. Epidermis of pollen sac apices bears stomata and rare trichome bases. Pollen small, tricolporate, finely reticulate. Lumina forming labyrinthine pattern. Aperture membrane granular.

Krassilovianthus sarbaensis N. Maslova, Tekleva et Remizowa, gen. et sp. nov.

Plate I, 1–8; **Plate II**, 1–6; **Plate III**, 1–11; **Plate IV**, 1–6; **Plate V**, 1–6; **Plate VI**, 1–6; **Plate VII** – 1–10.

Etimology: From the Sarbay locality.

Holotype: # 417/101; Borissiak Paleontological Institute RAS, (Pl. I, 4), designed here.

Diagnosis: Sessile staminate heads 2–3 mm in diameter. Up to 40 flowers per head. Perianth well-developed, exceeding stamen length. Epidermis of outer and inner perianth elements differs. Flowers with two stamens. Stamen filaments lacking. Anthers bisporangiate and dithecate. Pollen sacs narrow, elongated, with almost parallel margins, occasionally confluent basally, but free for most of their length. Connective indistinguishable. Epidermis of pollen sac apices bears stomata and rare trichome bases. Pollen small, tricolporate and finely reticulate. Lumina varying in shape and size and forming labyrinthine pattern. Colpi length about 2/3 of polar axis; aperture membrane granular.

Type locality: Western Kazakhstan, Sarbay locality, near Rudnyi city.

Stratigraphic position: Zhirkindekskaya Formation.

Age: Cenomanian–Turonian.

Description: The staminate inflorescence consists of a rather massive longitudinally striate axis about 1 mm in diameter with heads of 2.5–3.0 mm in diameter (**Plate I**, 1, 2). Parenchyma cells of the axis are rectangular, 40–60 µm long and 10–20 µm wide; the cell walls with small rounded pits (**Plate I**, 7, 8). Only fragmentary inflorescences were found. Each fragment bears only a single head and the number of heads per axis is unknown. Heads are rather loose, with the central core of about 1 mm in diameter and up to 40 flowers per head.

The flower microstructure was studied with the help of SEM and also in anatomical sections in transmitted light. The flowers are about 850 µm long and 350–560 µm wide, with two stamens (**Plate I**, 5, 6; **Plate III**, 1–5; **Plate VI**, 1, 2). The perianth is longer than the stamens; however, in most cases the apices of perianth elements were broken during fossilisation due to their fragility and loose arrangement (**Plate I**, 4, 5; **Plate V**, 2; **Plate VI**, 1, 2).

Two types of perianth elements were revealed. The epidermis of the outer perianth elements differs in the basal and apical parts of the elements (**Plate II**, 2). Basally, it consists of strongly elongated cells arranged in longitudinal rows (**Plate II**, 3), whereas apically the cells vary in shape and size from rectangular and spindle-shaped to triangular and polygonal (**Plate II**, 4). The walls of epidermal cells of the outer perianth

Plate I. *Krassilovianthus sarbaensis* gen. et sp. nov. 1–3 – under reflected light, 4–8 – SEM.

1. Inflorescence architecture. Macerated 3-D preserved inflorescence. Specimen no. 417/106.
2. Inflorescence architecture. Macerated 3-D preserved inflorescence. Specimen no. 417/102.
3. Fragment of the inflorescence in the rock. Specimen no. 417/103.
4. Inflorescence architecture. Holotype no. 417/101.
5. Flower, two stamens (white arrows) and perianth (black arrows) are visible. Holotype no. 417/101.
6. Flower, perianth elements (black arrows), pollen sacs (white arrows). Specimen no. 417/102.
- 7, 8. Fragment of inflorescence axis, cells walls of the ordinary parenchyma with round pores are seen. Specimen no. 417/102.

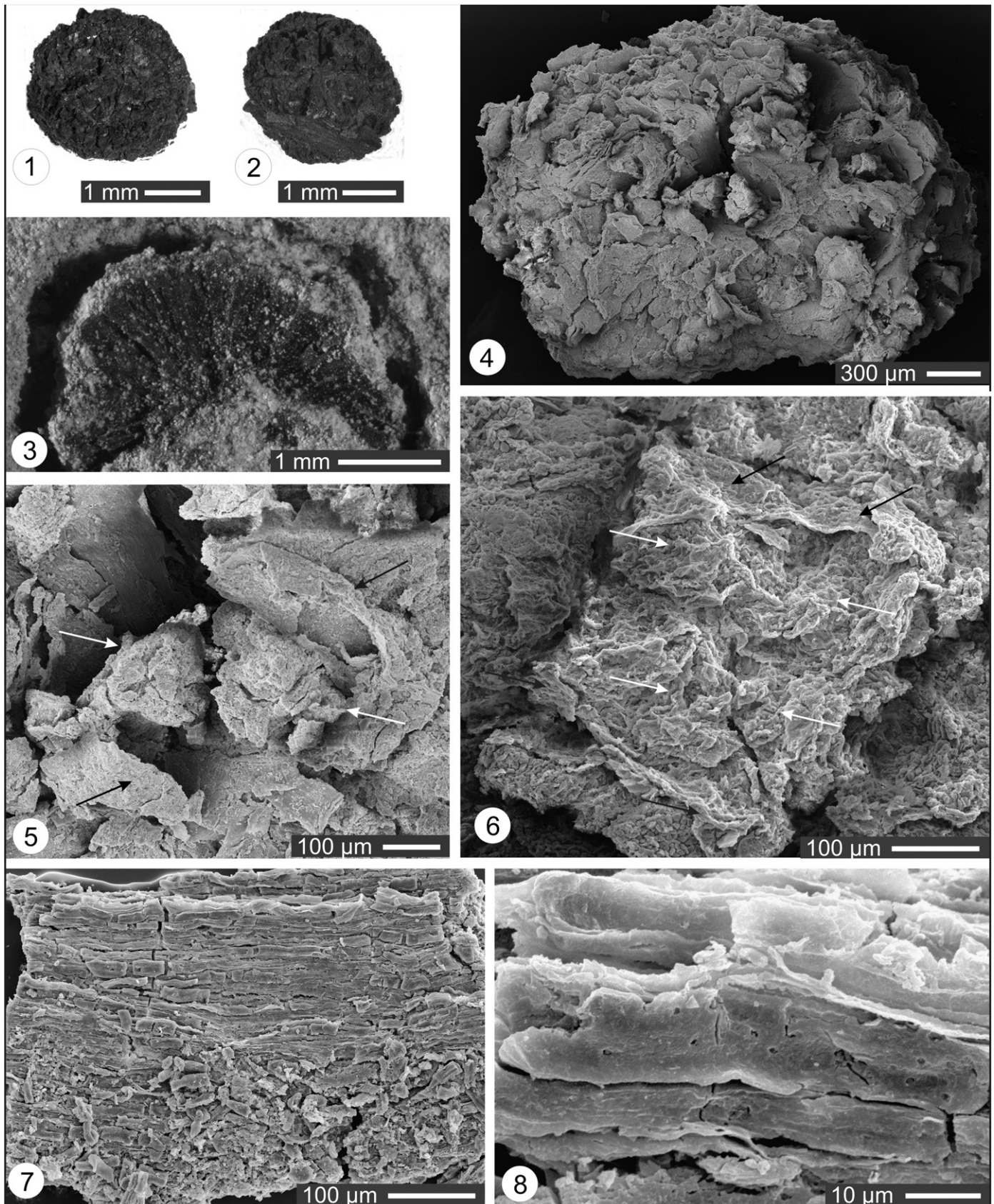
Plate II. *Krassilovianthus sarbaensis* gen. et sp. nov., specimen no. 417/102, SEM. 1–4. Outer perianth elements: 1, 3 – non-macerated cuticle, 2, 4 – macerated cuticle; 1–3 – view from the outside, 4 – view from the inside.

1. Outer perianth element in apical part of flower.
2. Cuticle of outer perianth element, view from the outside.
3. Outer perianth element in basal part of flower.
4. Cuticle of apical part of outer perianth element, view from the inside.
5. Basal part of inner perianth element.
6. Apical part of inner perianth element.

elements are strongly cutinised. At the apices, the anticlinal walls of the epidermal cells bear small cuticular folds, which are oriented in parallel to the long axis of the cell (Plate II, 1). The inner perianth elements have a thinner cuticle. Since the epidermal cells are weakly cutinised,

the shape of the cells is often unclear. In places, rectangular elongated cells are distinguishable (Plate II, 5, 6).

