

New Genus *Sarbaicarpa* gen. nov. (Hamamelidales) from the Cenomanian–Turonian of Western Kazakhstan

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Abstract—Anatomically preserved infructescences of *Sarbaicarpa shilinii* gen. et sp. nov. are described from the Cenomanian–Turonian of Kazakhstan and assigned to the Hamamelidales on the basis of their microstructure. The infructescence consists of about 30 free broadly cuneate fruits. The fruits are monocarpellate, without stylode, and basally with hairs. The seed is solitary and anatropic. Two types of sterile elements are present: (1) semispherical structures that are comparable in size to the fruits and densely covered with rounded trichomes and (2) narrow linear structures reaching more than a half of the fruit length. The new genus is characterized by a mosaic of platanaceous and hamamelidaceous characters. The plant remains are found associating with fossil leaves of the typically *Platanus* aspect.

Key words: Hamamelidales, reproductive structures, Cenomanian–Turonian.

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INTRODUCTION

The systems of angiosperm plants proposed by Takhtajan (1966, 1997) and Cronquist (1981) consider the families Platanaceae and Hamamelidaceae within the order Hamamelidales, which occupies a key position within the Hamamelidae. The recently published system of angiosperms based on molecular data abolished the order Hamamelidales and classifies the families Platanaceae and Hamamelidaceae within the orders Proteales and Saxifragales, correspondingly, thereby having destroyed the earlier concept about probable relationships between the two families (APG, 2003). The discrepancy between systems based on morphological and molecular data is far from being understood, and this is in particular true for the position of the families in question. Whereas paleobotanical proofs of relationships between the Platanaceae and Proteales as well as Hamamelidaceae and Saxifragales are virtually lacking, data in support of the origin of the Platanaceae and Hamamelidaceae from a common stock are considerably representative. Thus, leaf remains are known combining characters of the Platanaceae and Hamamelidaceae (Golovneva, 1994; Maslova, 2002; and others). Such leaves were found associating with both platanaceous and hamamelidaceous reproductive structures (e.g., Maslova, 2002; Maslova and Herman, 2004).

Of particular interest are reproductive structures combining characters of the two families (Crepet et al., 1992; Maslova et al., 2005, 2007). The supposed phylogenetic relationships between these families were earlier discussed (Crepet et al., 1992; Maslova, 2003,

2007; Maslova and Herman, 2004; Maslova et al., 2005, 2007). As far as the new genus shows a mosaic combination of characters of these two families, and no molecular data are available for the genus, I follow the systems of Takhtajan and Cronquist and consider the Platanaceae and Hamamelidaceae within the Hamamelidales. The existing problem unequivocally needs additional studies.

To date, 16 genera of the Platanaceae have been described on the basis of staminate and pistillate infructescences (Krassilov, 1973, 1976; Manchester, 1986, 1994; Crane et al., 1988, 1993; Friis et al., 1988; Pedersen et al., 1994; Krassilov and Shilin, 1995; Magallón-Puebla et al., 1997; Maslova, 2002; Maslova and Krassilov, 2002; Maslova and Kodrul, 2003; Mindell et al., 2006).

Data on the geological history of the Hamamelidaceae are much less numerous; nonetheless, nine fossil genera have been described on the basis of reproductive structures (Endress and Friis, 1991; Manchester, 1994; Magallón-Puebla et al., 1996, 2001; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou et al., 2001; Maslova and Herman, 2004). Five of them are capitate inflorescences and infructescences, morphologically similar to platanaceous heads.

The present description of *Sarbaicarpa* gen. nov. contributes to our knowledge about the diversity of fossil capitate reproductive structures, showing a mosaic combination of platanaceous and hamamelidaceous characters. Of interest is the association between these infructescences and leaf remains, which main morpho-

type is typical of the modern plane tree. Leaf remains of this morphotype accompany heads of some members of the Platanaceae (Krassilov and Shilin, 1995; Maslova and Herman, 2006), Hamamelidaceae (Maslova and Herman, 2004), and reproductive structures combining characters of the two families and, therefore, only determinable up to the order Hamamelidales (Maslova et al., 2005). *Sarbaicarpa* gen. nov. is recorded from the same deposits as the earlier described staminate inflorescences of *Sarbaya*, assigned by its authors to the Platanaceae (Krassilov and Shilin, 1995).

MATERIAL AND METHODS

The material comes from gray Cenomanian–Turonian clays of Sarbai quarry in western Kazakhstan, near town of Rudnyi. The plant remains were collected and described by Shilin (1986). The flora includes *Asplenium dicksonianum* Heer, *Gleichenia* sp., *Sphenopteris* sp., *Sequoia heterophylla* Velen., *Cedrus* sp., *Platanus pseudoguillelmae* Krass., *P. cuneiformis* Krass., *Dalbergites simplex* (Newb.) Sew., and *Ilex* sp. Later, the infructescence under description was discovered and kindly provided by Shilin to the present author for the study. Collection, no. 5266 is kept at the A.A. Borisiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN).

The collection contains two fragments of anatomically preserved infructescences. After preparation, individual structures were photographed under a CITOVAL stereomicroscope (LM). Isolated fruits and a fragmentary head were cleaned from rock remains with fluoric acid and mounted on SEM stubs. Some structures were also studied under SEM after maceration with nitric acid and alkali. Microphotographs were made under a CamScan SEM in PIN.

SYSTEMATIC PALEOBOTANY

Order Hamamelidales Wettstein

Genus *Sarbaicarpa* N. Maslova, gen. nov.

Etymology. From the Sarbai locality and the Latin *carpus* (fruit).

Type species *Sarbaicarpa shilinii* N. Maslova sp. nov.

Diagnosis. Sessile spherical infructescence 10 mm in diameter, consists of about 30 relatively loosely arranged fruits, about 30 radiating from central core. Fruit widely cuneate, monocarpellate, without stylode. Fruit wall with solitary large glands. Fruit naked, basally with hairs. Seed solitary and anatropic. About eight semispherical sterile structures are situated between fruits, nearly as large as fruits, covered with numerous rounded trichomes, which leave rounded pits after abscission. Several narrow linear sterile structures surround fruit reaching half of its length.

Genus composition. Type species.

Comparison. *Sarbaicarpa* gen. nov. is characterized by a mosaic of characters, some of which are diagnostic of *Platanus* L. as well as of several members of the Hamamelidaceae. The new genus is close to modern *Platanus* by the capitate infructescence, absence of a developed perianth, presence of hairs at the base of the fruit, more or less synchronously maturing fruits in the infructescence, a solitary seed in the fruit, and the presence of sterile elements in the infructescence. Members of the modern genus *Platanus* differ from the new genus by a much greater number of flowers per inflorescence (up to 300), numerous apocarpous carpels in one flower (five–nine), hairy fruits (most species), smaller sizes and different shape of sterile structures, and orthotropic seeds. The main difference of ancient platanaceous genera from *Sarbaicarpa* gen. nov. is a greater number of carpels in the flower: five in *Friisicarpus* (Friis, Crane et Pedersen) N. Maslova et Herman¹ and *Macginicarpa* Manchester (Manchester, 1986) and dividable on four (four or eight) in *Quadriplatanus* Magallón-Puebla, Herendeen et Crane (Magaláon-Puebla et al., 1997). *Friisicarpus* has orthotropic seeds. The carpel of *Quadriplatanus* contains a solitary and non-orthotropic seed. In addition, fossil members of the Platanaceae differ from the new genus by their developed and often differentiated perianths.

Considering members of the Hamamelidaceae, *Sarbaicarpa* gen. nov. shows the maximal similarity to modern Altingioideae and related fossil members and to members of the Hamamelidoideae. The similarity to modern Altingioideae includes the number of flowers per head, lacking perianth, presence of monocarpellate gynoecium, anatropic seed, morphology of spermoderm, and the presence of sterile structures in the infructescence. Although bicarpellate gynoecium dominates, monocarpellate forms are also present in this subfamily (Wisniewski and Bogle, 1982; Bogle, 1986). The main distinguishing feature of *Sarbaicarpa* gen. nov. from modern Altingioideae is a solitary seed in the fruit. Among fossil members of the Altingioideae, *Anadyricarpa* N. Maslova et Herman resembles the new genus by the presence of monocarpellate gynoecium; regrettably, the type and number of seeds in its fruit is unknown because of the insufficiently preserved fossil remain (Maslova and Herman, 2004). The recently described *Kasicarpa* N. Maslova, Golovneva et Tekleva from the Turonian of Chulym-Yenisei Depression has a monomeric gynoecium with a solitary seed and combines characters of platanaceous and hamamelidaceous reproductive structures (Maslova et al., 2005). The main differences between *Kasicarpa* and the new genus are the presence of a developed perianth, absence of sterile structures in the infructescence, asyn-

¹ Maslova and Herman (2006) proposed the new name *Friisicarpus* (Friis, Crane et Pedersen) N. Maslova et Herman for the earlier described *Platanocarpus* Friis, Crane et Pedersen (Friis et al., 1988), which is a later invalid homonym of *Platanocarpus* Jarmolenko.

chronously maturing fruits, and orthotropic seed of the former genus. The similarity between *Sarbaicarpa* gen. nov. and modern Hamamelidoideae includes the presence of a solitary anatropic seed in the fruit and a developed endosperm.

Remarks. Capitate infructescences of *Sarbaicarpa* gen. nov. associate with leaves of the morphotype typical of the modern plane tree and with staminate inflorescences of *Sarbayia* (Krassilov and Shilin, 1995).

