

# A diverse pollen assemblage found on *Friisicarpus* infructescences (Platanaceae) from the Cenomanian–Turonian of Kazakhstan



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## ARTICLE INFO

### Article history:

Received 3 June 2015

Received in revised form

10 August 2015

Accepted in revised form 24 August 2015

Available online xxx

### Keywords:

Cretaceous

Platanaceae

Angiosperms

Exine ultrastructure

Reticulate sculpture

Entomophily

## ABSTRACT

Pollen grains found on, or within, pistillate reproductive structures are described for numerous gymnosperms and angiosperms. Attribution of these pollen grains to the macrofossils is often risky and requires additional evidence. This study, based on the material from the Cenomanian–Turonian of Kazakhstan, is the first to document in detail different types of pollen adhering to platanoid infructescences of *Friisicarpus sarbaensis*. Infructescence parts were examined under SEM in search of pollen. Pollen grains were removed from SEM stubs and studied with LM and TEM. About 250 pollen grains adhering to infructescence axes and carpels were studied; they are small, reticulate (rarely foveolate), tricolpate or tricolporate, and columellate. At least nine pollen types have been distinguished based mainly on the details of the exine sculpturing. The exine ultrastructure was characterized for four prevailing types. Considering pollen morphology and ultrastructure, three types were shown to be produced by platanoids and one was probably ranunculid. Other pollen types are harder to refer to a certain group, though one of them probably belongs to Hamamelidaceae and another one shows exine sculpturing similar to Chloranthaceae pollen. One of the types prevails (about 170 pollen grains) and resembles pollen found on inflorescences of other *Friisicarpus* species, so we consider that this type was produced by the parent plant. Pollen grains of another type are identical to pollen of *Sarbaya radiata* from the same locality. The diversity and abundance of different pollen types of the similar size and sculpture found on the infructescences of *Friisicarpus sarbaensis* favour entomophily of this plant but challenge specific plant–insect specialization.

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## 1. Introduction

The Cenomanian–Turonian Sarbay locality (western Kazakhstan) is characterized by a unique preservation of fossil plants. Reproductive structures are three dimensionally preserved, leaves have well-preserved cuticles, and this allows the study of the plant anatomy. A considerable number of platanoid taxa and related groups have been found such as staminate reproductive organs of *Sarbaya* (Krassilov & Shilin, 1995) and *Krassilovianthus* (Maslova, Tekleva, & Remizowa, 2012), pistillate reproductive organs of *Sarbaicarpa* (Maslova, 2009), and leaves of *Ettingshausenia sarbaensis* N. Maslova et Shilin (Maslova & Shilin, 2011). Platanoid capitate infructescences referred to *Friisicarpus sarbaensis* N. Maslova et Tekleva (Maslova & Tekleva, 2012) based on their micro-morphology have also been described from the Sarbay locality. We

found pollen grains adhering to carpel surfaces and infructescence axes of *F. sarbaensis*. Although all these pollen grains were small, (micro)reticulate, and tricolpate, at least three different morphological types could be distinguished among them (Maslova & Tekleva, 2012). At first sight, any of the found pollen types could have been produced by *F. sarbaensis*, as all discovered pollen had morphology similar to that of platanoid pollen. A further study of more specimens of inflorescence fragments revealed additional pollen types.

A number of studies have described fossils where pollen grains were found adhering to the fruit surface (Friis, Crane, & Pedersen, 1988; Maslova, Kodrul, Tekleva, & Aleksandrova, 2014; Moreau et al., 2013; Zhou, Crepet, & Nixon, 2001), and there is always a question of whether the pollen grains belonged to the same plant or were brought in by chance and are not related at all. Interestingly, so far one pollen type per a given species has been described for platanoid and related taxa (Crane, Pedersen, Friis, & Drinnan, 1993; Friis et al., 1988; Maslova, Golovneva, & Tekleva, 2005, 2011; Pedersen, Friis, Crane, & Drinnan, 1994; Wang, 2008).

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Besides, the pollen grains were of a common platanoid type and was believed with some certainty to belong to the same plant.

Considering already known and studied reproductive structures from the same locality that could have produced such pollen, along with information on the morphology and ultrastructure of similar pollen from the locality, it becomes particularly important to study adhering pollen in detail. This will help to determine which pollen type could have belonged to the plant with infructescences described as *Friisicarpus sarbaensis* and which types could have been produced by other members of the Sarbay flora. Also this could give grounds for associating taxa described for staminate inflorescences with the studied infructescences.

## 2. Material and methods

The fossil flora from the Cenomanian–Turonian deposits of Sarbay locality (quarry near Rudnyi city, western Kazakhstan, Shet-Irgiz Formation) was collected by Dr. P.V. Shilin (Institute of Botany and Plant Introduction, Almaty city) in 1978. He then gave a number of specimens for a microstructural study to one of us (N.P. Maslova) in 2009. The Shet-Irgiz Formation is interpreted as being of lacustrine to alluvial origin and consists mainly of silt, with some clay and sand (Levina et al., 1990; Frumin & Friis, 1999). A detailed map and description of the stratigraphy can be found in Shilin (1986), Levina et al. (1990), and Frumin and Friis (1999).

Pollen grains adhering to the surface of infructescences of *Friisicarpus sarbaensis* (see description of the infructescences in Maslova & Tekleva, 2012) were studied by means of light (LM), scanning (SEM) and transmission (TEM) electron microscopy.

Four specimens (417/88, 417/89, 417/98, 417/95) have been studied. Most pollen grains were obtained from the holotype 417/88, which is represented by the fragment of the axis with nine capitate infructescences. Fragments of infructescences were released from the rocks in hydrofluoric acid; some fragments were also macerated in concentrated nitric acid and alkali. The fruit elements (both after hydrofluoric acid and after maceration in concentrated nitric acid and alkali) were mounted on SEM stubs using nail polish and studied under SEM. The studied pollen grains (when possible) were removed from the infructescence parts for study with LM and/or TEM. Some of infructescence fragments were disintegrated and searched for pollen grains in LM before examination in SEM. The pollen grains were then studied with LM, SEM and TEM according to Tekleva, Naryshkina, and Evstigneeva (2014).

The work was performed at the A.A. Borissiak Paleontological Institute, Russian Academy of Sciences (Carl Zeiss Axioplan-2 LM) and at User Facilities Centers of M.V.Lomonosov Moscow State University and A.A. Borissiak Paleontological Institute, Russian Academy of Sciences (CamScan SEM, Jeol 100B TEM and Jeol 1011 TEM). The studied specimens 417/88, 417/89, 417/98, and 417/95 are housed at the A.A. Borissiak Paleontological Institute, Russian Academy of Sciences. The terminology follows Hesse et al. (2009).

## 3. Results

Nine types of pollen grains were found on the surface of the carpels and infructescence axes of *Friisicarpus sarbaensis* (Fig. 1). Pollen grains of all types are small, spheroidal to ellipsoidal, rounded or oval in equatorial view, rounded trilobate in polar view, tricolpate or tricolporate, (micro) reticulate, rarely foveolate, and columellate (Figs. 2–4). In dispersed state they can be referred to *Tricolpopollenites* (tricolpate pollen) and *Tricolpoporopollenites* (tricolporate pollen) according to the formal classification of pollen grains.