The androecium includes two sessile stamens. The anthers are bisporangiate and dithecate, basally attached. The pollen sacs are



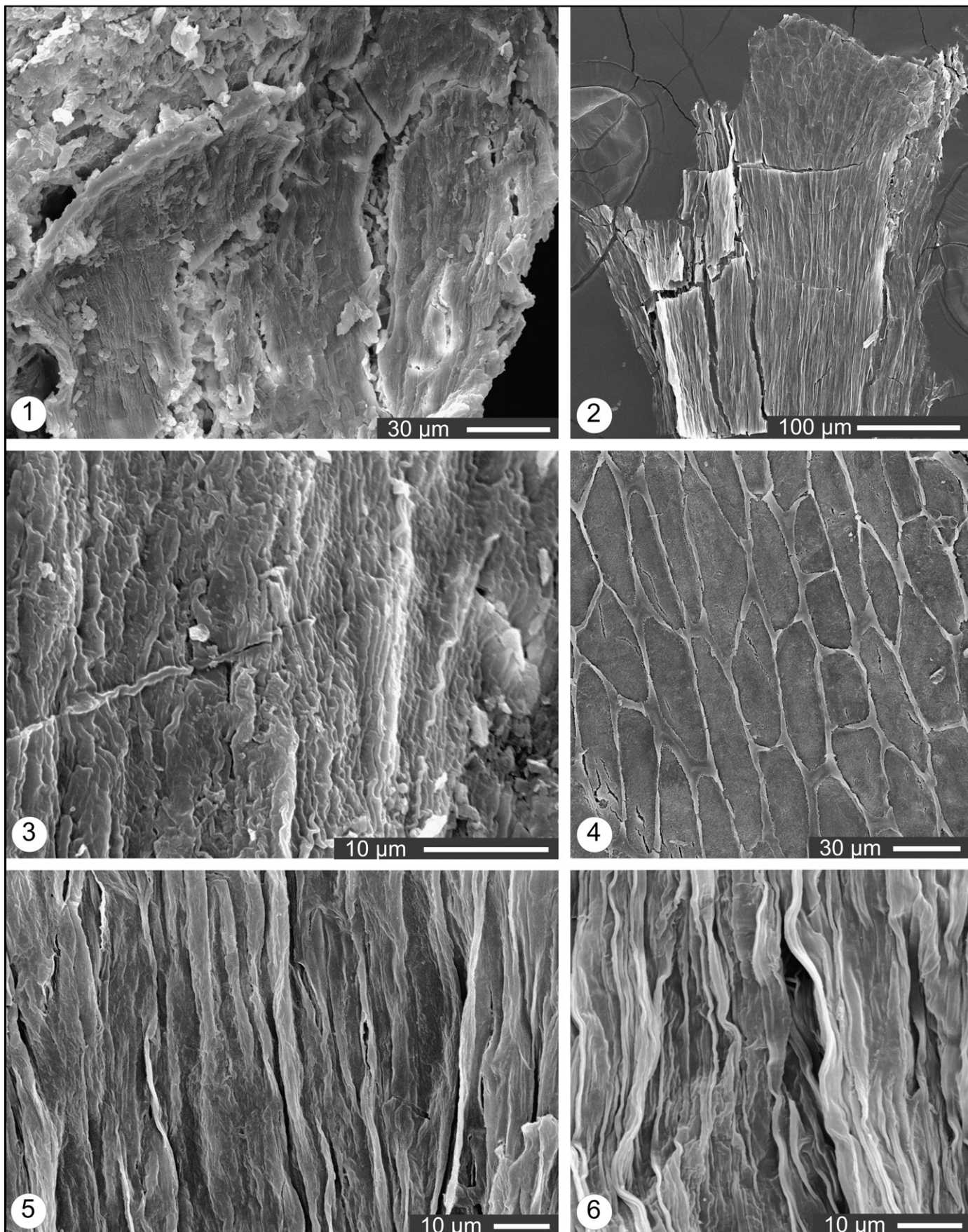


Plate II (caption on page 2).

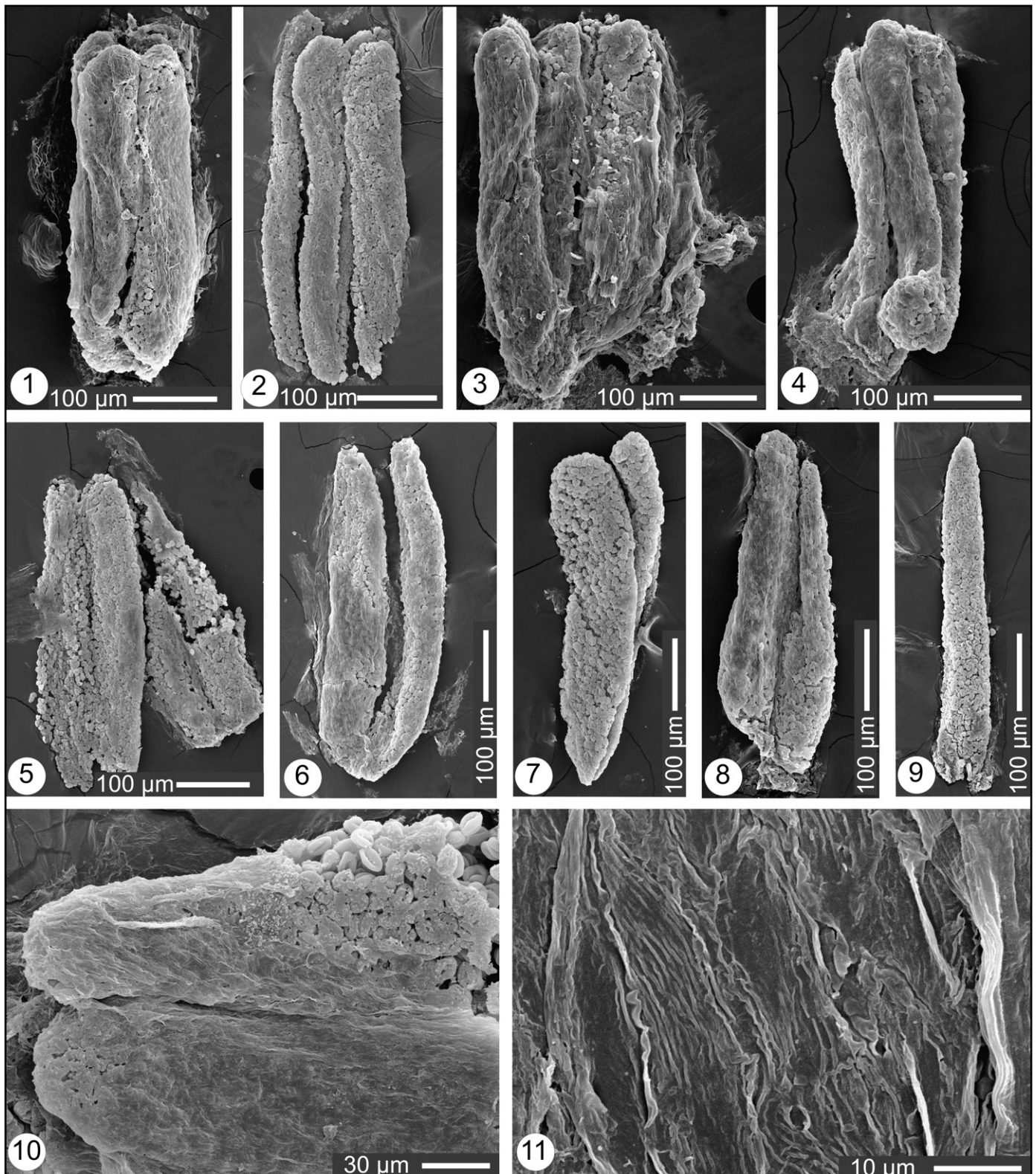


Plate III. *Krassilovianthus sarbaensis* gen. et sp. nov., specimen no. 417/102, SEM.

- 1–4. Macerated androecium, four pollen sacs are visible.
5. Two stamens of one flower.
6. Two basally confluent pollen sacs.
- 7, 8. Two pollen sacs.
9. Isolated pollen sac.
10. Apices of two pollen sacs.
11. Cuticle of central part of pollen sac, view from the outside.