Sarbaicarpa shilini N. Maslova, sp. nov.

Etymology. In honor of the paleobotanist P.V. Shilin (Almaty, Kazakhstan), who collected and studied the fossil flora of the Sarbai locality in western Kazakhstan.

Holotype. PIN, no. 1/5266; capitate infructescence; western Kazakhstan, Sarbai locality, Zhirkindekskaya Formation, Cenomanian–Turonian, Fig. 1a.

Diagnosis. As for the genus.

Description (Figs. 1–8). The sessile capitate infructescence 10 mm in diameter is situated on a relatively thick and longitudinally ribbed axis with the maximal diameter of 1.5 mm (Fig. 1a). The surface of the axis is covered with oval bases of trichomes (Figs. 1d, 1e).

The head consists of a central core about 2 mm in diameter and monocarpellate fruits radiating from the core and relatively loosely situated (Fig. 1b). The approximate number of fruits in the head does not exceed 30.

The microstructure of individual fruits was studied under SEM. Perianth elements are lacking. The length of the fruit is 1600–2200 μm , and the width varies from 600 to 900 μm . The fruits are broadly cuneate (Figs. 2a–2c), with a relatively narrow conical base (Fig. 2c). The styloide is lacking. Rare relatively large peltate glands about 30 μm in diameter occur predominantly in the lower part of the fruit (Figs. 3e, 3f). The cuticle of the fruit wall is relatively thick and with a distinct transverse striation (Fig. 3a). The external wall of the fruit is composed of two–four layers of morphologically similar cells differing in size. The epidermis of the external wall of the fruit is formed by isodiametric nearly rounded cells 10–20 μm in diameter (Fig. 3d). Towards the inner areas, several (three or less) layers of cells are present, the cells are rectangular in plan and 50 \times 80 μm in size (Fig. 3c).

The fruit contains a solitary anatropic seed 900–1100 μm long and up to 500 μm wide in its widest part (Figs. 4a, 4b, 4d, 5a). All seeds in the infructescence are approximately identical in size and shape. They are elongated ovate, strongly convex ventrally, and slightly flattened (Fig. 6a). The seed cuticle is relatively thick and with a distinct transverse striation (Fig. 6b). The spermoderm includes three cellular layers. The external cover of the seed is composed of one layer of cells, which are variable in size, polygonal, more often tetragonal, and predominantly orientated along the longitudinal axis of the seed (Fig. 4e). The largest cells (40–

60 μm in diameter) are situated in the central area of the seed. The cells diminish toward the periphery. The middle sclerenchyma layer is one–three cells thick. Cells of the middle layer are palisade, polygonal in plan, about 10 μm in diameter, and with very thick walls (Figs. 4f, 6e, 6f). The inner layer of the spermoderm is unicellular and formed by cells of 20–30 μm in diameter, with undulated walls (Figs. 4g, 4h). The seed suture is formed by small sclerenchyma cells with thickened walls and nearly lacking cellular content (Fig. 4e). In section, an undivided sclerenchyma layer is visible in the area of the suture (Figs. 6f, 6g). The endosperm is well developed (Fig. 6h) and formed of rectangular or nearly isodiametric cells 10–20 μm in diameter (Fig. 6i).

Remains of a hair bunch are visible at the base of the fruit. Hairs are mostly preserved which are adpressed to the fruit wall to a lesser or greater degree (Fig. 2d). Free hairs are preserved much more rarely (Fig. 2e), apparently because of their fragility. Since the fruits are quite loosely situated in the infructescence, hairs were not densely packed and mechanically suffered in course of fossilization. It is difficult to judge about their length; apparently, they exceeded a half of the fruit length.

The sterile structures are irregularly situated between the fruits. There are up to eight relatively large (950–1300 μm long and 1100–1300 μm wide) sterile structures (Figs. 1c, 7a), consisting of a small peduncle up to 180 μm wide (Fig. 7c) and a thick relatively flattened semispherical part (Fig. 7b). These structures are covered with numerous rounded trichomes about 10 μm in diameter (Figs. 7d, 7e), which leave distinct rounded bases after shedding. The inner surface of the cuticle bears relatively large cuticular thickenings surrounding the apertures of the trichomes (Fig. 7f).

One more type of sterile structures which are present in the infructescence is represented by needle-shaped, thin, about 60 μm wide, linear, basally attached and distally free structures, reaching at least a half of the fruit length (Figs. 8a, 8b). The maximal number of such structures per infructescence is about 15. Because of their linear outline, they are highly fragile and fragmentarily preserved; their apices are broken. The cuticle of these structures bears a distinct longitudinal striation (Fig. 8c). The epidermis is composed of distinct rows of elongated cells with strongly cutinized anticlinal walls (Fig. 8d).

Material. Holotype PIN, no. 1/5266 and fragmentary infructescence PIN, no. 2/5266.

DISCUSSION

General architecture of the infructescence. The heads of *Sarbaicarpa* gen. nov. are sessile, with a longitudinally striate axis and oval bases of trichomes. There are up to 30 fruits, radiating from the central core of the head. They are loosely situated and do not fuse with each other. The diameter of the infructescence of *Sarbaicarpa* gen. et sp. nov. is 10 mm. The evolution-

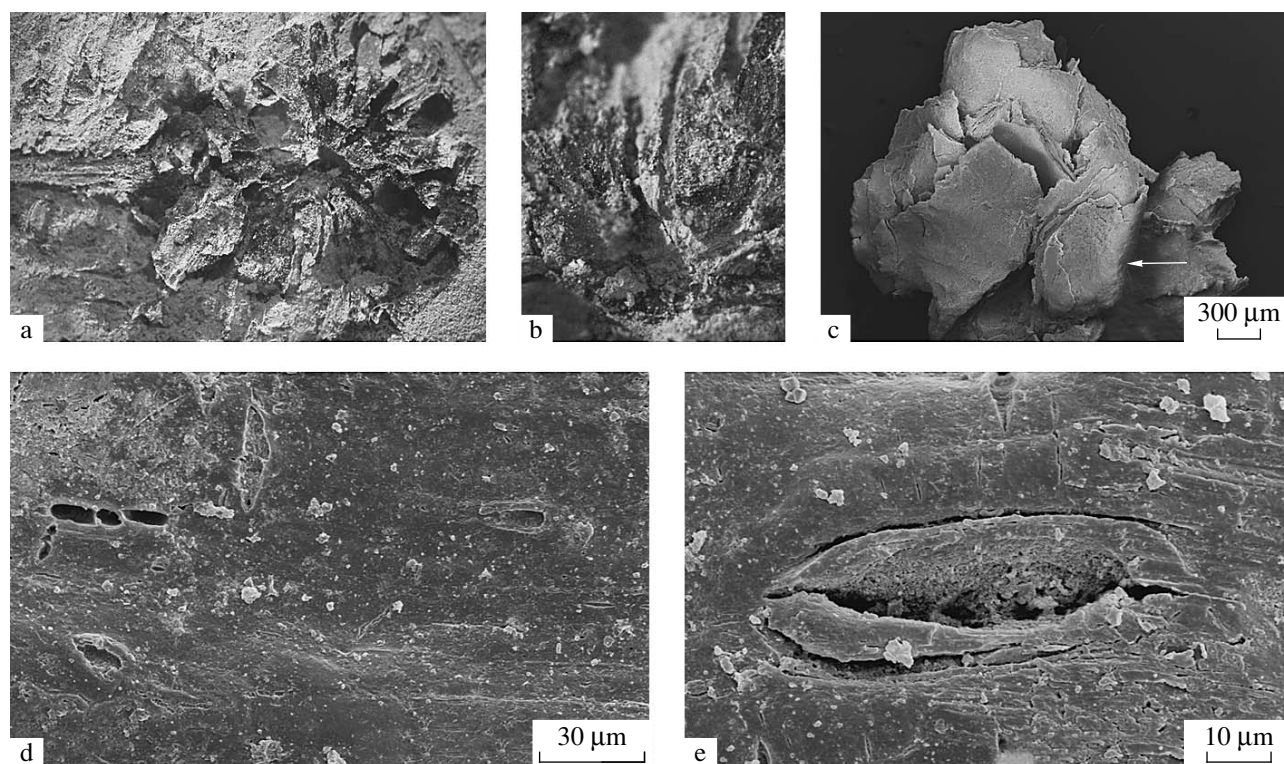


Fig. 1. *Sarbaicarpa shilinii* gen. et sp. nov., western Kazakhstan, Sarbai locality, Zhirkindeskaya Formation, Cenomanian–Turonian: (a, b) LM; (c–g) SEM; (a) holotype PIN, no. 1/5266, capitata infructescence on an axis, $\times 5$; (b) holotype PIN, no. 1/5266, two fruits, $\times 18$; (c) PIN, no. 2/5266, fragmentary head, note fruits and a spherical sterile structure (arrow); (d) PIN, no. 2/5266, axis surface with trichome bases; (e) PIN, no. 2/5266, oval base of a trichome.

any trend of heads increasing in size is known in both the Platanaceae and Hamamelidaceae. Thus, the diameter of the infructescences in different species of Cretaceous *Friisicarpus* varies from 3 to 6 mm (Friis et al., 1988; Crane et al., 1993). Heads of Eocene *Macginicarpa* reach 10–16 mm (Manchester, 1986; Pigg and Stockey, 1991). Heads of the modern plane tree often exceed 30–35 mm. The size of capitata infructescences of the Altingioideae also varies. The smallest infructescences reaching up to 7 mm are found in Turonian *Microaltingia* Zhou, Crepet et Nixon (Zhou et al., 2001). The infructescence of Miocene *Liquidambar changii* Pigg, Ickert-Bond et Wen is about 25 mm in diameter (Pigg et al., 2004). Heads of modern species of *Liquidambar* reach 30 mm in diameter.