### 3.1. Pollen type 1 (Fig. 2A–R)

Number of pollen grains: 169 or more, found as single grains and in clumps.

SEM. The polar axis is 11.1 (8.9–14.5)  $\mu\text{m}$ , and the equatorial diameter is 8.5 (5.7–11.7)  $\mu\text{m}$ . The sculpture is microreticulate with rounded polygonal or elongated lumina. On average there are about two reticulum meshes per 1  $\mu\text{m}$ . The muri are rounded and 0.25 (0.14–0.5)  $\mu\text{m}$  thick. The colpus margin is bordered by an uneven row of somewhat smaller reticulum meshes. The pollen grains appear to be tricolporate, colpi are 8 (6–12.1)  $\mu\text{m}$  long, ora are from 1.1 to 1.4  $\mu\text{m}$  in diameter. Ora were seen on several pollen grains only (Fig. 2E, G, J, K, N), as the pollen usually has closed colpi (Fig. 2I). The aperture membrane is granular (Fig. 2M, N). The exine structure is seen on broken pollen with a tectum 0.24–0.3  $\mu\text{m}$  thick, columellae 0.29–0.33  $\mu\text{m}$  high and 0.21–0.25  $\mu\text{m}$  wide, and an inner layer 0.21–0.25  $\mu\text{m}$  thick (Fig. 2F).

TEM. The ectexine is about 0.99–1.24  $\mu\text{m}$  thick, and the tectum is 0.33–0.44  $\mu\text{m}$  thick. The columellae are 0.21–0.35  $\mu\text{m}$  high and 0.15–0.25  $\mu\text{m}$  wide. The foot layer is about 0.33–0.4  $\mu\text{m}$  thick. The endexine is two-layered, more electron dense than the ectexine; in non-apertural regions the outer layer is more or less uniform in thickness throughout the pollen and is about 0.06–0.08  $\mu\text{m}$  thick, the inner layer is about 0.06  $\mu\text{m}$  thick or thicker, especially towards the apertural regions (Fig. 2L, O, R). The inner endexine layer is homogeneous in non-apertural regions and finely lamellate in apertural ones, and the outer endexine layer is granular (Fig. 2L, P, Q).

### 3.2. Pollen type 2 (Fig. 3A–J)

Number of pollen grains: 40, found mostly in clumps.

SEM. The polar axis is 15.7 (13.6–18.6)  $\mu\text{m}$ , and the equatorial diameter is 12.8 (10.6–15.7)  $\mu\text{m}$ . The sculpture is microreticulate. The lumina are of two types, rounded and elongated, which are intermixed; on average there are about 2.5 reticulum meshes per 1  $\mu\text{m}$ . The muri are rounded and 0.2 (0.18 – rarely up to 0.27)  $\mu\text{m}$  thick. Close to the colpus margin the reticulum breaks up, and some of the lumina open towards the aperture membrane (Fig. 3D, E). The pollen grains are tricolporate, colpi are 10.1 (7.9–11.8)  $\mu\text{m}$  long, the aperture membrane is granular (Fig. 3A, B, E).

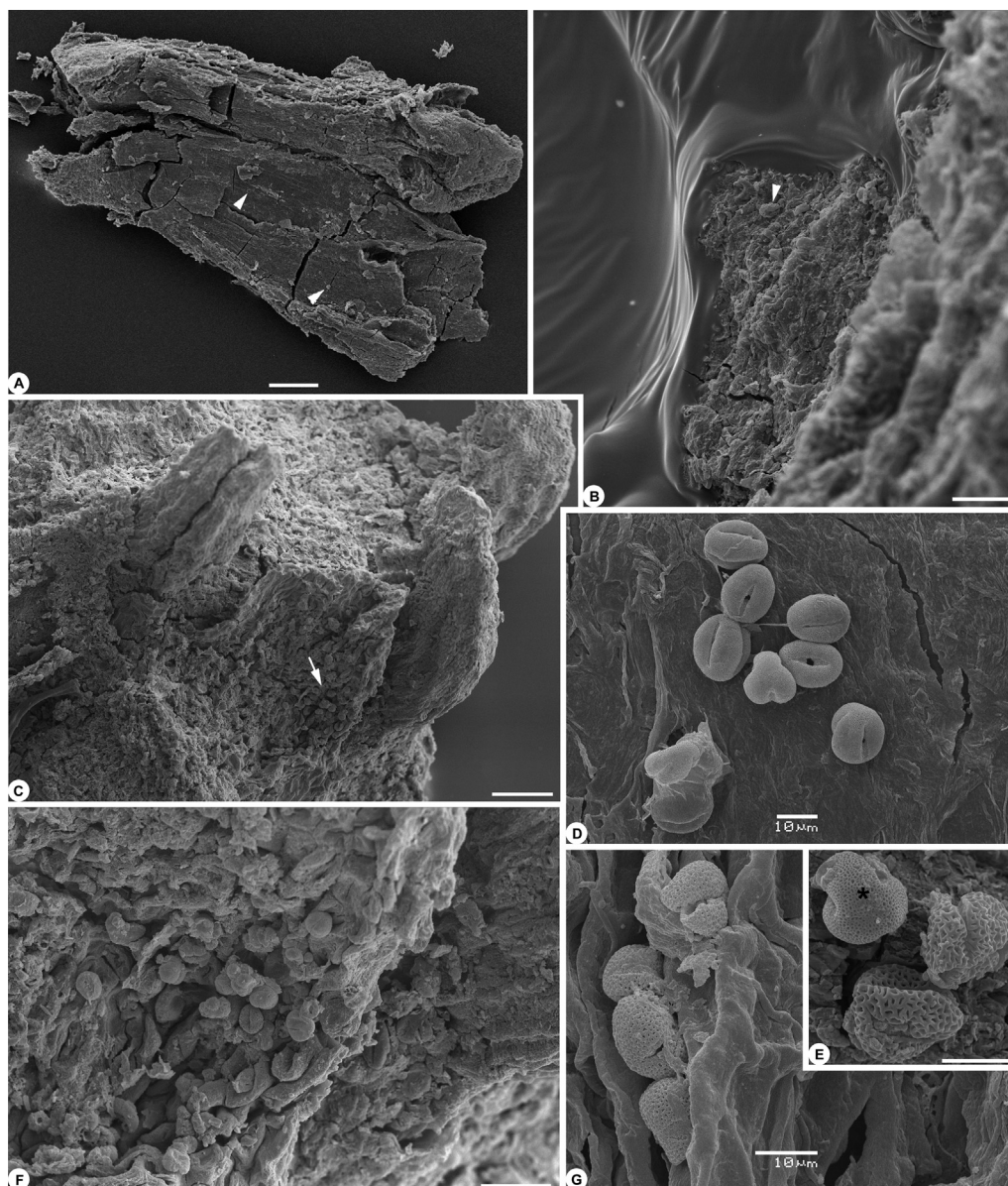
TEM. The ectexine is about 1.03–1.15  $\mu\text{m}$  thick, and the tectum is about 0.39–0.55  $\mu\text{m}$  thick consisting of muri with acute tops. The columellae are about 0.16–0.26  $\mu\text{m}$  high and 0.11–0.26  $\mu\text{m}$  wide; the foot layer is about 0.46–0.55  $\mu\text{m}$  thick. The endexine is more electron dense than the ectexine, granular, about 0.37–0.41  $\mu\text{m}$  thick in non-apertural regions, greatly increasing in thickness towards apertures (Fig. 3G). The endexine is probably two-layered, but its preservation does not allow clear distinction of the layers (Fig. 3I, J).