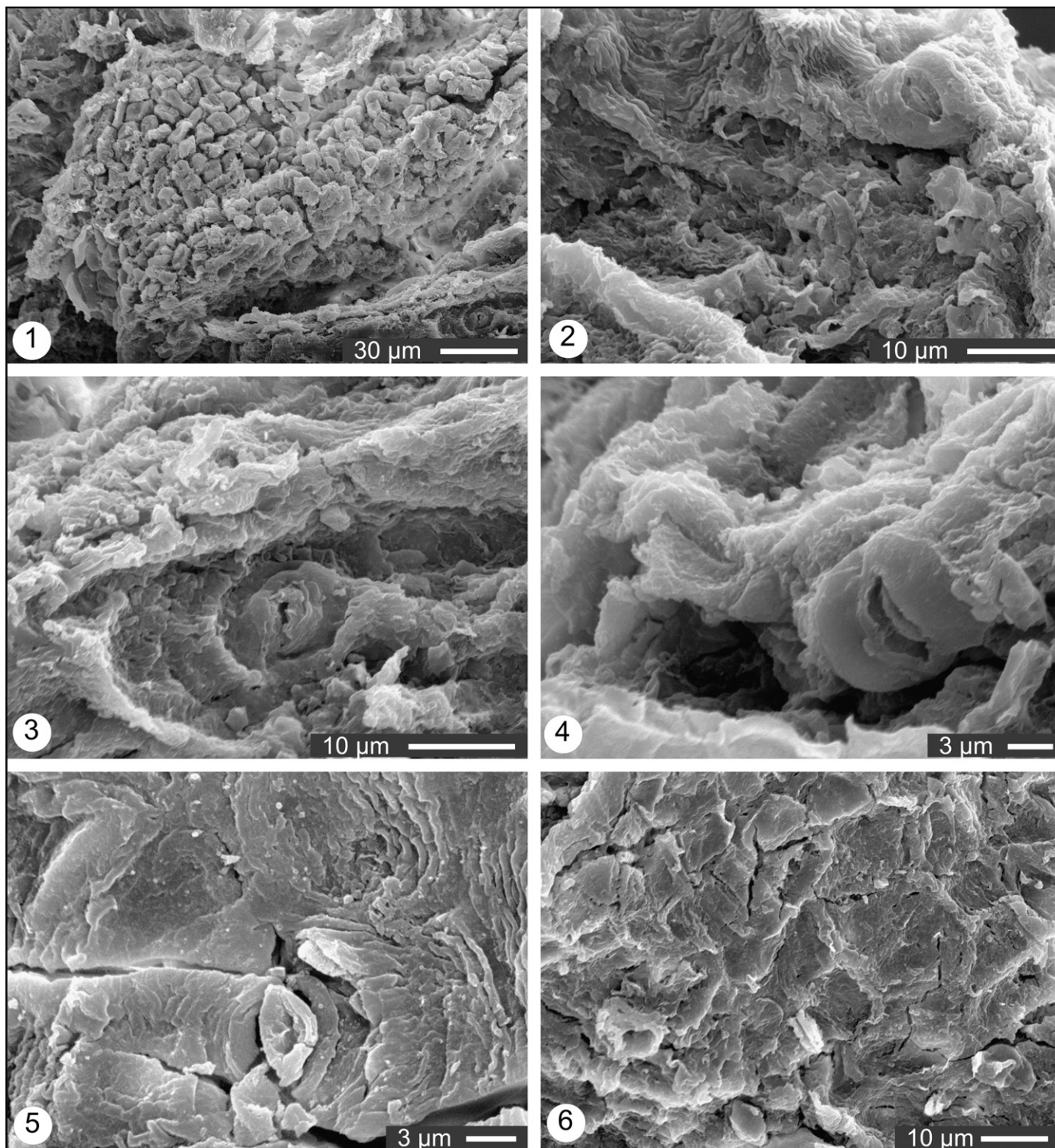


Plate IV. *Krassilovianthus sarbaensis* gen. et sp. nov., specimen no. 417/102, SEM.

1. Fragment of the surface of pollen sac apex, epidermis is removed to show cells of endothecium.
2. Fragment of preserved epidermis of pollen sac apex; finely striate cuticle and stoma seen.
3. Stomata in epidermis of pollen sac apex, smaller specialized subsidiary cells forming a ring with transverse cuticle folds.
- 4, 5. Stomata in epidermis of pollen sac apex.
6. Epidermis of pollen sac apex, square ordinary cells and trichomes with broken apices.

narrowly spindle-shaped with parallel margins and slightly pointed tips. They are free along the most their length, but often confluent in the basal part. Occasionally, the pollen sacs vary in size within the anther (Plate III, 5–10). The connective is indistinguishable. Transverse sections show no connective tissue between the thecae along the

whole length of the stamen. During the androecium maceration, no other cuticles, besides those of the pollen sac, were found. In transverse sections, the outlines of the pollen sacs vary from rounded (Plate VI, 6) to oval (Plate V, 3–6; Plate VI, 3, 4) and triangular (Plate V, 3, 4). The cuticle of the pollen sacs is finely striate; the folds are parallel to the

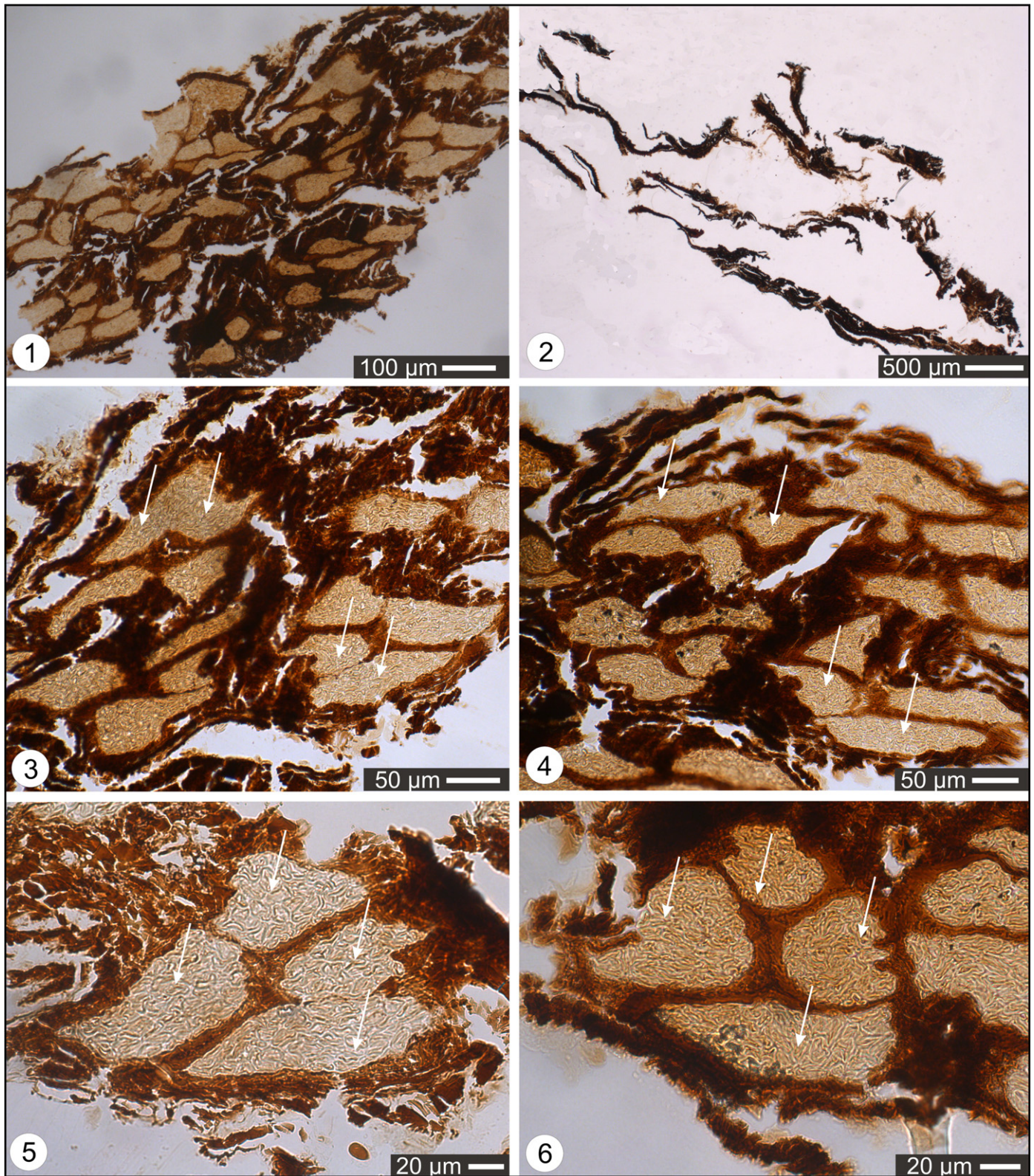


Plate V. *Krassilovianthus sarbaensis* gen. et sp. nov., transverse sections of inflorescence fragment. Specimen no. 417/106. LM