Sarbaicarpa gen. nov. resembles members of the Altingioideae (Hamamelidaceae) by the number of fruits in the infructescence (up to 30). Thus, up to 25 flowers are known in modern *Altingia* Nor. and 26–40 in *Liquidambar* (Bogle, 1986; Ickert-Bond et al., 2005). Miocene *L. changii* has approximately 25–30 fruits. Speaking about fossil members of the Platanaceae, the genera *Sarbaya* Krassilov et Shilin (Krassilov and Shilin, 1995) and *Archaranthus* N. Maslova et Kodrul (Maslova and Kodrul, 2003) have a smaller number of flowers in inflorescences (about 24 and 15, correspondingly). As a rule, platanaceous heads consists of a

greater number of flowers. *Quadriplatanus* has about 40 tetramerous flowers (Magallón-Puebla et al., 1997); inflorescences of *Friisicarpus* and some species of *Platananthus* Manchester have a slightly greater (50) number of pentamerous flowers (Manchester, 1986; Friis et al., 1988); about 100 flowers occur in inflorescences of some species of Late Cretaceous *Platananthus*; the number of flowers can reach 300 in heads of the modern plane tree.

Capitate inflorescences and infructescences are usually very dense, making difficult if ever possible the determination of the number of flowers in the head. Thus, heads of the modern plane tree are very dense, flowers are tightly adpressed to each other, and margins between individual flowers are virtually indistinguishable. Fossil platanaceous genera with a developed perianth, e.g., *Platananthus* or *Friisicarpus*, show distinct margins between flowers, nonetheless, the heads are dense. The main type of hamamelidaceous inflorescences is a spike or a compound spike (Endress, 1977). Racemes or compound and variously shortened racemes are known in some genera. Inflorescences of some members of the Hamamelidoideae and Exbucklandioideae are shortened in such a degree that they look as heads. Thus, *Exbucklandia* R. Brown has distinctly developed capitata inflorescences (Kaul and Kapil, 1974). Capitata inflorescences are also known in

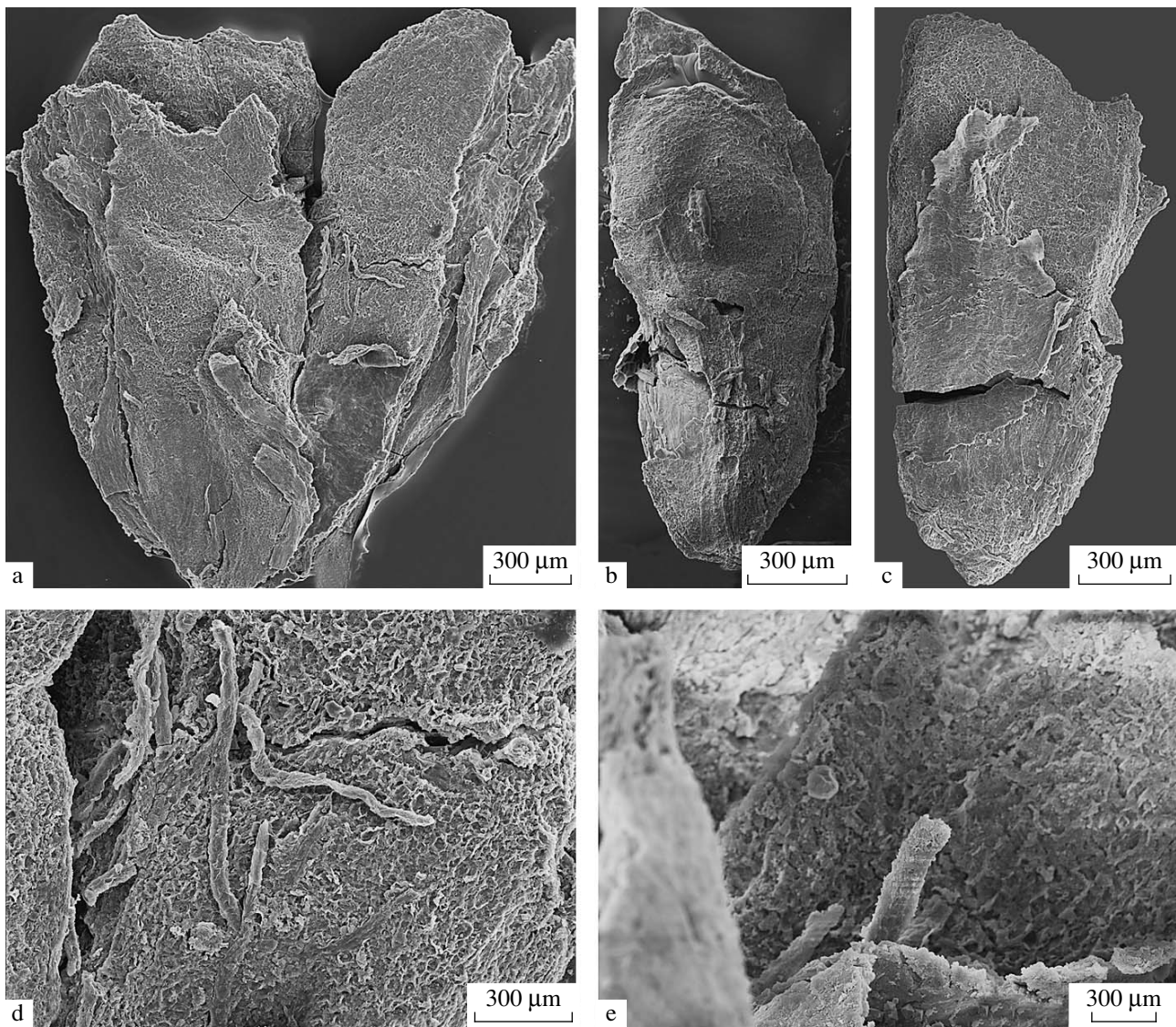


Fig. 2. *Sarbaicarpa shilinii* N. Maslova, western Kazakhstan, Sarbai locality, Zhirkindekskaya Formation, Cenomanian–Turonian: (a) holotype PIN, no. 1/5266, fragments of two fruits, remnants of elongated sterile structures are visible at the base; (b, c) holotype PIN, no. 1/5266, fruits; (d) holotype 1/5266, hairs adpressed to the fruit surface; (e) PIN, no. 2/5266, free hair.

three modern genera of the Altingioideae: *Altingia*, *Liquidambar*, and *Semiliquidambar* Chang (Bogle, 1986). Pistillate inflorescences and infructescences of modern members of the Platanaceae and Altingioideae (Hamamelidaceae) are remarkably different by their general morphology. However, such structures can be virtually identical in fossil state. The spectrum of their morphological variations can only be deduced from the anatomy.

Infructescences of modern *Liquidambar* vary in density dependent on the fusion between carpels. The majority of species have cuneate or fusiform fruits with two locules. The fruits are more or less fused basally and free distally. However, fruits of *L. acalycina* Chang and the related genus *Altingia* are relatively loosely situated, do not fuse with each other and disintegrate under mechanical pressure (Ickert-Bond et al., 2005,

2007). The architecture and density of infructescences and the shape of fruits make *Sarbaicarpa* gen. nov. close to *Liquidambar acalycina*.

The recently described *Bogutchanthus* N. Maslova, Kodrul et Tekleva (Maslova et al., 2007), which shows a peculiar combination of platanaceous and hamamelidaceous characters, is also characterized by flowers loosely situated in the head.

Perianth. Perianth is lacking in *Sarbaicarpa* gen. nov. Mature fruits of *Sarbaicarpa* gen. nov. show no fragments of perianth elements which could have testified to the presence of a perianth at earlier stages of the flower development and their later disappearance. Apparently, the flower of *Sarbaicarpa* gen. nov. was originally naked.