### 3.3. Pollen type 3 (Fig. 3K–W)

Number of pollen grains: 13, found in clumps.

SEM. The polar axis is 14.7 (11.6–18.2)  $\mu\text{m}$ , and the equatorial diameter is 12.2 (9.2–14.4)  $\mu\text{m}$ . The sculpture is microreticulate with polygonal, mostly pentagonal lumina. On average there are about 2.5–3 reticulum meshes per 1  $\mu\text{m}$ . The tops of the muri are acute, rather thin and 0.13 (0.08–0.17)  $\mu\text{m}$  thick. Close to the colpus margin the reticulum breaks up and some of the lumina open towards the aperture membrane (Fig. 3R). The pollen grains are tricolporate, the colpi are 8.6 (5.8–8.9)  $\mu\text{m}$  long, the ora are from 1.3 to 2.3  $\mu\text{m}$  in diameter. The aperture membrane is granular (Fig. 3L, P, Q).

TEM. The ectexine is about 0.95–1.36  $\mu\text{m}$  thick, the tectum is 0.42–0.52  $\mu\text{m}$  thick. The columellae are 0.2–0.28  $\mu\text{m}$  high and 0.18–0.2  $\mu\text{m}$  wide, and the foot layer is about 0.38–0.41  $\mu\text{m}$  thick. The endexine is two-layered in non-apertural regions,



**Fig. 1.** Parts of the inflorescence bearing pollen of different types, SEM. A–C. Pollen grains (arrowheads and arrow) seen as single grains or in clumps. An enlarged photograph of a pollen grain figured in B is shown in Fig. 4S. D. Group of Type 2 pollen. E. Three pollen grains of Type 1 (asterisk) and Type 5. F. Enlarged view of pollen from C. G. Several pollen grains of Type 4. Scale bar in A = 200 µm; in B, F = 30 µm; in C = 100 µm; in D, E, G = 10 µm.

approximately 0.23–0.45 µm thick with the outer, less electron dense layer about 0.05 µm thick and homogeneous, and the inner layer granular (Fig. 3T, U). The endexine is more electron dense than the ectexine and increases considerably in thickness towards the apertural regions, where the outer endexine layer becomes finely lamellate (Fig. 3V, W).

#### 3.4. Pollen type 4 (Fig. 4A–H)

Number of pollen grains: 10, found in clumps.

SEM. The polar axis is 13.4 (11.5–14.4) µm, and the equatorial diameter is 12.1 (9.6–13.4) µm. The sculpture is microreticulate with rounded or elongated lumina. On average there is up to one reticulum mesh per 1 µm. The muri are rounded and 0.44–0.5 µm thick. The colpus margin is mostly bordered by a continuous line of the same thickness as the muri (Fig. 4A, C, D). The pollen grains are tricolpate, the colpi are 10.1 (8.5–11.9) µm long, the aperture

membrane is granular with densely packed granules (Fig. 4A–D).

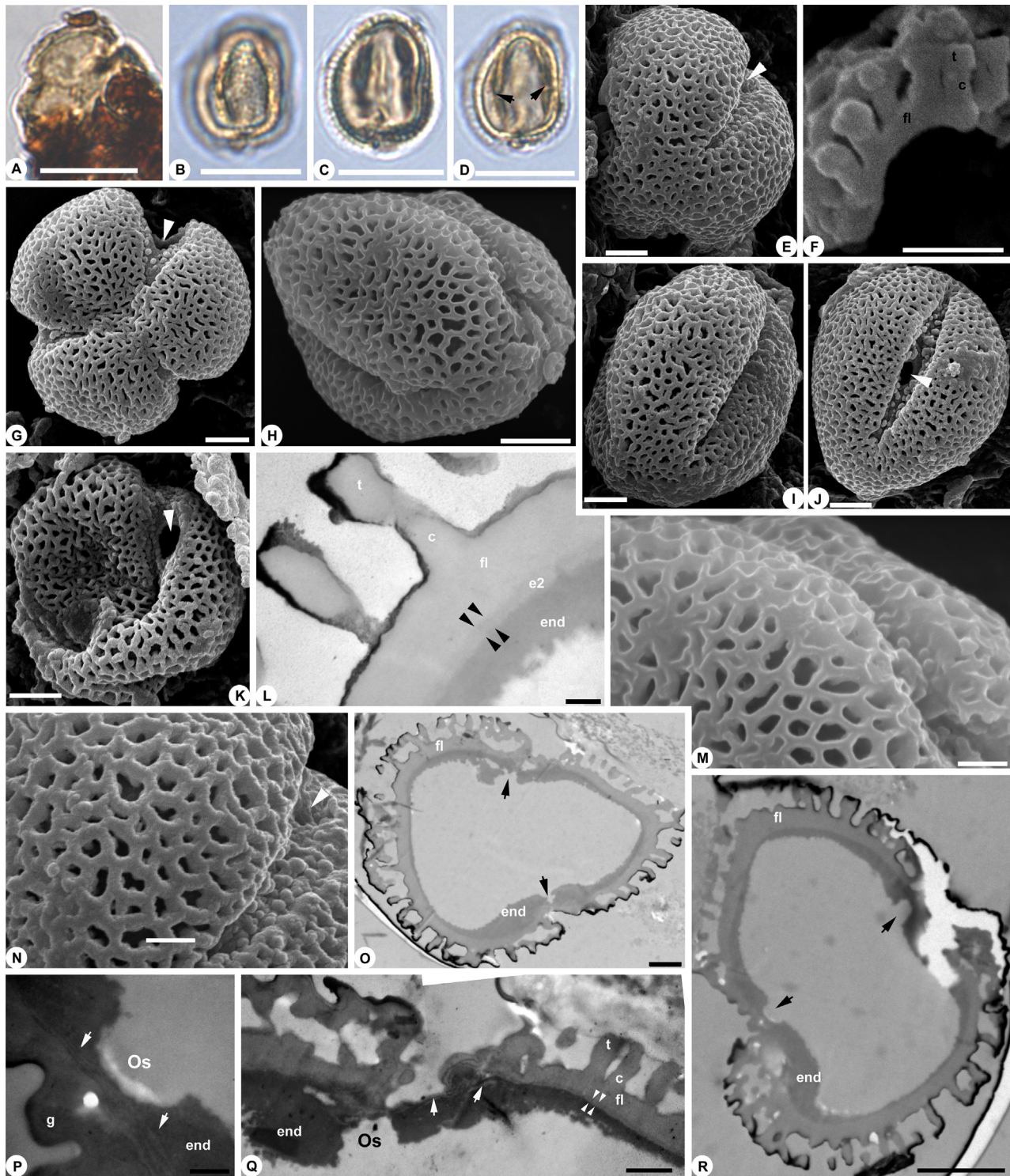
TEM. The ectexine is 0.76–1.13 µm thick with a tectum about 0.42–0.58 µm (sometimes it is about 0.25 µm thick in depressions). The columellae are about 0.17–0.25 µm high and 0.1–0.2 µm wide. The foot layer is about 0.13–0.17 µm thick. The endexine is about 0.03–0.1 µm thick in non-apertural regions, increasing slightly towards the apertures. The endexine appears homogeneous and is more electron dense than the ectexine (Fig. 4E–H).