1. Section of flower, bases.
2. Section of flower apices, only perianth elements are visible, the androecium is below the section level.
3. Section of flower bases, arrows indicate basally confluent pollen sacs.
4. Section of central part of flowers (the same fragment as in Fig. 3), arrows indicate almost free pollen sacs.
5. Section of central part of flower, pollen sacs (arrows) of stamens are not so far separated.
6. Section of apical part of flower, free pollen sacs (arrows), хорошо виден фиброзный слой.

long axis of the sac (Plate III, 11). The cuticle of the pollen sac tips is preserved fragmentarily, only endothecium cells are present here (Plate IV, 1). Preserved cuticle fragments show ordinary epidermal cells that are square in the apical part of the pollen sacs, from 10 to 20 μm , with a finely striate outer periclinal wall (Plate IV, 5, 6). There are stomata about 10 μm long (Plate IV, 2–5) and trichomes. The stomatal type was not determined, but the subsidiary cells are narrower than ordinary epidermal cells, about 5 μm wide, rather strongly cutinized with cuticle folds situated perpendicular to the stoma axis (Plate IV, 3). Trichomes are about 8 μm in diameter (Plate IV, 6), with broken apices. Preserved trichome fragments reach 5 μm in length. Endothecium cells with thickened walls are clearly seen in sections (Plate VI, 3, 5, 6).

Pollen grains are small, with the polar axis of 13.3 (12.0–14.6) μm and equatorial diameter of 10.3 (8.0–12.3) μm , tricolporate; ora are not always clearly seen (Plate VII, 1–4). The sculpture is finely reticulate with lumina varying in shape and size, occasionally elongated, curved or slit-like, from small to rather large (probably resulting from open-ended lumina); this is especially well seen in the meso- and apocolpium regions (Plate VII, 2–7). A combination of small and large lumina results in a labyrinthine pattern (Plate VII, 3, 7). The difference in lumina size is almost indistinct near the aperture margin where the lumina are very small and almost fused in a continuous rim in some pollen grains or not fused in others. The colp length is about 2/3 of the polar axis. The aperture membrane is granular (Plate VII, 3, 5, 6).

The exine is semitectate; the ectexine is less electron dense than the endexine (Plate VII, 8–10). The non-apertural ectexine is 0.94 (0.67–1.08) μm thick with the tectum 0.29 (0.24–0.35) μm thick, columellae 0.24 (0.2–0.33) μm high and 0.1 (0.08–0.13) μm wide, and the foot layer 0.43 (0.35–0.48) μm thick (Plate VII, 8, 9). The endexine is two-layered with the layers separating from each other, especially in the aperture region (Plate VII, 8, 10). The outer endexine layer is almost homogeneous, being 0.06 (0.03–0.08) μm thick in the non-aperture region and becoming thinner in the aperture region. It tightly adjoins the ectexine throughout the pollen perimeter. The inner endexine layer is granular, 0.18 (0.15–0.2) μm thick in the non-aperture region; it separates from the outer endexine layer and may slightly thicken towards the aperture region. Orbicules occur.

Comparison: The new genus shows a unique combination of characters. *Krassilovianthus* shares with extant *Platanus* L. the general architecture of the capitate inflorescence, fibrous endothecium, and tricolporate pollen. Also the two genera are similar in the reduction of the stamen filament. Anthers are sessile in *Krassilovianthus*, while *Platanus* possesses a short stamen filament. The listed characters occur in some other fossil platanoids with a well-developed perianth. The late Paleocene–early Eocene *Chemurnautia* N. Maslova is similar to the new genus in having rather loosely arranged pollen sacs, partly confluent at the base, and a well-developed fibrous layer, and in lacking a pronounced apical extension of the connective (Maslova, 2002). However, flowers in the inflorescence of *Chemurnautia* are packed less tightly, the perianth is almost lacking and the pollen grains differ being tricolpate (not tricolporate) with a different reticulum pattern.

Krassilovianthus differs from all species of Platanaceae by the floral structure. The perianth of *Krassilovianthus* is considerably longer than the androecium, which consists of two bisporangiate and dithecate stamens with free pollen sacs, so the connective is indistinguishable. A well-developed perianth has been described in the extinct subfamily Gynoplatananthoideae (Platanaceae). However, in Gynoplatananthoideae,

the perianth elements do not exceed the androecium or gynoecium length. Stamens of Platanaceae are exclusively tetrasporangiate and bisporangiate anthers have not been reported so far.

The loose flower arrangement in the head, bisporangiate stamens and perianth differentiated into outer and inner elements with different epidermal structure make the new genus comparable to the Paleocene *Bogutchanthus* N. Maslova, Kodrul et Tekleva (Maslova et al., 2007) of the family Bogutchanthaceae (Hamamelidales). However, in *Bogutchanthus* the perianth reaches only half of the androecium length, the androecium consists of both fertile stamens that possess well-developed connective with a slight apical extension and staminodes, the anthers differ in shape and size and produce pantocolpate pollen.

The similarities between the new genus and extant and fossil members of the Hamamelidaceae concern the general architecture of the capitate inflorescences, well-developed perianth, bisporangiate stamens with dithecate anthers, basally confluent pollen sacs and tricolporate pollen. Among extant Hamamelidaceae, capitate inflorescences with comparable macromorphology are known in the subfamily Altingioideae and in the genus *Exbucklandia* R. Brown (Exbucklandioideae) of the Exbucklandioideae (Kaul and Kapil, 1974; Bogle, 1986). Fossil capitate inflorescences referred to the Hamamelidaceae are also known (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a,b; Zhou et al., 2001). The majority of extant Hamamelidaceae possess tetrasporangiate stamens; unilocular thecae are described only in stamens of *Hamamelis* L. (Hamamelidoideae) (Schoemaker, 1905; Mione and Bogle, 1990) and *Exbucklandia* (Kaul and Kapil, 1974). Similarly to *Krassilovianthus*, *Parrotia* C.A. Mey and *Fothergilla* have pollen sacs that are confluent basally; however, the androecium in these two genera is partly fused with perianth elements (Bogle, 1970). In fossil Hamamelidaceae, bisporangiate stamens are known in the Hamamelidoideae. The late Santonian *Androdecidua* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla et al., 2001) possesses bisporangiate stamens in the outer whorl and tetrasporangiate stamens in the inner whorl. Bisporangiate stamens have been observed in *Archamamelis* Endress et Friis from the Santonian–Campanian of Sweden (Endress and Friis, 1991). The Cretaceous genera *Archamamelis* (Endress and Friis, 1991) and *Androdecidua* (Magallón-Puebla et al., 2001) are represented by detached flowers; there are no data on the architecture of their inflorescences.

In sum, the extant genus *Exbucklandia* shows the greatest similarity to the new genus (capitate inflorescences and bisporangiate stamens), but differs in having crescent-shaped pollen sacs and pantocolpate pollen.