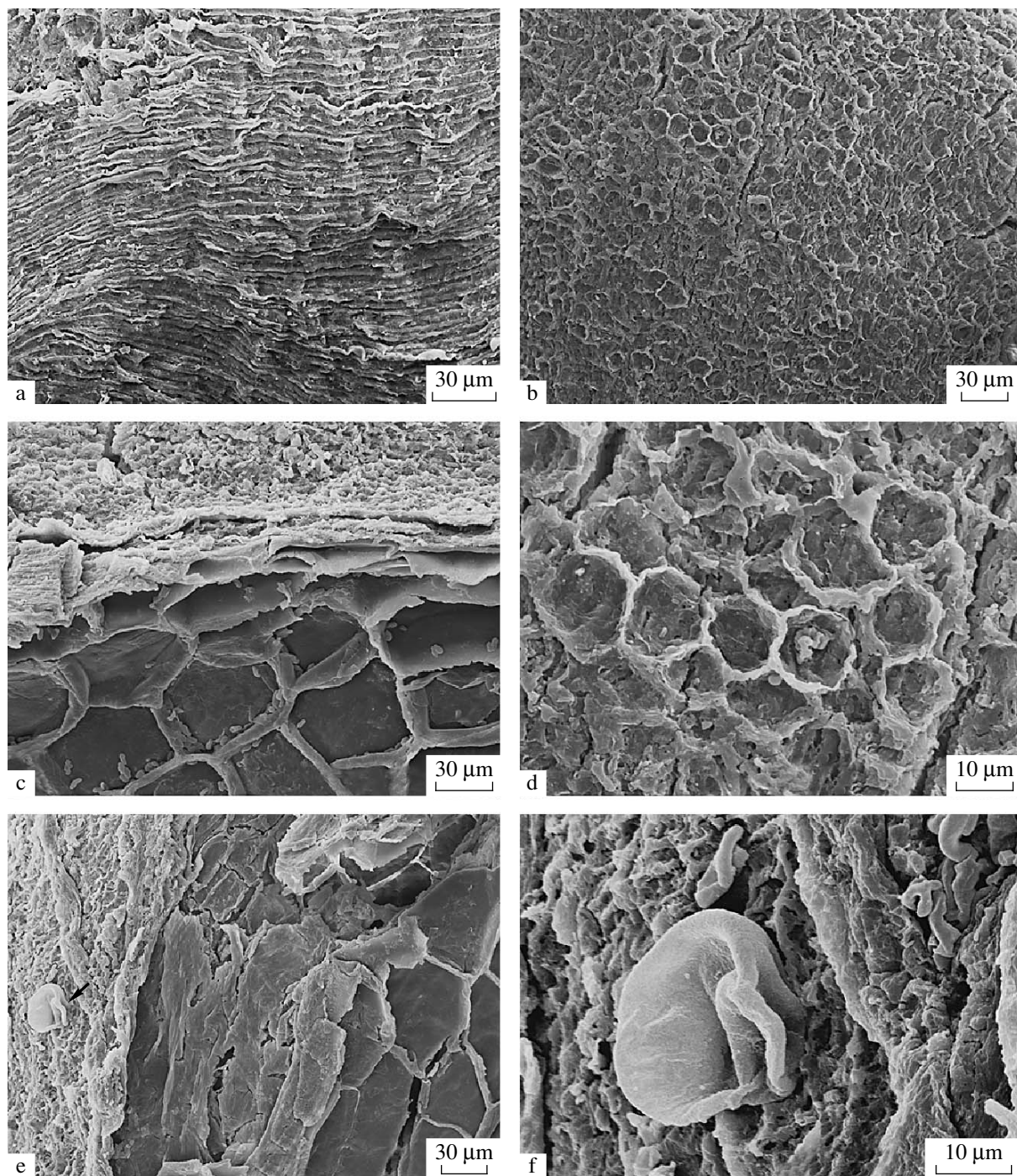


Fig. 3. *Sarbaicarpa shilini* N. Maslova, western Kazakhstan, Sarbai locality, Zhirkindekskaya Formation, Cenomanian–Turonian, holotype, no. 1/5266, SEM: (a) transversely striate cuticle of the fruit; (b, d) epidermal cells of the fruit; (c) cells constituting fruit wall; (e) fragment of the external wall of the fruit, note a gland (arrow); (f) gland on the fruit surface.

The modern plane tree also has a naked flower according to the opinion of some scientists. Contrariwise, the majority of fossil members of the Platanaceae had well-developed and often differentiated perianths (*Friisicarpus*, *Macginicarpa*, *Platananthus*, *Quadriplatanus*, *Hamatia* Pedersen, Friis, Crane et Drinnan, *Tanyoplatanus* Manchester, and *Archaranthus*).

Among modern Hamamelidaceae, members of the Altingioideae are characterized by naked flowers, which lack perianth elements even at early ontogenetic stages (Wisniewski and Bogle, 1982). Many genera of other subfamilies of the Hamamelidaceae also have naked flowers. Thus, within the Hamamelidoideae, *Distylium* Sieb. et Zucc. lacks a perianth, and *Sycopsis dunnei* Hemsl. and

Parrotiopsis Schneider have a highly reduced perianth (Bogle, 1970). Within the Exbucklandioideae, naked flowers characterize *Chunia* Chang, and a calyx is only present in flowers of *Exbucklandia* at early ontogenetic stages (Bogle, 1986).

Most of known fossil flowers of the Hamamelidaceae have well-developed perianths. *Lindacarpa* N. Maslova of the Altingioideae has a perianth that is attached slightly above the base of the gynoecium and embraces the flower along a nearly entire length (Maslova and Golovneva, 2000a). In *Anadyricarpa*, perianth elements form a floral tube, which persists in mature fruits (Maslova and Herman, 2004). Various developed perianths are found in ancient Hamamelidoideae, such as *Allonia* Magallón-Puebla, Herendeen et Endress (Magallón-Puebla et al., 1996), *Archamamelis* Endress et Friis (Endress and Friis, 1991), and *Androdecidua* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla et al., 2001).

Gynoecium. Modern *Platanus* is characterized by an apocarpous gynoecium of unstable number of elements (five–eight or, more rarely, three–nine carpels) arranged in two or three circles and supplied with relatively long stylodes. Extinct members of the Platanaceae are characterized by a constant number of carpels in the flower. *Friisicarpus* and *Macginicarpa* had five carpels per flower, and *Quadriplatanus*, *Sarbaya*, and *Archaranthus* had strictly tetramerous flowers. Monomeric gynoecium, a characteristic feature of *Sarbaicarpa* gen. nov., is unknown in modern and fossil Platanaceae.

A syncarpous half-inferior ovary of two carpels is one of the key characters of the Hamamelidaceae. This character dominates in the Hamamelidoideae, Exbucklandioideae, Rhodoleioideae, and Altingioideae. However, unstable number of carpels is known in some genera of the Hamamelidaceae. For instance, *Exbucklandia* of the Exbucklandioideae has one to five carpels, with a dominating bicarpellate gynoecium (Kaul and Kapil, 1974). One to three carpels are present in flowers of *Parrotiopsis* of the Hamamelidoideae (Kapil and Kaul, 1972). Monocarpellate gynoecia are found among dominating bicarpellate gynoecia in *Altingia* and *Liquidambar* (Wisniewski and Bogle, 1982; Bogle, 1986). A monocarpellate gynoecium only occurs in some genera of modern Hamamelidaceae and never prevails. However, the Late Albian–Early Cenomanian genus *Anadyricarpa* (Altingioideae) is exclusively characterized by a monocarpellate gynoecium. This character as well as the shape and size of the infructescences and the number of fruits per head make this genus closer to *Sarbaicarpa* gen. nov. On the other hand, *Anadyricarpa* has a perianth that nearly completely embraces the gynoecium resulting in a floral tube, which persists in mature fruits; its fruit is narrowly elliptical unlike the broadly cuneate fruit of *Sarbaicarpa* gen. nov. In addition, no sterile structures are found in heads of *Anadyricarpa*.

Recently published Turonian *Kasicarpa* has a monomeric gynoecium and is characterized by a mixture of platanaceous and hamamelidaceous characters, namely, those of the subfamilies Altingioideae and Hamamelidoideae (Maslova et al., 2005). Other distinguishing features of this genus are a developed differentiated perianth, orthotropic seed, and the platanaceous morphology of the spermoderm.

It should be noted that although modern members of the Proteales also have a monomeric gynoecium, other floral characters of the Proteales differ from those of *Sarbaicarpa* gen. nov.

The fruit of *Sarbaicarpa* gen. nov. is broadly cuneate with a conical base. Such a shape is described in fruits of Coniacian *Lindacarpa* (Altingioideae). The new genus resembles modern *Liquidambar acalycina* by the general outlines of the fruit. Carpels of this species are similar to those of Late Turonian *Microaltingia* of the Altingioideae (Zhou et al., 2001) and Miocene *Liquidambar changii* (Pigg et al., 2004).

Rare peltate glands were observed on the fruit wall of *Sarbaicarpa* gen. nov. Similar, but more numerous, structures are present on the surface of stamen thecae and carpels of *Quadriplatanus georgianus* Magallón-Puebla, Herendeen et Crane (Platanaceae) from the Coniacian–Santonian of southeastern North America (Magallón-Puebla et al., 1997).

A bunch of hairs is present at the base of the fruit of *Sarbaicarpa* gen. nov., but it is difficult to judge about their length, because the hairs are too fragile. The hairs are only situated at the base of the fruit; the rest of the fruit surface lacks hairs. Such bunches of hairs, although developed in a greater degree, are known in the modern plane tree as an anemochorous adaptation. Different species of *Platanus* show variously developed bunches of hairs. Thus, *P. occidentalis* L. has numerous hairs reaching the half of the fruit length, and the surface of the fruit is also covered with shorter hairs. *P. kerrii* Gagnep. has naked fruits and rare hairs at the fruit base nearly reaching the fruit apex (Takhtajan, 1991).

Seed. The fruit of *Sarbaicarpa* gen. nov. contains a solitary anatropic seed, which tightly fits to the walls and occupies virtually entire volume. Among the Platanaceae, fruits of modern *Platanus* (Boothroyd, 1930; Cronquist, 1981) and fossil *Macginicarpa* and *Friisicarpus* (Manchester, 1986; Friis et al., 1988; Crane et al., 1993) also have a solitary, but orthotropic seed. The only exception is *Quadriplatanus georgianus*, which has non-orthotropic ovules (Magallón-Puebla et al., 1997). Unfortunately, the insufficiently preserved material did not allow a detailed description of the seed morphology. It was only reliably found that the seed has a narrow median bar resembling a narrow wing, and no micropyle was found in the area opposite to the point of the seed attachment.