#### 3.5. Pollen type 5 (Fig. 4I–N)

Number of pollen grains: 7, found as single grains.

SEM. The polar axis is 15 (11–18.9) µm, and the equatorial diameter is 11.8 (8.6–15.7) µm. The sculpture is reticulate with polygonal to rounded lumina. Many elongated lumina tend to be folded and closed in the dehydrated pollen state. On average there is one reticulum mesh per 1 µm. The muri are rounded and 0.4



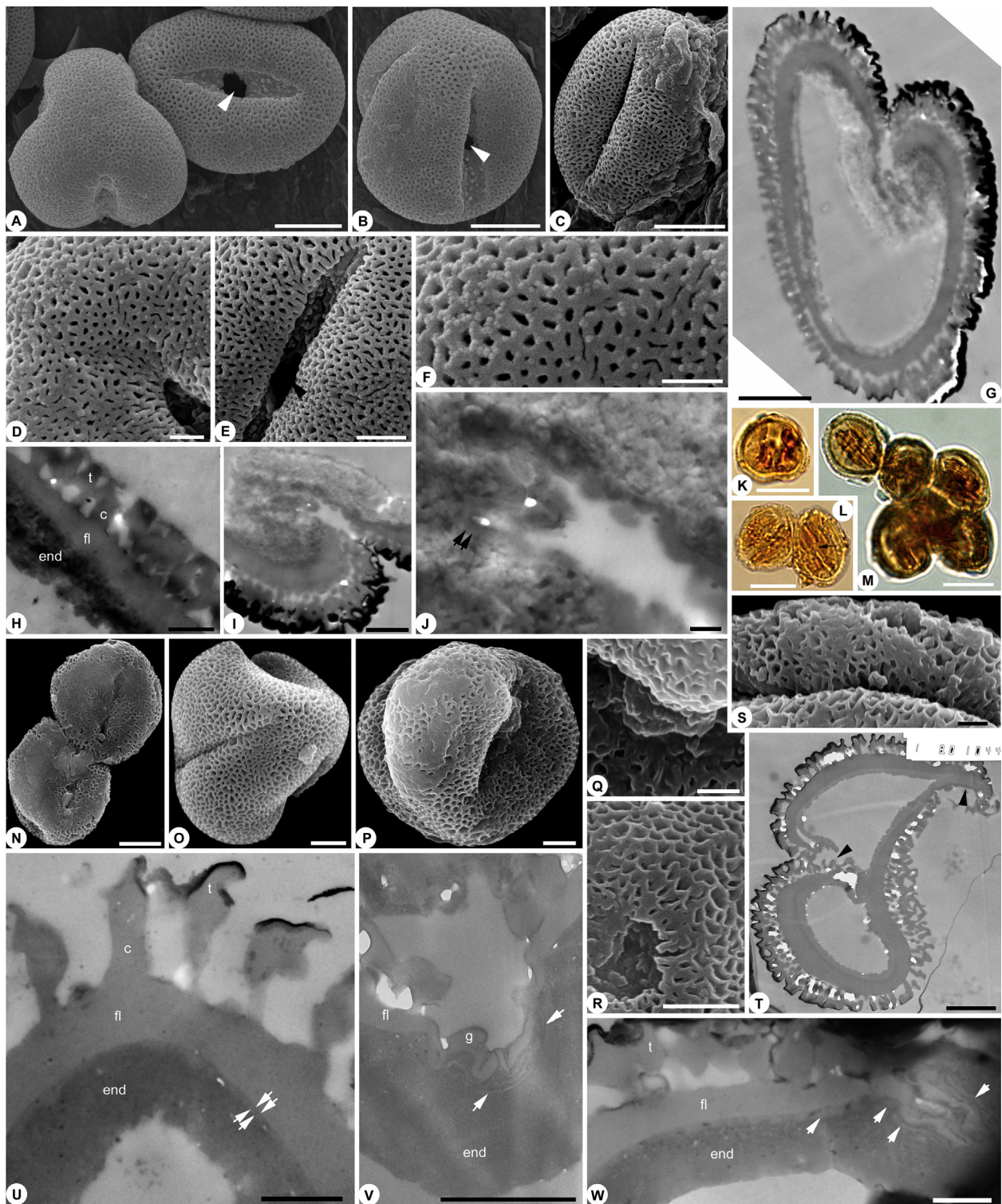


**Fig. 2.** Pollen grains of Type 1, LM (A–D), SEM (E–K, M, N), TEM (L, O–R). TEM sections are from the pollen grain figured in H. A. Polar view. B–D. Equatorial view, different foci, arrows point to ora. E, G, K. Polar view, showing os (arrowhead). F. Fractured pollen grain, showing exine layers. H–J. Equatorial view, showing os (arrowhead). L. Part of the exine, non-apertural region, arrowheads border an outer, less electron-dense endexine layer. M, N. Details of sculpture, granular aperture membrane and os (arrowhead). O, R. Sections through the whole pollen grain, ora (arrowheads) are cut at different depths. P. Aperture region with os, two-layered endexine with outer finely lamellated layer (arrows). Q. Aperture region, outer, less electron dense, homogeneous endexine layer (bordered with arrowheads) becomes finely lamellated (arrows) under aperture. Abbreviations: t – tectum, c – columella, fl – foot layer, end – endexine, e2 – outer endexine layer, Os – os. Scale bar in A–D = 10  $\mu$ m; in E, G, I–K, P = 2  $\mu$ m; in F, N, O 1  $\mu$ m; in H, M = 3  $\mu$ m; in L, Q = 0.2  $\mu$ m; in R = 0.5  $\mu$ m.