4. Discussion

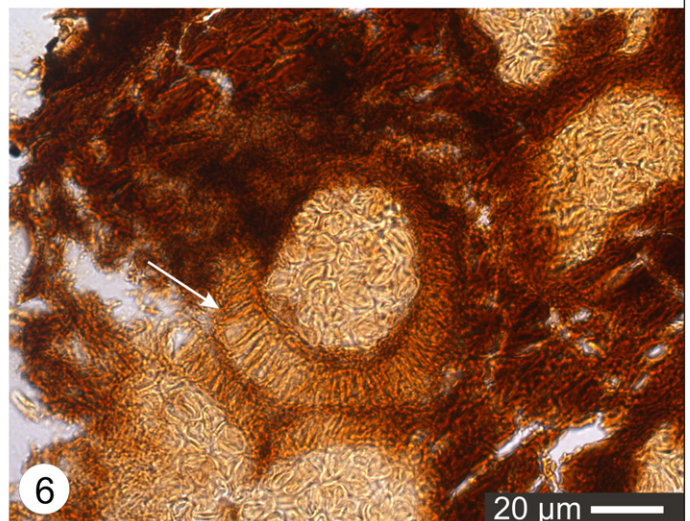
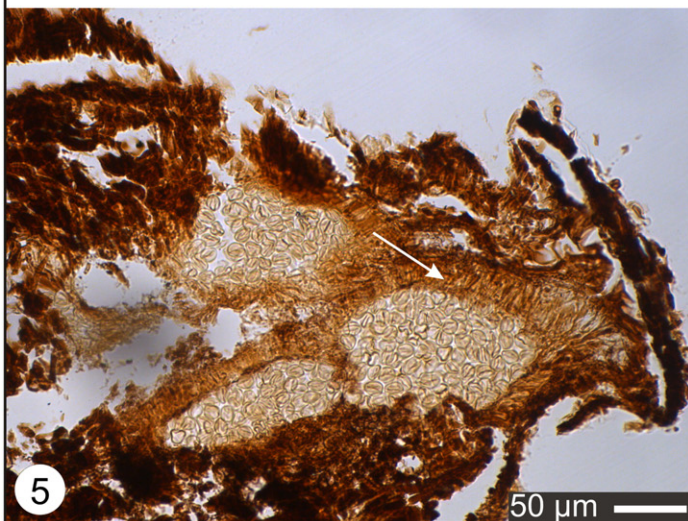
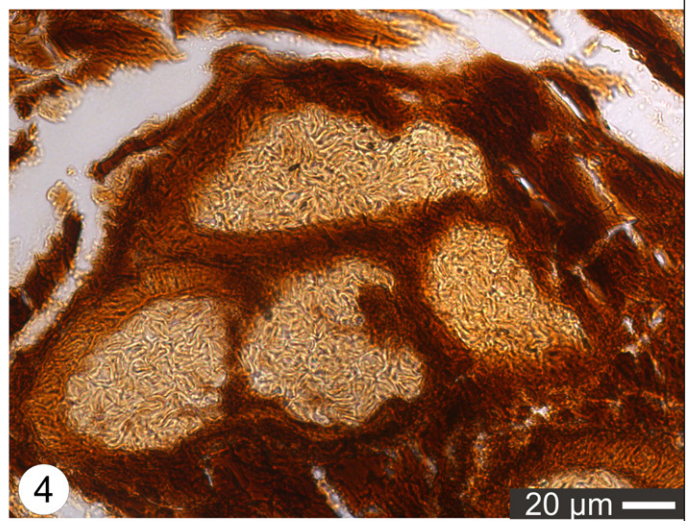
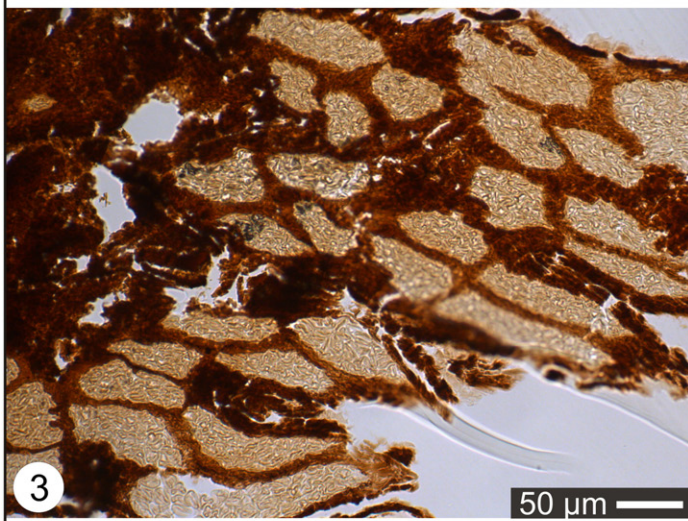
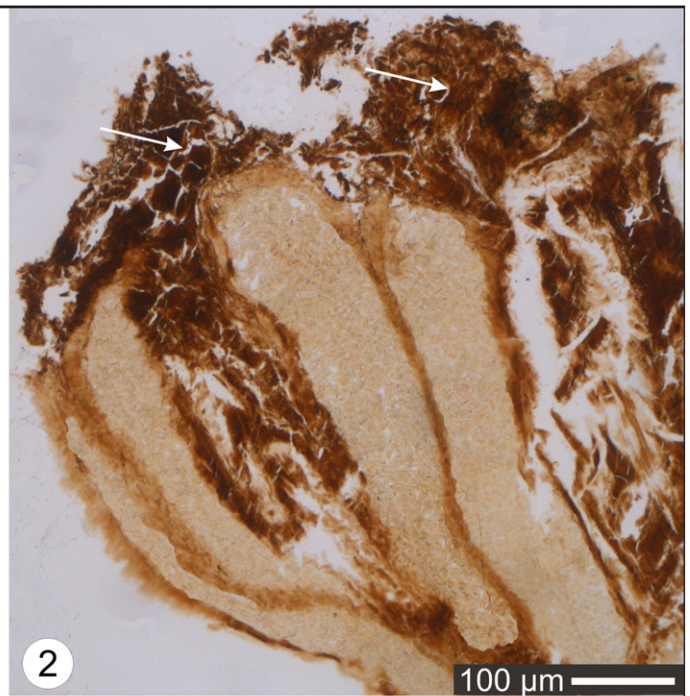
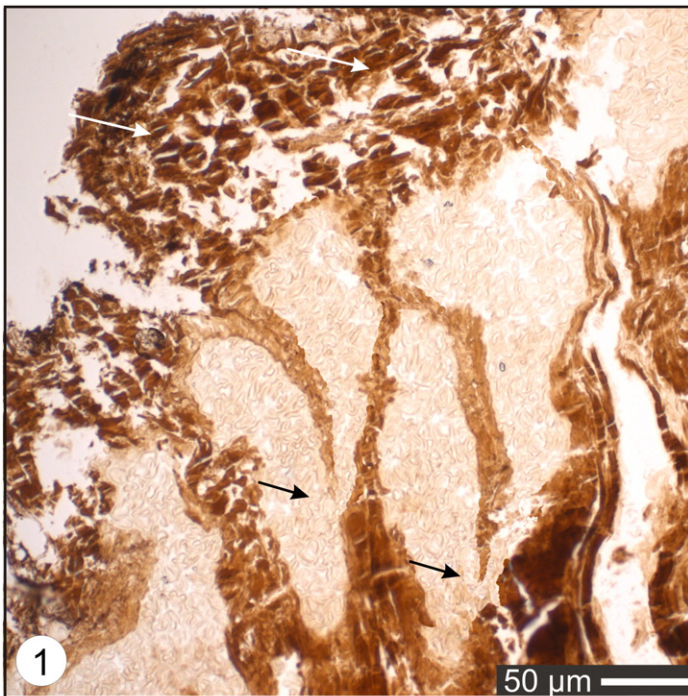
4.1. Inflorescence architecture

Inflorescences of *Krassilovianthus* are axes with sessile heads. Number of heads per axis cannot be determined as there are only detached heads. The majority of the Platanaceae are characterized by sessile heads. Among fossil staminate inflorescences, pedunculate heads are known in Cretaceous *Platananthus scanicus* Friis, Crane et Pedersen (Friis et al., 1988) and *P. speirsae* Pigg et Stockey (Pigg and Stockey, 1991) and in *Archaranthus krassilovii* N. Maslova et Kodrul of the Bogutchanthaceae from the Paleocene (Maslova and Kodrul, 2003).

In *Krassilovianthus*, the general morphology of heads is rather peculiar. Individual flowers are arranged quite loosely, but boundaries between them cannot be traced because the perianth almost twice

Plate VI. *Krassilovianthus sarbaensis* gen. et sp. nov., specimen no. 417/106. LM.

- 1, 2. Longitudinal sections of flower, two stamens with basally confluent pollen sacs (black arrows) and perianth elements (white arrows) considerably exceeding stamen length.
3. Transverse section of inflorescence fragment in the apical part, pollen sacs of different shape in section.
4. Transverse section of flower, pollen sacs of different shape.
- 5, 6. Transverse section in the central part of flowers, endothecium cells (arrows) with thickened walls.