Anatropic seeds characterize of all members of the Hamamelidaceae, which are significantly variable by

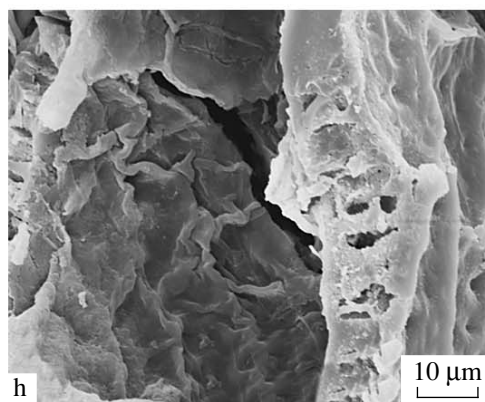
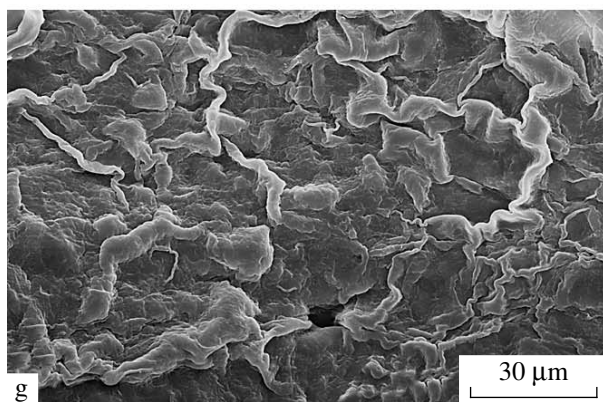
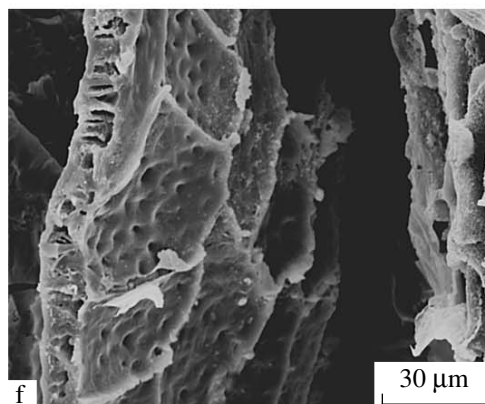
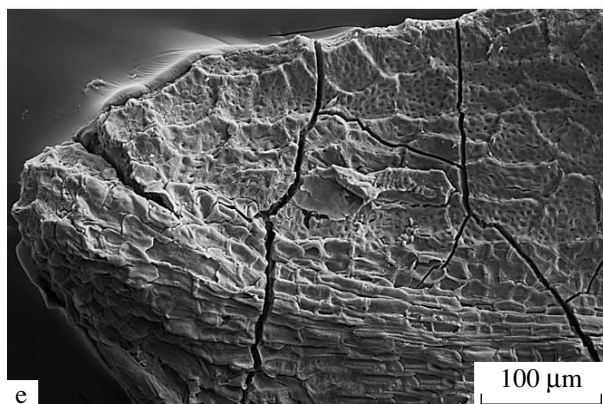
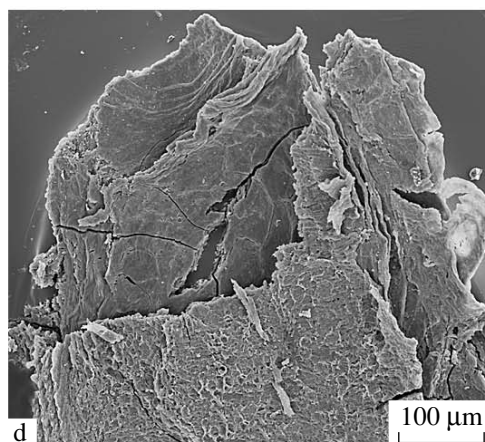
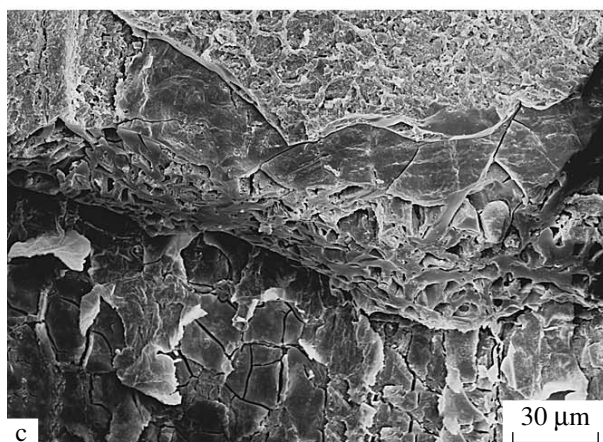
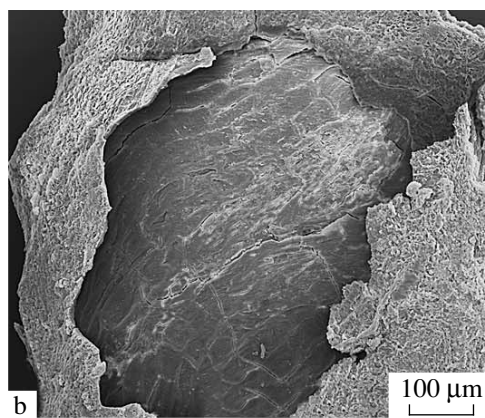
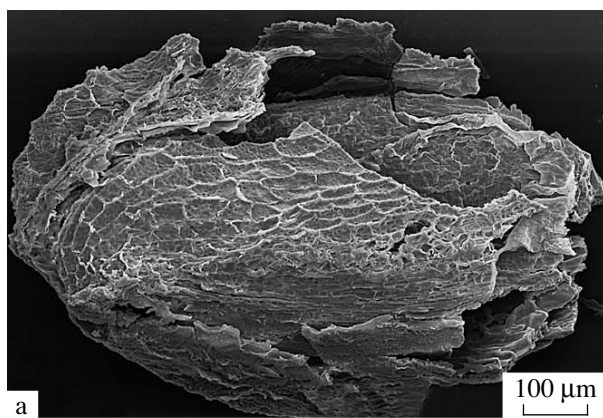


Fig. 4. *Sarbaicarpa shilinii* N. Maslova, western Kazakhstan, Sarbai locality, Zhirkindekskaya Formation, Cenomanian–Turonian, holotype PIN, no. 1/5266, SEM: (a, b, d) fruit with a solitary seed; (c) transverse section of fruit wall and seed; (e) seed fragment; (f) spermoderm section, note remnants of the anticlinal walls of polygonal cells of the external spermoderm layer and layer of small palisade sclerenchyma cells; (g) inner layer of the spermoderm, formed by cells with undulate anticlinal walls; (h) longitudinal section of the spermoderm showing cells of three layers.

the number of ovules per ovary. All members of the Hamamelidoideae have one ovule in the ovary. Genera of other subfamilies have 5–8 (*Disanthus* Maxim., *Exbucklandia*, *Mytilaria* Lecomte, and *Chunia*), 10–20 (*Rhodoleia* Champ. ex Hook), 20–30 (*Liquidambar*), and 28–47 (*Altingia*) ovules (Endress, 1989a). *Sarbaicarpa* gen. nov. is comparable with members of the Hamamelidoideae by the number of ovules (one) and seed type (anatropic).

Anatropic seeds of modern Altingioideae bear more or less developed rounded or distal wings, whereas the majority of hamamelidaceous genera have ballistic wingless seeds (Tiffney, 1986). Wings in Altingioideae vary from a large distal wing in *Liquidambar formosana* Hense and *L. styraciflua* L. to a shorter wing in *L. orientalis*. *L. acalycina* has a small rounded or triangular wing, resembling that in *Altingia* and *Semiliquidambar*. The seed of Miocene *Liquidambar changii* has a rounded wing (Pigg et al., 2004); and the seed of Late Turonian *Microaltingia* lacks a developed wing, but has a distinct ring rib (Zhou et al., 2001). The seed of *Sarbaicarpa* gen. nov. lacks such structures.

The morphology of the spermoderm of *Sarbaicarpa* gen. nov. is similar to that of modern Altingioideae. The spermoderm of the new genus is relatively thin, formed by a few layers, and well differentiated. The seed surface of *Sarbaicarpa* gen. nov. resembles that of modern *Liquidambar acalycina* (Ickert-Bond et al., 2005). These authors noted that in species of *Liquidambar* cells of the seed surface are nearly isodiametric. *Sarbaicarpa* gen. nov. has epidermal cells diminishing from the medial area toward the periphery of the seed.

The similarity between *Sarbaicarpa* gen. nov. and members of the Altingioideae and Platanaceae also includes the morphology of the mechanical layer, composed of relatively small thick-walled palisade sclereids, nearly lacking cellular content. Similarly to members of the Altingioideae and Platanaceae, the number of cellular layers in *Sarbaicarpa* gen. nov. varies from one to three. The Hamamelidoideae differs by a thicker mechanical tissue, with a greater number of cellular layers and variable structure of sclereids (Takhtajan, 1991). Melikian (1973a, 1973b) concluded that the thin seed wall in *Liquidambar* and *Altingia* is more specialized in comparison to relatively thick walls in other members of the Hamamelidaceae s.s., which are considered more primitive according to many other botanists.

Sarbaicarpa gen. nov. has a relatively thick endosperm, which makes the new genus similar to members of the Hamamelidoideae. Unlike the Hamamelidoideae, the endosperm in the Altingioideae is very scanty. In modern species of *Platanus*, the endosperm is nearly completely digested by a growing embryo and is represented by a thin layer at the periphery of the mature seed (Poddubnaya-Arnol'di, 1982).