(0.21–0.54)  $\mu$ m thick. The colpus margin is mostly bordered by a continuous even murus having the same thickness as the muri elsewhere (Fig. 4J, K, M, N). The pollen grains are tricolpate (Fig. 4J, K) or appear to be tricolpate (Fig. 4I, L–N), the colpi are 11.4

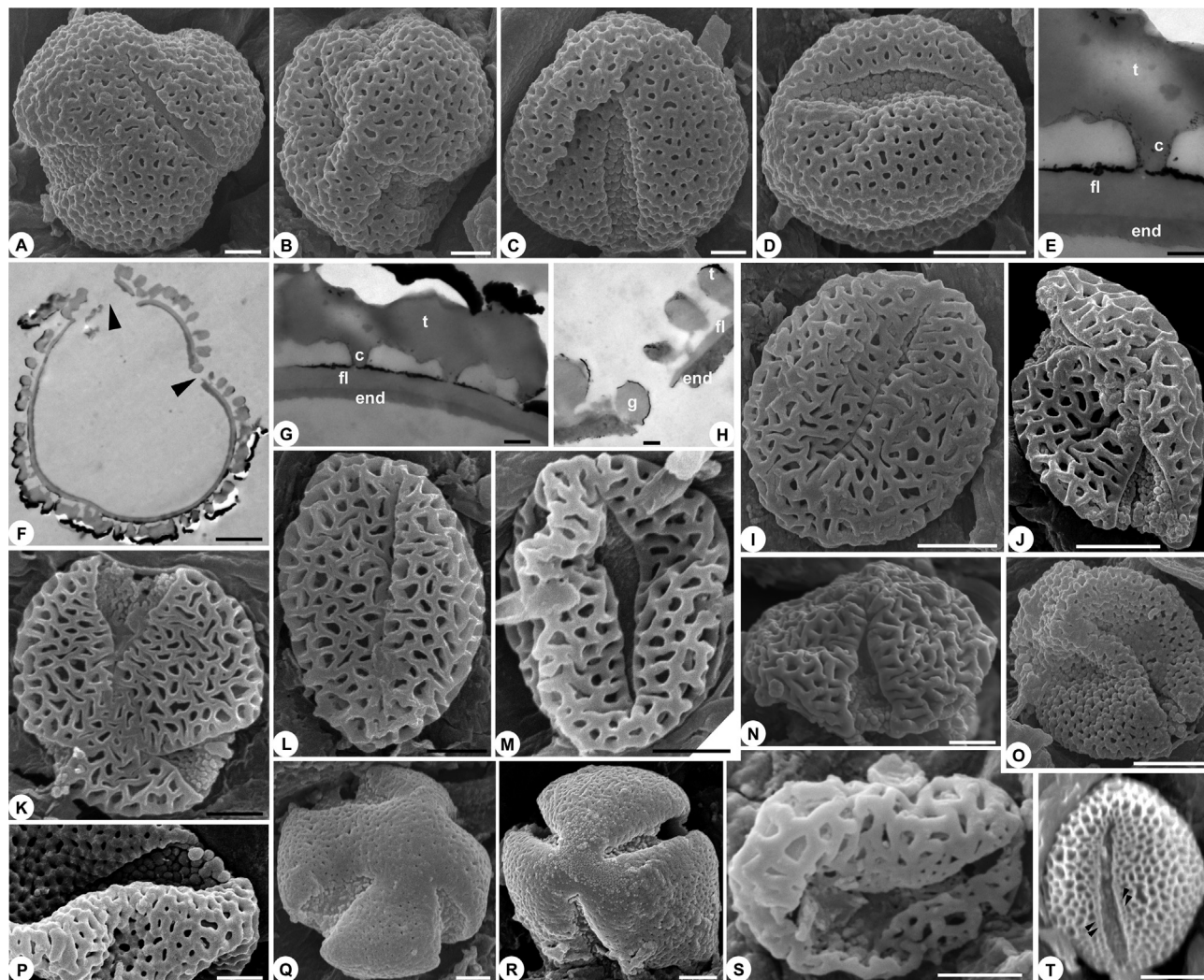
(7.9–13.9)  $\mu$ m long, the aperture membrane is granular with somewhat differently sized granules, where larger ones are in the center of the membrane (Fig. 4J, K, N). One pollen grain has a scabrate or almost smooth aperture membrane (Fig. 4M).





**Fig. 3.** Pollen grains of Type 2 (A–J) and Type 3 (K–W). LM (K–M), SEM (A–F, N–S), TEM (G–J, T–W). TEM sections of Type 2 are from the pollen grain figured in B, TEM sections of Type 3 are from the pollen grain figured in N, O, S. A. Two pollen grains in polar (left) and equatorial (right) views, showing granular aperture membrane and os (arrowhead). B, C. Equatorial views, showing granular aperture membrane and os (arrowhead). D–F. Details of the sculpture, granular aperture membrane and os (arrowhead). G. Section through the whole pollen grain. H. Part of the exine, non-apertural region. I, J. Aperture region, showing thin layer of the ectexine (arrows). K–M. Pollen grains, showing different foci, os (arrow). N. Two pollen grains, equatorial view. O. Polar view. P. Equatorial view, showing os. Q–S. Details of the exine, showing os (Q) and colpus margin (R). T. Section through the whole pollen grain, arrowheads indicating aperture regions. U. Part of the exine, non-apertural region, arrows border outer, less electron endexine layer. V, W. Aperture region, outer, less electron dense, homogeneous endexine layer becomes finely lamellated under aperture (arrows). Abbreviations: t – tectum, c – columella, fl – foot layer, end – endexine, g – granules of sporopollenin. Scale bar in A–C, N = 5  $\mu\text{m}$ ; in D, F, I, Q, S, V = 1  $\mu\text{m}$ ; in E, G, O, P, R = 2  $\mu\text{m}$ ; in H, U, W = 0.5  $\mu\text{m}$ ; in J = 0.2  $\mu\text{m}$ ; in K–M = 10  $\mu\text{m}$ ; in T = 1.25  $\mu\text{m}$ .





**Fig. 4.** Pollen grains of Type 4 (A–H), Type 5 (I–N), Type 6 (O, P), Type 7 (Q, R), Type 8 (S), and Type 9 (T), SEM (A–D, I–T) and TEM (E–H). A, B. Polar view, note granular aperture membrane. C, D. Equatorial view, showing granular aperture membrane. E, G. Part of the exine, non-apertural region, endexine consists of one layer. F. Section through the whole pollen grain, arrowheads indicate aperture regions. H. Aperture region. I, L, M. Equatorial views. J, K. Polar views. N. Granular aperture membrane. O. Polar view. P. Details of the sculpture, showing granular aperture membrane. Q. Polar view of a tetracolpate pollen grain with granular aperture membrane. R. Polar view. S. Equatorial view, note tiny lumina along colpus margin, showing a row of tiny lumina (arrowheads) along colpus margin. Abbreviations: t – tectum, c – columella, fl – foot layer, end – endexine, g – granules of sporopollenin. Scale bar in A–C, F, P–R = 2  $\mu\text{m}$ ; in D, I, J, O = 5  $\mu\text{m}$ ; in E, G = 0.2  $\mu\text{m}$ ; in H = 0.5  $\mu\text{m}$ ; in K–N, S, T = 3  $\mu\text{m}$ .