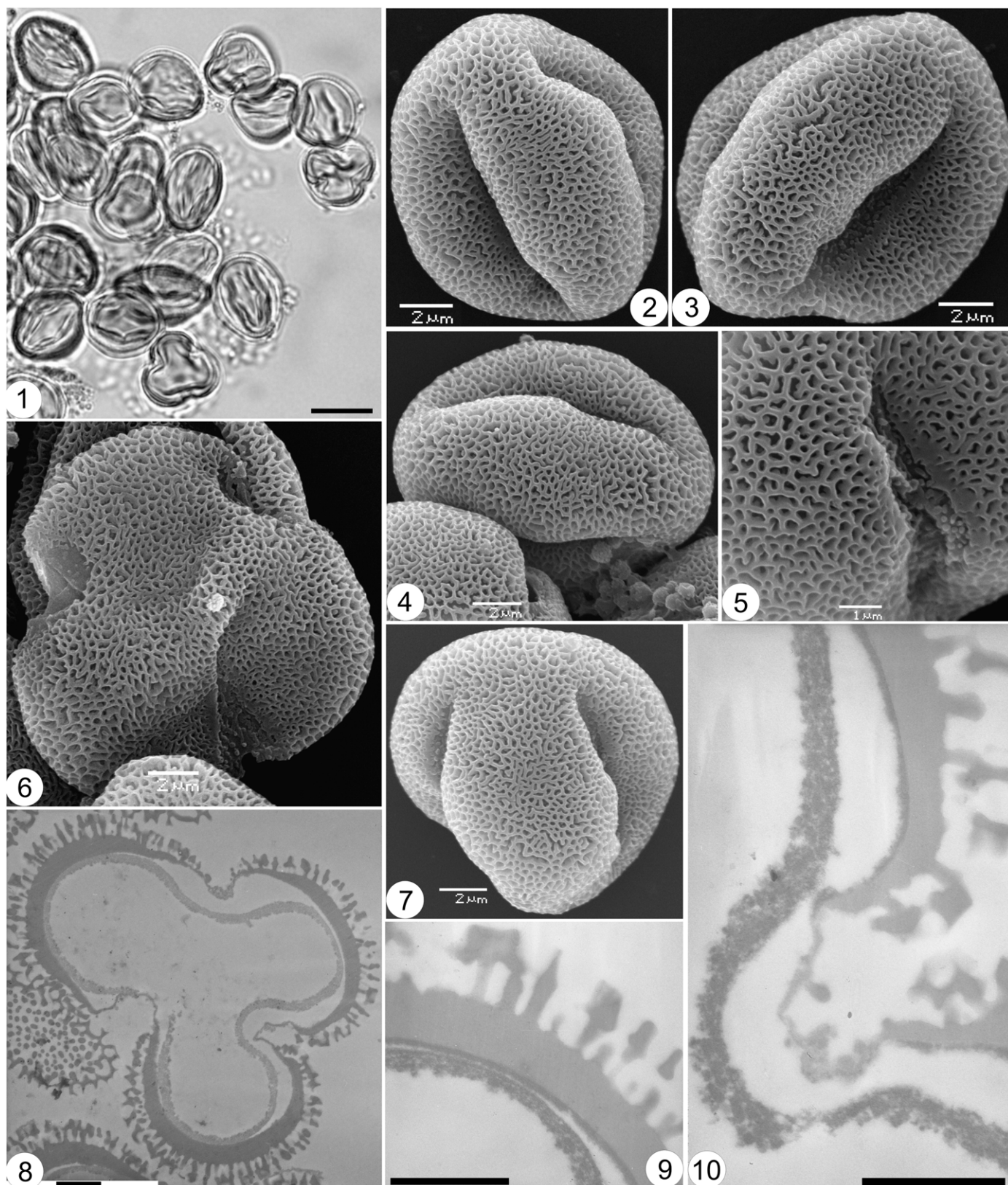


Plate VII. *Krassilovianthus sarbaensis* gen. et sp. nov., specimen no. 417/102. 1 – LM, 2–7 – SEM, 8–10 – TEM.

1. Pollen mass in LM, ora can be seen, scale bar 10 μm .
- 2–4, 7. Pollen from equatorial view, scale bar 2 μm .
5. Higher magnification of the pollen, showing aperture margin, scale bar 1 μm .
6. Pollen from polar view, scale bar 2 μm .
8. Section through a whole pollen grain, scale bar 1 μm .
9. Part of the section showing non-aperture region, scale bar 1 μm .
10. Part of the section showing aperture region, scale bar 1 μm .

exceeds the androecium in length. The boundaries between flowers can be revealed only using transverse anatomical sections. Thin and long perianth elements were broken during fossilization. More or less free arrangement of flowers in the staminate inflorescence has been also observed in the Paleocene genus *Bogutchanthus*, *Bogutchanthaceae* (Maslova et al., 2007).

The new genus *Krassilovianthus* is comparable in the number of flowers (40) to the fossil genera of *Bogutchanthaceae*–*Bogutchanthus* and *Quadriplatanus* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla et al., 1997). As a rule, staminate inflorescences of *Platanaceae* contain numerous flowers. For example, inflorescences of *Platananthus* number from 50 to 100 flowers. Extant *Hamamelidaceae* with capitate inflorescences have 8–13 flowers per head as in *Exbucklandia* (Kaul and Kapil, 1974), 6–25 flowers in *Altingia* Noronha, and up to 40 flowers in *Liquidambar* L. (Bogle, 1986).

Heads of the extant plane tree as well as those of the majority of fossil *Platanaceae* genera consist of a relatively massive receptacle and radiating flowers. The extant plane tree has very dense heads with tightly packed flowers. Boundaries between individual flowers are virtually indistinct due to tiny (if ever existing) perianth elements. Members of fossil *Platanaceae* that are characterized by a relatively well-developed perianth have heads with distinct boundaries between individual flowers (e.g., *Platananthus*).

The main type of the inflorescence in *Hamamelidaceae* is a spike or a compound spike (Endress, 1977). Some genera are characterized by variously compact racemes or compound racemes. Some members of *Hamamelidoideae* and *Exbucklandioideae* possess inflorescences that are extremely compact and superficially resemble heads. For example, *Exbucklandia* has capitate inflorescences (Kaul and Kapil, 1974). The three extant members of *Altingioideae*, *Altingia*, *Liquidambar* and *Semiliquidambar* Chang, have heads that are similar in morphology to *Platanaceae* heads (Bogle, 1986).

4.2. Perianth

The perianth of *Krassilovianthus* is up to twice longer than the androecium (Plate VI, 1). Epidermal cells of the base of the outer elements differ from those of their apices. The inner elements of the perianth have a considerably thinner cuticle in comparison to more strongly cutinized outer elements. Distinct perianths have been earlier observed in the majority of fossil *Platanoid* flowers; however, their length did not exceed that of the androecium. Among fossil *Platanaceae* that have been described on the basis of staminate inflorescences, well-developed perianths are known in *Platananthus* (Albian-Eocene, Manchester, 1986; Friis et al., 1988; Pigg and Stockey, 1991) and *Hamatia* Pedersen, Crane et Drinnan (Albian, Pedersen et al., 1994). The perianth is extremely reduced in *Chemurnautia* (late Paleocene-early Eocene, Maslova, 2002). Von Balthazar and Schönenberger (2009) consider extant *Platanus* to have an extremely reduced perianth, while others (Griggs, 1909; Bretzler, 1924; Douglas and Stevenson, 1998) believe mature flowers to be naked.

Members of the fossil *Bogutchanthaceae*, *Quadriplatanus* (Coniacian-Santonian, Magallón-Puebla et al., 1997), *Archaranthus* and *Bogutchanthus* (Danian, Maslova and Kodrul, 2003; Maslova et al., 2007), possess flowers with well-developed perianths. *Quadriplatanus* is characterized by a simple perianth. There are differences in the epidermal structure between the outer and inner perianth elements in *Archaranthus* and *Bogutchanthus*. The perianth is scarcely visible in *Sarbaya* Krassilov et Shilin (Cenomanian-Turonian, Krassilov and Shilin, 1995).