Sterile elements. Two types of sterile structures are known: phyllomes and staminodes. Staminodes are reduced stamens, able (to a greater or lesser extent) to produce sterile pollen. Phyllomes are sterile structures in pistillate flowers, different from staminodes. Their functions are still a matter of discussion. Sterile structures in reproductive organs of modern and especially fossil plants are difficult to interpret. Thus, Tong (1930)

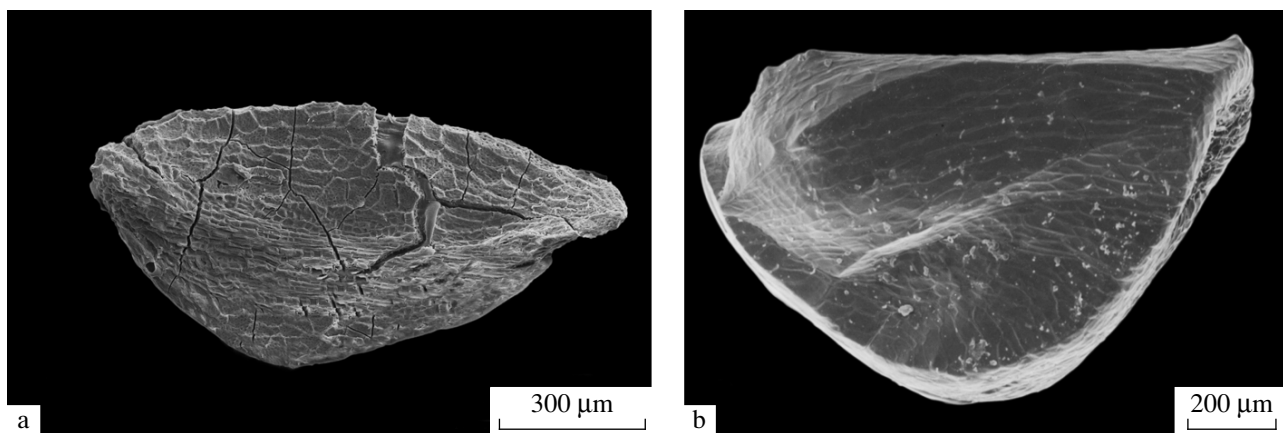


Fig. 5. *Sarbaicarpa shilinii* N. Maslova, western Kazakhstan, Sarbai locality, Zhirkindekskaya Formation, Cenomanian–Turonian (a) and modern *Liquidambar formosana* L. (b), SEM: (a) holotype PIN, no. 1/5266; (b) collection of N. Maslova.

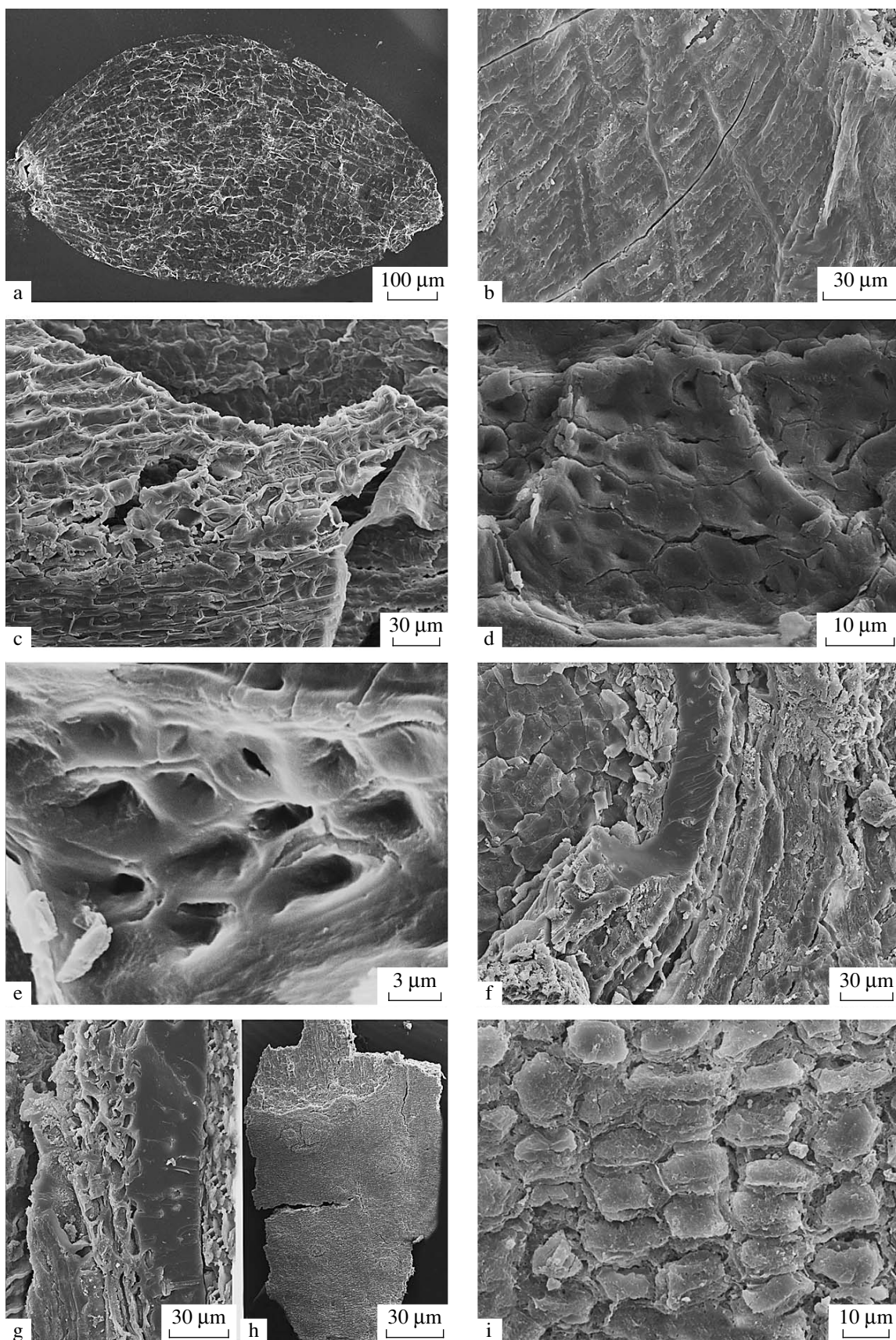


Fig. 6. *Sarbaicarpa shilini* N. Maslova, western Kazakhstan, Sarbai locality, Zhirkindekskaya Formation, Cenomanian–Turonian, holotype PIN, no. 1/5266, SEM: (a) anisotropic seed after maceration; (b) cells of the seed surface showing cuticle striation, perpendicular to the longer axis of the cells; (c) fragment of seed surface; (d) remnants of the anticlinal walls of a trapezoid cell of the external layer of the spermoderm, thick-walled sclerenchyma cells of the second layer of the spermoderm are visible in plan; (e) thick-walled sclerenchyma cells of the second layer of the spermoderm; (f, g) longitudinal section of the seed in the area of the suture, note an entire sclerenchyma layer; (h) endosperm; (i) endosperm cells.

believed that there are no crucial differences between staminodes and phyllomes and considered them as one type of sterile structures in the flower.

Sterile structures vary in size, shape, and position within the flower (intrafloral) or outside it (extrafloral). As far as such structures are very small and occur in small and dense inflorescences, the study of their morphology and typology is complicated. Thus, Croizat (1947) believed that phyllomes were situated at the periphery of the flower and came directly from the receptacle. Later, it was shown that these structures are supplied with the same conductive bundles as stamens and carpels, and there are no proofs of the extrafloral nature of phyllomes (Bogle, 1986).

The position of sterile elements is not always reliably determinable, and their homologation is not always unequivocal, that is particularly true in case of fossil material. When phyllomes are situated between the stamen circle and ovary, one can suppose that they are rudiments of these floral elements (Vink, 1957). Some authors believe that they are elements of the calyx (Clarke, 1858; Hooker and Thomson, 1858; Oliver, 1867), underdeveloped styles in sterile flowers occurring among normal flowers (Harms, 1930), staminodes (Tong, 1930), papillae (Schmitt, 1965), or nectaries (Leeuwen, 1938).

Krassilov (1989) believed that intrafloral phyllomes were originally sterile and their similarity to elements of perianth, stamens, and carpels was derived, as well as functions acquired in relation to insect pollination.

Extrafloral phyllomes were interpreted as bracts supporting flowers (Guillaumin, 1920), bracteoles or modified leaves associating with inflorescences (Gifford and Foster, 1989), or groups of undeveloped flowers (Ickert-Bond et al., 2005).

Extrafloral phyllomes are known in modern members of several hamamelidaceous subfamilies, such as *Altingia* and *Liquidambar* of the Altingioideae, *Exbucklandia* of the Exbucklandioideae, and *Rhodoleia* of the Rhodoleioideae, as well as in *Platanus*. They vary in size and shape; the latter character is specific of some species. Thus, needle-shaped phyllomes are known in *Liquidambar formosana* and *L. acalycina*; wider and cone-shaped, in *L. styraciflua*; and wide and slightly emerging, in *L. orientalis*. Smaller verrucate structures were found in the same position in *Altingia* (Ickert-Bond et al., 2005, 2007). According to Bogle (1986), phyllomes in some species of *Liquidambar* are superficially similar to abortive pistils, but no receptacle-resembling structures or indices of ovule formation were detected. Moreover, Wisniewski and

Bogle (1982) showed that these structures appear later than stamens and carpels during ontogenesis. The function of phyllomes is still unclear, though, for example, they are glandular in *Rhodoleia* (Bogle, 1987).