### 3.6. Pollen type 6 (Fig. 4O, P)

Number of pollen grains: 4, found as single grains.

SEM. The polar axis is about 13.8–14.9  $\mu\text{m}$ , the equatorial diameter is about 10.5–11.7  $\mu\text{m}$ . The sculpture is microreticulate, the lumina are rounded or elongated, on average there are about 1–1.5 reticulum meshes per 1  $\mu\text{m}$ , the muri are flattened, with granular suprasculpture, 0.41 (0.38–0.5)  $\mu\text{m}$  thick. Close to the colpus margin, the reticulum breaks up and some of the lumina open towards the aperture membrane. The pollen grains appear to be tricolpate, the colpi are about 9.3–11.1  $\mu\text{m}$  long, the aperture membrane is granular with densely packed granules (Fig. 4P).

### 3.7. Pollen type 7 (Fig. 4Q, R)

Number of pollen grains: 2, found as single grains.

SEM. Pollen grains have been found in polar views with approximate equatorial diameters of 10.7 and 11.8  $\mu\text{m}$ . One pollen grain has four colpi, the sculpture is foveolate, the aperture membrane is

granular (Fig. 4Q). The other one has three colpi and is probably tricolpate and foveolate to microreticulate and nearly imperforate at the poles, the aperture membrane is granular (Fig. 4R).

### 3.8. Pollen type 8 (Fig. 4S)

Number of pollen grains: 1, found as single grains.

SEM. The polar axis is 10.7  $\mu\text{m}$ , and the equatorial diameter is 7.3  $\mu\text{m}$ . The sculpture is reticulate, the lumina are polygonal and often elongated (except for colpus margins). On average there is one reticulum mesh per 2  $\mu\text{m}$  (0.5 lumen per 1  $\mu\text{m}$ ). The muri are rounded and about 0.5–0.57  $\mu\text{m}$  thick. Close to the colpus margin there are two or three rows of small lumina. The pollen grain is tricolpate with the colpi about 8.7  $\mu\text{m}$ .

### 3.9. Pollen type 9 (Fig. 4T)

Number of pollen grains: 2, found as single grains.

SEM. The polar axis  $\times$  equatorial diameter are 10.5  $\times$  8.6  $\mu\text{m}$  and

$9.9 \times 7.6 \mu\text{m}$  for the two pollen grains. The sculpture is micro-reticulate with rounded polygonal lumina. On average there are slightly fewer than two reticulum meshes per  $1 \mu\text{m}$ . The muri are acute on top and thin, about  $0.18 \mu\text{m}$  thick. The colpus margin is bordered by a row of tiny lumina, which are about three times smaller than those elsewhere on the grain. The pollen grains are tricolpate, the colpi are about  $5.6\text{--}8.1 \mu\text{m}$  long, the aperture membrane is granular.

#### 4. Discussion

While being similar in size, aperture and sculpture characters, pollen grains found on platanoid infructescences of *Friisicarpus sarbaensis* form several types. Pollen grains of these types were evidently produced by different plant species, related to several families. It is hard to determine which species produced each of the pollen types, as in most cases we have data on exine sculpturing only and this is of a rather common type among angiosperms. However, a comparison with previously studied platanoid pollen, especially from the Sarbay locality, can provide some evidence on whether any of the pollen types could have been associated with known platanoid taxa. This will shed light on which staminate reproductive structures could have been associated with *F. sarbaensis*. A number of the pollen types under study can be compared to the pollen of other angiosperm taxa.

##### 4.1. Comparison with in situ platanoid pollen found from the Sarbay locality

Among platanoid and related taxa from the Sarbay locality, *in situ* pollen grains from inflorescences of *Sarbaya radiata* Krassilov et Shilin (Krassilov & Shilin, 1995) and *Krassilovianthus sarbaensis* N. Maslova, Tekleva et Remizowa (Maslova et al., 2012) have been studied by means of LM, SEM and, in the case of *Krassilovianthus*, TEM. These two species are characterized by having microreticulate pollen grains, which are similar to our pollen types 2 and 3. Type 2 is rather similar to *Krassilovianthus* pollen in exine ultrastructure but there are significant differences in details of exine sculpturing. First, the sculpturing in pollen type 2 is quite uniform, while *Krassilovianthus* pollen grains show differently sized and shaped lumina forming a peculiar labyrinthine pattern. In addition, muri in pollen type 2 pollen are rounded but in *Krassilovianthus* pollen they look acute, and the latter have a sporopollenin rim near the colpus margins. Comparing pollen type 2 with *Sarbaya* pollen there are no evident differences in the exine sculpturing: the exine ultrastructure of *Sarbaya* was not studied. Both pollen of *Sarbaya* and pollen type 2 are distinctly tricolporate with uniform microreticulate sculpture and granular aperture membranes. We suppose that type 2 could have been produced by *Sarbaya radiata*. Pollen type 3 is more similar to *Krassilovianthus* pollen in having acute muri; in contrast to *Krassilovianthus* pollen their colpi do not have a sporopollenin rim and their lumina are rather uniform. Pollen grains of *Krassilovianthus* are the smallest among the discussed pollen types; however, in general, all these types fit in the small size range and this character cannot be considered significant for distinguishing between these species.

##### 4.2. Comparison with pollen adhering to infructescences of other *Friisicarpus* species

Besides *Friisicarpus sarbaensis*, six additional species of the genus *Friisicarpus* have been described: *F. brookensis* (Crane, Pedersen, Friis et Drinnan) N. Maslova et Herman (Crane et al., 1993; late Albian, USA), *Friisicarpus marylandensis* (Friis, Crane et Pedersen) N. Maslova et Herman (Friis et al., 1988; late Albian, USA),

*F. elkneckensis* (Pedersen, Friis, Crane et Drinnan) N. Maslova et Herman (Pedersen et al., 1994; late Albian, USA), *F. dakotensis* Wang, Dilcher, Schwarzwald et Kvaček (Wang, Dilcher, Schwarzwald, & Kvaček, 2011; Albian, USA), *Friisicarpus kubaensis* N. Maslova, Tekleva et Sokolova (Maslova et al., 2011; Albian–Cenomanian, Russia), *F. carolinensis* (Friis, Crane et Pedersen) N. Maslova et Herman (Friis et al., 1988; Santonian–Campanian, USA). In addition, there are three specimens of *Friisicarpus* sp. (indicated as *Friisicarpus* spp. 1–3) described by Wang (2008) from the Albian–Cenomanian of the USA, one *Friisicarpus* sp. described by Friis et al. (1988) from the Santonian–Campanian of Sweden, and one *Friisicarpus* sp. described by Maslova and Herman (2006) from the Cenomanian of Russia.