There is no perianth in extant *Hamamelidaceae* with capitate reproductive structures (Bogle, 1970, 1986). Only *Exbucklandia* has a separate calyx in early ontogenetic stages (Bogle, 1986). However, fossil capitate inflorescences and infructescences referred to or related to the *Altingioideae* (*Hamamelidaceae*) are usually characterized by well-developed perianths. The perianth of the Cretaceous genus *Lindacarpa* N. Maslova is attached somewhat higher than the base of the

gynoecium and envelopes the flower almost along the full length (Maslova and Golovneva, 2000a). The Cenomanian genus *Viltyungia* N. Maslova, which combines features of three subfamilies, *Altingioideae*, *Exbucklandioideae* and *Hamamelidoideae*, has a well-developed perianth with differentiated elements: the inner ones are narrower; the outer ones are wide and bear trichomes (Maslova and Golovneva, 2000b). Fossil *Hamamelidoideae* differ in degree of perianth development. The Campanian genus *Allonia* Magallón-Puebla, Herendeen et Endress had a corolla of narrow parallel-margined petals and an irregularly developed calyx (Magallón-Puebla et al., 1996). Flowers of the late Santonian genus *Androdecidua* have spindle-shaped petals with tapering bases and apices, partly fused with stamens of the outer whorl (Magallón-Puebla et al., 2001). The Santonian–Campanian genus *Archamamelis* is characterized by hexa- or heptamerous perianth with triangular petals that are wide at their bases (Endress and Friis, 1991).

Well-developed perianths that form floral tubes, persisting in mature fruits, have been described for the Cenomanian genus *Anadyricarpa* N. Maslova et Herman (Maslova and Herman, 2004) and the Turonian *Kasicarpa* N. Maslova, Golovneva et Tekleva (Maslova et al., 2005) of the order *Sarbaicarpales* (Maslova, 2010).

4.3. Androecium

The androecium of *Krassilovianthus* differs from that of other flowers with capitate inflorescences macromorphologically similar to those of *Platanoids*. Flowers of *Krassilovianthus* are distemonous; stamens are bisporangiate and dithecate. Extant *Platanus* is characterized by unstable number of floral organs: the number of stamens varies from three to five per flower (Boothroyd, 1930; von Balthazar and Schönenberger, 2009). Most fossil *Platanaceae* have pentamerous flowers with a constant number of elements: *Platananthus*, *Gynoplatananthus* Mindell, Stockey et Beard (Mindell et al., 2006) and probably *Hamatia* (Pedersen et al., 1994). Tetramerous flowers have been described for the genera *Bogutchanthus* (Maslova et al., 2007), *Archaranthus* (Maslova and Kodrul, 2003), *Sarbaya* (Krassilov and Shilin, 1995) and *Quadriplatanus* (Magallón-Puebla et al., 1997) of the *Bogutchanthaceae* as well as for staminate and pistillate heads from the Turonian of the Raritan Formation, New Jersey with characters of *Platanaceae* and *Hamamelidaceae* (Crepet et al., 1992; Crepet and Nixon, 1996).

Bisporangiate stamens are unknown in the *Platanaceae*. *Platanus* is characterized by tetrasporangiate anthers and well-developed connective with an apical extension. In contrast to *Platanus*, *Krassilovianthus* has bisporangiate stamens.

Bisporangiate stamens were described for *Bogutchanthus* of the extinct family *Bogutchanthaceae* (Maslova et al., 2007). The androecium of *Bogutchanthus* is formed of four free stamens with sessile anthers. The stamens were originally tetrasporangiate, but at maturity they appeared as bisporangiate since septa between the lobes of the anther disappeared. We consider the presence of bisporangiate and tetrasporangiate stamens within the same head as evidence for their non-simultaneous maturity. The majority of the extant *Hamamelidaceae* possess tetrasporangiate stamens, though *Hamamelis* (Schoemaker, 1905) and *Exbucklandia* (Kaul and Kapil, 1974) develop monothecious anthers. Magallón-Puebla et al. (2001) have observed bisporangiate and tetrasporangiate anthers in stamens of the outer and inner whorls respectively in flowers of *Androdecidua*. *Archamamelis* has bisporangiate stamens (Endress and Friis, 1991).

Endress and Stumpf (1990) documented and reviewed the cases of non- tetrasporangiate anthers. The bisporangiate condition can be achieved via asymmetrical reduction of one theca (monothecal stamens) or via symmetrical reduction of one of two sporangia in each theca (dithecal stamens). In the first case, two remaining sporangia are situated on the same radius, while in the second case they are situated in the tangential plane. Monothecal bisporangiate stamens are common among highly specialized zygomorphic flowers. In such

flowers, apart from the functional fertile theca the second theca is also present as a sterile appendage and functions as a part of pollination apparatus (Endress and Stumpf, 1990). This structural elaboration clearly does not fit the morphology of *Krassilovianthus* with its symmetrical stamens and relatively simple flowers. In *Krassilovianthus* (Plate VI, 1) the pollen sacs form a bilaterally symmetrical anther with pollen sacs being clearly situated in the tangential plane, e.g. both pollen sacs lie parallel the perianth. They are almost free but confluent (also tangentially) at the anther base. Thus, the stamens are dithecal.

In a number of angiosperms, bisporangiate stamens and confluent pollen sacs correlate with shortened stamen filament as well as with pollen releasing by small portions through the apical aperture of the pollen sac. Such correlations were revealed, in general, for entomophilous plants (Endress and Stumpf, 1990). The mechanism of pollen releasing is unclear for *Krassilovianthus* but it might have occurred through the apical aperture. The idea on correlation between the massive perianth and entomophily were previously discussed (Manchester, 1986; Crane et al., 1993; Wang, 2008).

In the families related to Platanaceae by molecular data (e.g., APG, 2003), two genera of Proteaceae, *Conospermum* Sm. and *Synaphea* R. Br. (see e.g. Takhtajan, 2009), have bisporangiate dithecal stamens, but inflorescences of Proteaceae do not resemble those in Platanaceae, though they can be rather dense and composed of unisexual flowers. The perianth in members of Proteaceae is always well-developed and exceeds stamens in length. According to Soltis et al. (2011), Sabiaceae is another family related to Proteaceae, Nelumbonaceae and Platanaceae. The sabiaceous genus *Meliosma* Blume has both sterile and fertile stamens (Wanntorp and Ronse de Craene, 2007). The fertile stamens are bisporangiate and dithecal. Flowers of Sabiaceae are bisexual, with a double perianth of five sepals and five petals, and aggregated in pedunculate cymes (Wanntorp and Ronse de Craene, 2007; Takhtajan, 2009).

In *Krassilovianthus*, pollen sacs of the same stamen are almost identical in their shape, but may somewhat differ in size. Unequally developed pollen sacs within each theca of tetrasporangiate stamens and as a consequence asymmetrical thecae are characteristic of extant *Platanus* (Hufford and Endress, 1989). *Krassilovianthus* is similar to extant *Platanus* and Late Paleocene-Early Eocene *Chemurnautia*, Platanaceae (Maslova, 2002) in having extended pollen sacs with parallel margins. Pollen sacs that are similar in shape and with unequal length are described in *Bogutchanthus*, Bogutchanthaceae (Maslova et al., 2007); although pollen sacs of *Bogutchanthus* vary from narrowly elongated with almost parallel margins to asymmetric and crescent-shaped.

Pollen sacs of *Krassilovianthus* are basally confluent. Among Platanaceae, narrow and linear pollen sacs are known in *Chemurnautia*; they do not form distinct thecae and are partly confluent at the base. Basal confluence of pollen sacs as well as their confluence with staminodes is reported for *Bogutchanthus*.

In stamens of *Krassilovianthus*, the connective is indistinguishable. The majority of fossil Platanaceae have more or less well-developed connectives, which end with a triangular conical apical extension. Apical extensions of the connectives can be distinct to a variable degree: from weakly developed (*Aquia brookensis* Crane, Pedersen, Friis et Drinnan; Crane et al., 1993) to more or less massive and of different shapes (conical in *Platananthus synandrus* Manchester, Manchester, 1986; *P. speirsae*, Pigg and Stockey, 1991; triangular in *P. scanicus*, Friis et al., 1988; *Archaranthus krassilovii*, Maslova and Kodrul, 2003; flattened in *Platananthus hueberi* Friis, Crane et Pedersen, Friis et al., 1988; or peltate in *P. potomacensis* Friis, Crane et Pedersen, Friis et al., 1988).

There are trichomes and stomata in the epidermis of the apices of pollen sacs of *Krassilovianthus*. Subsidiary cells of the stomata are narrower than ordinary epidermal cells, but the stomatal type cannot be recognized. Among fossil Platanaceae, hairy anthers are known in *Platananthus hueberi* (Friis et al., 1988), *P. synandrus* (Friis et al., 1988), *Aquia brookensis* (Crane et al., 1993) and *Macginistemon mikaneides*

(MacGinitie) Manchester (Manchester, 1986). It is noteworthy that extant *Platanus* has hairy apical extensions of the connectives (von Balthazar and Schönenberger, 2009). Trichomes and stomata in the anther epidermis are also known in the Bogutchanthaceae. The epidermis of the connective of *Archaranthus krassilovii* bears rare rounded trichome bases and numerous anomocytic stomata (Maslova and Kodrul, 2003). The apical extension of the connective of *Quadriplatanus* is massive and with anomocytic stomata (Magallón-Puebla et al., 1997). Presence of stomata in the epidermis of the pollen sac is a quite rare condition in angiosperms. For example, stomata are found in such entomophilous plants as *Pyrostegia* C. Presl (Bignoniaceae, Lamiales) and *Geranium* L. (Geraniaceae, Geraniales) (Kamelina, 2009).