Sarbaicarpa gen. nov. is characterized by two morphologically different types of extrafloral sterile structures. The former type includes relatively large elements, which are comparable in size with the fruits and consist of a small peduncle and a massive and slightly oblate semispherical part. They are irregularly distributed within the infructescence. They are less numerous than needle-shaped sterile structures: about eight per infructescence. From eight to twelve extrafloral phyllomes occur in modern species of *Liquidambar*; they are uniform within a species and vary in shape and size among the species (Ickert-Bond et al., 2005). Such large sterile structures are unknown in modern and fossil members of the Platanaceae and Hamamelidaceae. Flowers of Late Turonian *Microaltingia* (Altingioideae) have two or three circles of fleshy rounded phyllomes, situated concentrically at the margin of the hypanthium and bearing stomata. They are slightly similar in shape to sterile structures of the second type of *Sarbaicarpa* gen. nov., but much smaller in absolute sizes as well as comparing to the length of the carpel. The surface of the semispherical sterile structures of *Sarbaicarpa* gen. nov. is covered with numerous rounded trichomes, which leave distinct rounded bases after shedding. Distinct cuticular thickenings around the trichome aperture are visible on the inner surface of the cuticle of these structures. Similarly, leaves of modern *Platanus* have rounded bases of trichomes on the adaxial surface, which have apertures on the inner surface of the cuticle, armored with additionally deposited cutin (Carpenter et al., 2005). Cuticular formations surrounding stomatal apertures are also detected on the inner surface of the leaf cuticle of modern *Liquidambar*.

Extrafloral structures of the first type in *Sarbaicarpa* gen. nov. most probably attracted insect-pollinators. It is not excluded that these structures could have produced nectar, and numerous gland trichomes probably had a secretory function. Nectar production is unknown in modern *Platanus* and fossil Platanaceae. Several fused scales situated between the androecium and gynoecium produce nectar in some hamamelidaceous genera: *Loropetalum* R. Brown ex Reich., *Tetrathirium* Benth., *Maingaya* Oliv., *Corylopsis* Sieb. et Zucc., *Fortunearia* Rehd. et Wils., and *Rhodoleia* (Endress, 1967). In *Hamamelis*, staminodes produce nectar (Endress, 1967). Nectaries are situated at the base of petals in *Disanthus* (Mizushima, 1968; Endress, 1989).

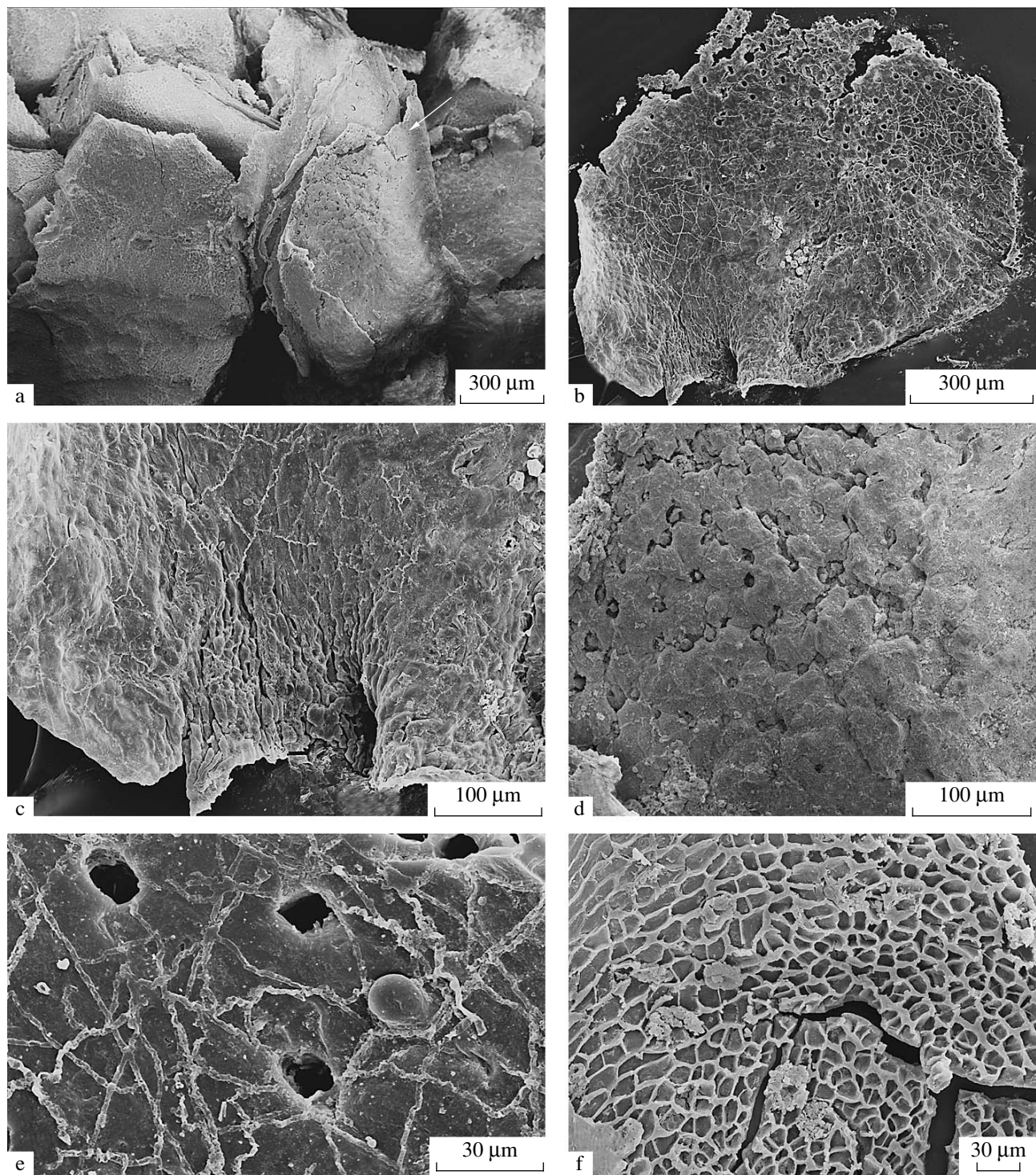


Fig. 7. *Sarbaicarpa shilini* N. Maslova, western Kazakhstan, Sarbai locality, Zhirkindekskaya Formation, Cenomanian–Turonian, SEM: (a) PIN, no. 2/5266; (b–f) holotype PIN, no. 1/5266; (a) fragmentary head, note fruits and a semispherical sterile structure (arrow); (b) semispherical sterile structure after maceration; (c) peduncle of a semispherical sterile structure; (d, e) surface of a semispherical sterile structure before (d) and after (e) maceration; (f) inner surface of the cuticle, note cuticular thickenings.

Nectar disks of *Exbucklandia* are occasionally erroneously interpreted as a calyx (Endress, 1989a). There is a hypothesis that sterile structures of *Liquidambar styraciflua* can be glands or nectaries judging from their

morphology and the moment of appearance during the ontogenesis; however, there are no data about their secretory activity or histology (Wisniewski and Bogle, 1982).