Pollen grains adhering to the carpels or perianth elements have been documented for all of them except for *Friisicarpus* sp. 2 (Wang, 2008), *Friisicarpus* sp. in Maslova and Herman (2006), and *F. dakotensis*. Interestingly, only one kind of pollen has been observed for each type of infructescence. An association with staminate inflorescences has been suggested for a number of *Friisicarpus* species (*F. brookensis*–*Aquia brookensis* Crane, Pedersen, Friis et Drinnan (Crane et al., 1993; Albian, USA); *F. elkneckensis*–*Hamatia elkneckensis* Pedersen, Friis, Crane et Drinnan (Pedersen et al., 1994; Albian, USA); *F. marylandensis*–*Platananthus potomacensis* Friis, Crane et Pedersen (Friis et al., 1988; Albian, USA); *F. carolinensis*–*Platananthus hueberi* Friis, Crane et Pedersen (Friis et al., 1988; Santonian–Campanian, USA); and probably *Friisicarpus* sp. in Friis et al. 1988 and *Platananthus scanicus* Friis, Crane et Pedersen (Friis et al., 1988; Santonian–Campanian, Sweden). Pollen grains from the anthers of these inflorescences were of the same or similar type as those found on the corresponding *Friisicarpus* species.

Pollen grains described for *F. elkneckensis*–*Hamatia elkneckensis* and *F. marylandensis*–*Platananthus potomacensis* are similar to our pollen type 1, but the latter differs in having lumina which do not decrease in size towards the apertures. Pollen grains from dispersed stamens from the Santonian–Campanian of Sweden tentatively assigned by Friis et al. (1988) to Platanaceae are also similar to our pollen type 1, but they are often covered by a substance that may fill the lumina or cover the whole grain and it is difficult to compare them with the pollen under study. Pollen type 3 shows similarity to pollen observed in *Friisicarpus* sp. (Friis et al., 1988) and *Platananthus scanicus*. Pollen grains adhering to *Friisicarpus* sp. 1 are similar to pollen type 1, but in contrast to the latter they also show decreasing of lumina size towards apertures. Pollen grains found on the surface of tepals of *Friisicarpus* sp. 3 (Wang, 2008) also resemble our type 1 but they are shown at low magnification and the only pollen grain at high magnification is not in focus and has closed colpi, so it is impossible to make a proper comparison. Pollen grains found on the fruitlet surface of *F. kubaensis* are similar to our pollen type 3, though the muri thickness and spacing are somewhat intermediate between type 1 and type 3.

##### 4.3. Comparison with pollen of other platanoid taxa

Among published platanoid and related taxa our pollen type 1 is similar to pollen grains of *Quadriplatanus georgianus* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla, Herendeen, & Crane, 1997; Coniacian–Santonian, USA), and pollen type 2 – to that of *Platanus quedlinburgensis* Pacltová emend. Tschan, Denk et von Balthazar (Tekleva & Denk, 2012; Santonian, Germany), *Platanus neptuni* (Ettings.) Bůžek, Holý et Kvaček (Bůžek, Holý, & Kvaček, 1967; Friis, 1985; Miocene, Europe) and *Kundurianthus mirabilis* Kodrul, N. Maslova et Tekleva (Kodrul, Maslova, Tekleva, & Golovneva, 2013; Campanian, Russia). Pollen type 3 can be



compared to pollen of *Archanthus krassilovii* N. Maslova et Kodrul (Tekleva & Maslova, 2004; Paleocene, Russia), *Platananthus speirsae* Pigg et Stockey (Pigg & Stockey, 1991; Paleocene, Canada), *P. synandrus* Manchester (Manchester, 1986; Eocene, USA and Canada), and *Chemurnautia staminosa* N. Maslova (Tekleva & Maslova, 2004; late Paleocene–early Eocene, Russia), but the pollen grains under study lack a sporopollenin rim along the colpi, in contrast to these species. The sculpture and size of pollen type 9 resemble those of *Ambiplatanus washingtonensis* Mindell, Karafit et Stockey (Mindell, Karafit, & Stockey, 2014; Coniacian, Canada). Pollen grains of *A. washingtonensis* differ in having numerous small lumina in addition to larger ones and the colpus margin is not bordered by a row of tiny lumina as in our type 9.

#### 4.4. Comparison with angiosperm taxa from the Sarbay and Kachar, Kazakhstan

A number of works have documented angiosperm remains from the Sarbay locality (Shilin, 1986; Krassilov & Shilin, 1995; Frumin & Friis, 1996, 1999; Frumin, Eklund, & Friis, 2004; Maslova, 2009; Maslova & Shilin, 2011; Maslova & Tekleva, 2012). Taxa from Magnoliaceae, Lauraceae, Illiciaceae, Chloranthaceae, Platanaceae, Sarbaicarpaceae, and Bogutchanthaceae have been reported. Frumin and Friis (1999) also reported several species of possible lauralean affinity and species with affinities to Ranunculales, Urticales, Rosales, Myrtales and Celastrales. Maslova et al. (2012) recently described the new genus *Krassilovianthus*, which was not referred to a particular family but was considered to resemble Platanaceae and Hamamelidaceae.

Ponomarenko (in Levina et al., 1990) described a pollen spectrum from the Sarbay locality (Shet-Irgiz Formation) with a high content of angiosperm pollen mostly assigned to *Tricolpopollenites* and *Tricolpoporopollenites* but with some compared to pollen of modern families: Fagaceae (*Quercites sparsus* (Martius) emend. Samoilovitch, and *Quercus* sp.), Menispermaceae (*Menispermum turonicum* Mtchedlishvili), Platanaceae (*Platanus orientalisformis* Samoilovitch), Hamamelidaceae (*Corylopsis* sp.), and Rhamnaceae.

Remains of angiosperms are also diverse in the Kachar quarry (Novozyrevsky Formation, Kustanay region, Northern Kazakhstan, Cenomanian–Turonian). Hvalj (2001) reported Magnoliaceae (*Liriodendroidea* seeds), Platanaceae (*Platanocarpus* (= *Friiscarpus*) infructescences), possible Droseraceae (seeds) and Hamamelidaceae (*Klikovispermum* Knobloch et Mai seeds), and a number of taxa (described from seed remains) considered at a wider systematic level (*Orysium* sp. with affinity to Illiciales–Nymphaeales–Winterales, *Cathiaria* infructescences to Urticales, seeds of cf. *Allerica*, cf. *Saurauia* and possible *Zolythene* with affinities to Actinidiales–Theales–Ericales), and *Saccospermum* Knobloch et Mai (probably Nymphaeales). He also described some taxa without referring them to a particular plant group (seeds of *Anivia*, *Saccospermum*, and *Borrigium*, seeds and fruits of *Spirella*, *Euryia*, and *Donyca* and *Vanikia* fruits). Golovneva and Oskolski (2007) described *Cathiaria zhilini* Golovneva et Oskolski of uncertain affinity from the same deposits. They wrote that the genus shared most of its features with Moraceae among modern taxa and presumed that these infructescences, staminate flowers of *Freyantha sibirica* Krassilov et Golovneva and leaves of *Liriodendropsis simplex* (Newberry) Newberry could have been produced by the same plant. A similarity of *Freyantha* inflorescences to those of Menispermaceae gives grounds to consider that the genus belongs within Ranunculales (Krassilov & Golovneva, 2004).