A subepidermal fibrous layer of cells with thickened walls is characteristic of pollen sacs of extant *Platanus* as well as those of *Krassilovianthus* and *Chemurnautia* (Maslova, 2002).

4.4. Pollen grains

Pollen grains under study are of a wide-spread angiosperm type – small, tricolporate, reticulate, columellate. Macromorphological features of the plant show similarities to the Platanaceae and Hamamelidaceae. While most of the Platanaceae and many of the Hamamelidaceae species have tricolpate pollen, some authors (Bogle and Philbrick, 1980 and references therein) reported tricolporate and tricolporoidate pollen for several extant genera of the Hamamelidaceae (*Exbucklandia*, *Hamamelis*, *Corylopsis* Siebold et Zuccarini, *Disanthus* Maximowicz, *Eustigma* Gardner et Champion, *Fortunaria* Rehder et E.H. Wilson, *Fothergilla* Murray, *Loropetalum* R. Brown ex Reichenbach, *Mytilaria* Lecomte, *Rhodoleia* Champion ex Hook, *Sinowilsonia* Hemsley, *Tetrathyrum* Benth and *Trichocladus* Persoon), Hesse (1978) and Zavada and Dilcher (1986) described tricolporate pollen grains in some of them, e.g. *Hamamelis*, *Corylopsis* and *Rhodoleia*.

Among Platanaceae these are *Hamatia* (Pedersen et al., 1994) and probably dispersed pollen masses described by Doyle et al. (1975) that show similarity to *Platananthus potomacensis*. Pollen grains of *Krassilovianthus* differ in the reticulum pattern and more or less uniform lumina size from these species and in the ratio of ectexine elements (the portion of the foot layer in the ectexine of pollen grains of *Hamatia* is considerably smaller). *Sarbaya radiata* was described from the same locality as *Krassilovianthus*; an endoaperture was observed in both taxa. Ora are clearly seen in pollen grains of *Sarbaya radiata* in transmitted light, and the sporoderm is definitely thicker than that of pollen grains of *Krassilovianthus*. Pollen grains of *Sarbaya radiata* are larger and bear a more uniform reticulum pattern.

Thus, in the Sarbay locality, several types of small tricolporate reticulate pollen were found in pollen organs (*Sarbaya radiata*, *Krassilov* and Shilin, 1995) or on the surface of carpels (Tekleva and Maslova, in preparation); however, they differ in their reticulum pattern from the pollen of *Krassilovianthus*.

Among tricolpate platanoid pollen, pollen grains of *Friisicarpus kubaensis* show the greatest similarity to the new taxon in the reticulum pattern and pollen size (Maslova et al., 2011). Tricolporate pollen grains are known in some extant Hamamelidaceae, though they differ considerably from pollen of *Krassilovianthus* in the reticulum pattern (Bogle and Philbrick, 1980; Li et al., 2011). No pollen grains with endoapertures are known in fossil Hamamelidaceae.

The sporoderm ultrastructure of *Krassilovianthus* is quite similar to that of fossil platanoid and hamamelid pollen. *Krassilovianthus* has pollen grains with a two-layered endexine, similar to that found in several platanoid taxa, with the layers are separated from each other in aperture regions. The two-layered endexine has been so far reported from merely a few species. Due to the fossil state one cannot be absolutely sure about its origin, whether this can be defined as an endexine or another sublayer of the sporoderm (Tekleva and Denk, submitted for publication).

4.5. Other finds from the Sarbay locality related to Platanaceae and Hamamelidaceae

Palaeobotanical finds from the Sarbay locality are of excellent anatomical preservation. In addition to *Krassilovianthus*, Platanaceae and related taxa published to date from the locality include staminate inflorescences of *Sarbaya* (Krassilov and Shilin, 1995), infructescences of *Sarbaicarpa* N. Maslova (Maslova, 2009) and leaves of *Ettingshausenia sarbaensis* N. Maslova et Shilin (Maslova and Shilin, 2011). Infructescences of a new species of *Friiscarpus* N. Maslova et Herman were found in the same locality (Maslova and Tekleva, in press). Although these male and female reproductive organs were found in the same layer, they did not occur in the organic connection. Moreover, they show a unique and essentially different structure. *Sarbaicarpa* infructescences and *Krassilovianthus* staminate inflorescences do not show close analogies to other angiosperms. In sum, it is impossible to propose that any of the reproductive structures belong to the same plant.

Staminate inflorescences of *Sarbaya* are characterized by tetramerous flowers with extremely reduced perianth which does not exceed one third of the stamen length, and tricolporate pollen (Krassilov and Shilin, 1995). Maslova (2010) placed the genus *Sarbaya* in the extinct family Bogutchanthaceae, Hamamelidales, of her system. Despite a considerable similarity between inflorescences of *Sarbaya* and *Krassilovianthus* in general morphology, they differ significantly in microstructure: (1) flowers of *Sarbaya* have four stamens in contrast to flowers of *Krassilovianthus*, which possess two stamens; (2) stamens in *Sarbaya* are tetrasporangiate in contrast to bisporangiate stamens of *Krassilovianthus*; (3) the perianth in *Sarbaya* is reduced, whereas it is well-developed in *Krassilovianthus*; (4) pollen grains of *Sarbaya* are larger and their sporoderm is thicker than that in *Krassilovianthus*; (5) and the reticulum pattern is different in the two taxa.

Infructescences of *Sarbaicarpa* are distinct by the mosaic combination of platanaceous and hamamelidaceous characters (see Maslova, 2009). The infructescence consists of about 30 freely arranged and widely cuneate fruits. Fruits are monocarpellate, without a stylodium and with a bunch of hairs at the base. The ovule is solitary and anatropous. There are two types of sterile structures: the first ones are similar to the fruits in size, hemispherical and covered by dense rounded trichomes, while the second ones are narrow, linear, reaching more than half of the fruit length. Maslova (2010) assigned this genus to the extinct family Sarbaicarpaceae of the order Sarbaicarpales because of the unique combination of characters of different families (Maslova, 2010).

Heads of the genus *Friiscarpus* consist of numerous pentamerous flowers, surrounded by a well-developed perianth, the carpels lack distinct stylodia (Friis et al., 1988). The heads of *Friiscarpus* from the Sarbay locality show all diagnostic characters of the genus; the finds will be assigned to a new species on the basis of some features of the morphology and epidermal structure (Maslova and Tekleva, in press).

Platanus-like leaves are also known from the Sarbay locality. Shilin (1986) identified these leaves as two species of the genus *Platanus*: *P. pseudoguillelmae* and *P. cuneiformis*. These species were distinguished solely on the basis of general morphology; no epidermal characters were used. Maslova and Shilin (2011) analyzed the morphological and epidermal characters of these leaves and distinguished two types of leaf blades: laminae that correspond to *P. pseudoguillelmae* (morphotype I) and *P. cuneiformis* (morphotype II), as well as transitional forms between them making a morphological series. For the first time, a unique epidermal structure has been shown for fossil leaves of platanoid appearance: a combination of encyclocytic, laterocytic and paracytic stomata and trichomes, which develop on one or two to seven epidermal cells. The identical peculiar epidermal features of both morphotypes gave ground for uniting these finds in one species. The two morphotypes (*P. pseudoguillelmae* and *P. cuneiformis* sensu

Shilin, 1986) were considered to represent sun and shade leaves of the same species of *Ettingshausenia sarbaensis* on the basis of variation of morphological and epidermal characters.

Stomata in the epidermis of the apices of pollen sacs in *Krassilovianthus* have specialized subsidiary cells: they are narrower than those of ordinary epidermal cells and rather strongly cutinized with cuticle folds oriented perpendicular to the stoma axis. Stomata of *Krassilovianthus* are similar to those of *Ettingshausenia sarbaensis* in these features; unfortunately the stomatal type of *Krassilovianthus* cannot be recognized.

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