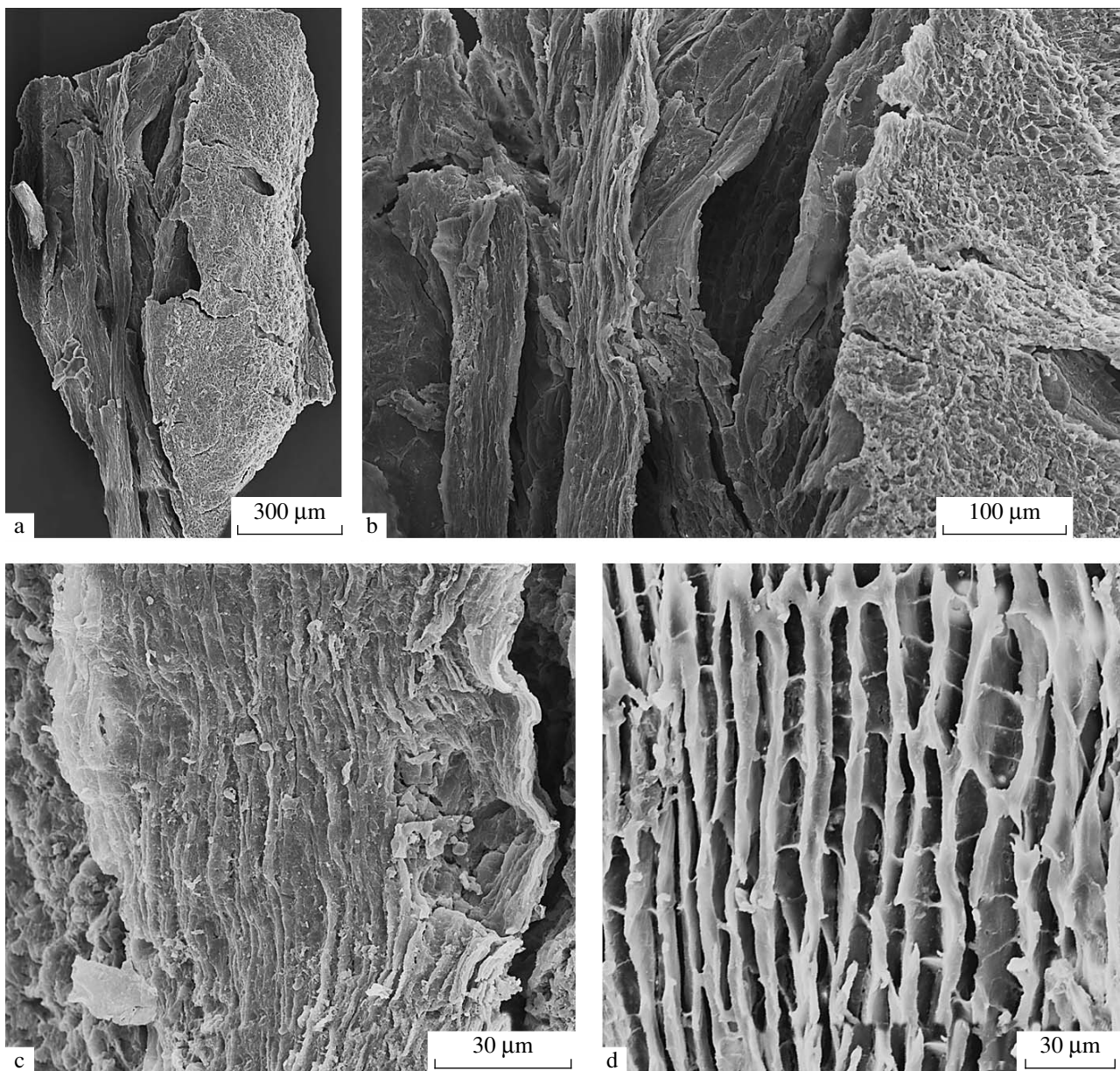


Fig. 8. *Sarbaicarpa shilini* N. Maslova, western Kazakhstan, Sarbai locality, Zhirkindekskaya Formation, Cenomanian–Turonian, holotype PIN, no. 1/5266, SEM: (a, b) fruit and two linear sterile structures; (c) linear sterile structure, note transversely striated cuticle; (d) epidermal cells of a linear sterile structure, inside view.

Extrafloral sterile structures of *Sarbaicarpa* gen. nov. of the second type are narrow, parallel-margined, needle-shaped elements, reaching at least a half of the fruit length. Since fruits were relatively loosely situated in the infructescences of *Sarbaicarpa* gen. nov. and the needle-shaped structures were very fragile, their apices were broken during fossilization. It is difficult to deduce whether the apices differed from the basal parts and showed a more elaborated morphology. No regularity was detected in the arrangement of these structures. They were situated chaotically among the fruits, occasionally, in pairs (Fig. 8a); in total, about 15 such struc-

tures occurred in one infructescence. These structures resemble the fruits by the degree of cutinization: both are relatively strongly cutinized, the cuticles are striate, but the fruit cuticle is transversely striate, and the cuticle of the needle-shaped sterile structures is longitudinally striate. It is difficult to hypothesize about the function of these structures, particularly because no apices are preserved. It is unlikely that they were staminodes, since no pollen grains were found either on them or other elements of the infructescence. The idea that they could have been perianth elements is contradicted by the fact that they are irregularly situated among fruits.

Their shape is similar to that of needle-shaped extrafloral phyllomes in *Liquidambar formosana* and *L. acalycina*; however, they are much longer than phyllomes in modern species of *Liquidambar* and differ by strongly cutinized striate surfaces. There is a possibility that they are comparable with bracts, supporting inflorescences in some members of the Hamamelidaceae and attracting insects by their bright coloring (e.g., *Parrotiopsis*, Kapil and Kaul, 1972); however, it cannot be said with confidence because of their irregular distribution.

Sterile structures in fossil flowers have been extremely rarely recorded. Maslova and Krassilov (1997) found two types of such structures differing in size and shape in *Evacarpa* N. Maslova et Krassilov (Altingioideae). The smaller and narrower structures were interpreted as phyllomes, and larger and wider structures were interpreted as staminodes, which apparently produced no pollen. *Viltyngia* N. Maslova, a genus combining characters of the hamamelidaceous subfamilies Exbucklandioideae, Hamamelidoideae, and Altingioideae, probably had staminodes which produced a considerable amount of pollen (Maslova and Golovneva, 2000b). Aggregations of stuck underdeveloped pollen grains, which are much smaller than fertile pollen, were found on the surface of the gynoecium. Staminodes are known in Santonian–Campanian *Archamamelis* of the Hamamelidoideae (Endress and Friis, 1991) and in Eocene staminate heads related with *Hamamelis* and *Corylopsis* by several characters (Manchester, 1994). Heads from the Turonian Raritan Formation of New Jersey, which show both platanaceous and hamamelidaceous characters, contained in their staminate flowers normal stamens and staminodes bearing nectary glands (Crepet et al., 1992; Crepet et al., 1996). Staminodes in staminate flowers of *Bogutchanthus* resembled mature stamens in shape and were situated between mature stamens and perianth elements, probably partially fusing to their bases (Maslova et al., 2007).

Associating staminate inflorescences and leaves.

Staminate heads of *Sarbaya* of the Platanaceae were earlier described from the same deposits (Krassilov and Shilin, 1995). They are characterized by tetramerous flowers without a perianth and tricolporate pollen grains.

Lobate leaves earlier assigned to *Platanus pseudoquillelmae* Krass. and *P. cuneiformis* Krass. (Shilin, 1986) were found associating with the infructescence of *Sarbaicarpa* gen. nov. Among typically *Platanus*-like characters, these leaves show some peculiarities that make them closer to members of the Altingioideae. In particular, these are repeated intercalary veins that are situated between secondary veins and reach approximately a half of the distance to the leaf margin and well-developed marginal glands. Krassilov and Shilin (1995) showed that the epidermal morphology of these leaves shows characters of the Fagaceae. Maslova et al. (2005) already discussed that

the assignment of Cretaceous leaf remains superficially resembling leaves of the modern plane tree to the genus *Platanus* is unjustified.

CONCLUSIONS

1. Infructescences of the new genus *Sarbaicarpa* gen. nov. combine platanaceous and hamamelidaceous characters. Characters shared by the two families include the shape of the compound inflorescence (Platanaceae/Altingioideae and some members of the Exbucklandioideae), no perianth (modern *Platanus*/Altingioideae, some members of the Hamamelidoideae and Exbucklandioideae), a solitary seed in the fruit (Platanaceae/Hamamelidoideae), similar architecture of the spermoderm (modern *Platanus*/modern members of the Altingioideae), and sterile structures in infructescences (modern *Platanus*/Altingioideae, Rhodoleioideae, and some members of the Exbucklandioideae).

The characters only ascribed to the Hamamelidaceae and found in *Sarbaicarpa* gen. nov. are a monocarpellate gynoecium, which occurs, though does not dominate in some members of the Altingioideae and the Hamamelidoideae, an anatropic seed, which is present in all members of the Hamamelidaceae, and a developed endosperm, which is a character of the Hamamelidoideae. The presence of a hair bunch at the fruit base is only known in the Platanaceae (modern *Platanus* and some fossil members of the family).

2. *Sarbaicarpa* gen. nov. is distinctive by a combination of characters more or less characteristic of the four subfamilies of the Hamamelidaceae: the Altingioideae, Hamamelidoideae, Exbucklandioideae, and Rhodoleioideae. The new genus resembles the Altingioideae by such characters as the shape of the capitate infructescence, no perianth, a monocarpellate gynoecium (it rarely occurs in modern members of the Altingioideae), micromorphology of the seed surface, spermoderm morphology, and sterile structures in the infructescence. The common features with members of the Hamamelidoideae are the absence of the perianth (in some members, such as *Distylium*, *Sycopsis dunnei*, and *Parrotiopsis*), a monocarpellate gynoecium (occurs in *Parrotiopsis*), a solitary seed in the fruit, and a developed endosperm. *Sarbaicarpa* gen. nov. is similar to *Exbucklandia* and *Chunia* (Exbucklandioideae) by capitate infructescences, naked flowers, a monocarpellate gynoecium, and sterile elements in the infructescence. *Sarbaicarpa* gen. nov. resembles the Rhodoleioideae by the total absence of the perianth (or weak development in some species of *Rhodoleia*) and the presence of sterile structures. To conclude, the find of the Cenomanian–Turonian infructescence of *Sarbaicarpa* gen. nov. confirms the earlier expressed hypothesis (Maslova and Golovneva, 2000; Maslova, 2003) about the close relationships between the Altingioideae and other subfamilies of the Hamamelidaceae, and, particularly, the Hamamelidoideae and Exbuck-

landioideae and supports the supergeneric system of the Hamamelidaceae, proposed by Endress (1989a, 1989b).

3. The mosaic combination of morphological and anatomical characters in the Cenomanian–Turonian infructescence *Sarbaicarpa* gen. nov. and the association between these reproductive structure and leaves showing the typical morphology of the modern plane tree and some altingioid characters confirm the earlier expressed opinion about the close relationships between the Platanaceae and Hamamelidaceae. Earlier, a body of paleobotanical evidence was amassed in favor of relationships between the Platanaceae and Hamamelidaceae (Crepet et al., 1992; Crepet and Nixon, 1996; Maslova and Herman, 2004; Maslova et al., 2005, 2007).

4. Paleobotanical studies have shown a considerable heterogeneity of Cretaceous platanoids, which include more than one family. The taxonomic solution for these fossil finds apparently demands a completely new approach: their classification within extinct families, in various degrees related to the modern family Platanaceae. This approach contradicts the existing opinion about the wide occurrence of the modern families Platanaceae and Hamamelidaceae in the Cretaceous.

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