A pollen spectrum from the Novozyrevsky Formation is similar to that of the Shet-Irgiz Formation (Levina et al., 1990). Angiosperm pollen grains are numerous, particularly pollen of *Tricolpopollenites* and *Tricolpoporopollenites*. Pollen grains of

*Retitricolpites varireticulatus* Brenner, *R. fragosus* Hedlund et Norris, *Tricolpites micromunus* (Groot et Penny) Singh, *T. albiensis* Kemp, and *T. minutus* (Brenner) Dettmann were found. A considerable number of pollen types are similar to those of Fagaceae, Menispermaceae, Hamamelidaceae, Platanaceae, and Araliaceae. Rare pollen grains of *Liliacidites creticus* Mtchedlishvili, *Clavatipollenites hughesii* Couper, and *Typha* sp. were reported (Levina et al., 1990).

Unfortunately, few findings of reproductive organs with pollen are known from the Kazakhstan localities; most of them are the platanoids discussed above. Pollen grains found on juvenile fruits of *Cathiaria* (Golovneva & Oskolski, 2007) show somewhat similar sculpture to our Pollen type 1, but the former pollen grain is larger with larger lumina and narrower muri than in Pollen type 1. Golovneva and Oskolski (2007) indicate that the tricolpate pollen grains (nearly spherical,  $PxE = 16–18 \times 13–16$ , reticulate) found on the surface of juvenile fruits of *Cathiaria* were very similar to those from *Freyantha* anthers. They supposed that the pollen found on *Cathiaria* fruits could have been produced by *Freyantha*. The pollen ultrastructure of *Freyantha* is characterized by a very thin foot layer and endexine (Tekleva, 2007) in contrast to that of our Pollen type 1. The tectum structure of the pollen of the two species also differs. So, if we accept that the pollen on *Cathiaria* fruits was produced by that plant and associated with *Freyantha* inflorescences, then the pollen grains differ distinctly from our Pollen type 1. If either (or both) of the assumptions are not correct then the two pollen types differ in their quantitative characteristics only.

Apart from platanaceous plants, some of the studied pollen types show similarity to pollen grains of some Hamamelidaceae. For example, pollen type 9 can be compared to *Corylopsis* pollen, and type 5 (some pollen, Fig. 4J, K) shows some similarity to *Hamamelis* pollen. The aperture membrane of these types probably has coarser granules in the central part, which is characteristic of a number of Hamamelidaceae pollen. Pollen type 6 is similar in the exine sculpture to Chloranthaceae pollen but differs in having three apertures. Pollen type 5 is similar to some ranunculid (including, but not limited to Menispermaceae) pollen. Other pollen types are even harder to relate to a particular plant group as their sculpture patterns are very common. In addition, Pollen types 5 and 7 definitely include more than one morphology and may represent more than one species (e.g., compare Fig. 4J, K, and M for Pollen type 5, and Fig. 4Q and R for pollen type 7). As we had to describe them with SEM only and in the orientation they were found, the information is incomplete and the pollen grains were placed in these types tentatively.

Many of the plant groups reported from the Sarbay locality and other localities of similar age and geography in Kazakhstan have species with similar reticulate or foveolate pollen (e.g., Caprifoliaceae, Euphorbiaceae, Fabaceae, and Sapotaceae) and there are additional groups that were not reported for the localities but have similar pollen. Unfortunately, a reliable comparison of the present pollen cannot be made due to their widespread morphological features, the paucity and unfavourable orientation of the fossil grains, and the lack of comparative material for a detailed study.

#### 4.5. Application of the data to reconstruction of the parent plants

The study of the pollen grains found adhering to the infructescence parts raises several questions. Which pollen type (if any) was produced by the plant? Can it help in recognizing the association of the infructescence with any staminate reproductive structures?

To answer these questions we carried out a comparison with pollen grains associated or found *in situ* with platanoid plants. Only three types (1–3) of the studied pollen grains are similar in morphology and ultrastructure to platanoid pollen. This particularly includes the structure of the endexine characteristic of most



platanoids. It is usually two-layered, with layers differing both in structure and electron density. The outer endexine layer is thin, less electron dense, homogeneous in non-apertural regions and finely lamellate under apertures. The inner endexine layer is more electron dense and granular, the endexine thickens towards the aperture mostly at the expense of its inner layer, and the endoaperture is presumably also formed by this layer (Fig. 2O–R).

Among the first three types, type 1 is similar to pollen found on other *Friisicarpus* species. This type was also most abundant (more than 150 grains vs at most 40 for other Types) which makes it logical (along with the above-mentioned arguments) to suppose that these pollen grains could have been produced by the plant with infructescences of *F. sarbaensis*.

Two species described on the basis of staminate reproductive structures are known from the Sarbay locality: *Sarbaya radiata* and *Krassilovianthus sarbaensis*. The exine sculpture of these two species is characterized by a distinctly finer reticulum than that of Pollen type 1 and this rules out a relationship with *Friisicarpus sarbaensis*. Macromorphological features also do not support the idea that *Friisicarpus sarbaensis*, *Sarbaya radiata* or *Krassilovianthus* could have been fossil remains of the same parent plant (Maslova & Tekleva, 2012). As discussed above, Pollen type 1 is similar to pollen of *Platananthus potomacensis*, and to that adhering to *Friisicarpus marylandensis* and *Friisicarpus* sp. 1 and 3 shown in Wang (2008), and to pollen found in dispersed stamens described by Friis et al. (1988). The exine sculpture is also similar to that of *Quadriplatanus georgianus*. Data on macromorphology of the reproductive organs do not confirm association of these taxa and further information is necessary. It is evident that staminate inflorescences that belonged to the same plant as *Friisicarpus sarbaensis* are still to be found.

#### 4.6. Discussion on the pollination mode of *Friisicarpus sarbaensis*

Here we present data on a diverse assemblage of pollen grains found adhering to the infructescence parts of one species. Though different pollen grains have been repeatedly found in seeds of fossil and modern gymnosperms (e.g., Gomankov & Meyen, 1986; Jin et al., 2012; Zavialova, Gordenko, Nosova, & Polevova, 2014), this is a rather unusual discovery for fossil angiosperms so far. It is particularly interesting as until now one pollen type has been described per pistillate reproductive structure of a given platanaceous species (e.g., Friis et al., 1988; Wang, 2008; Maslova et al., 2011). Moreover our pollen grains are of a similar size, aperture type and exine sculpture, which makes it difficult to distinguish between different pollen types. This makes one curious to know what could have been the reason for this? Why are there so many different pollen types on infructescences of the same species? What does this tell us about the pollination mode of the plant?

The fact that there was only one pollen type for each specific kind of a fossil led Wang (2008) to suggest that *Friisicarpus* was entomophilous and there was some sort of specialization in which the insect could carry only a particular type of pollen grains to these platanoid plants.

Though modern *Platanus* L. is considered to be wind pollinated, entomophily has been suggested for at least some fossil platanoids, and certain morphological traits such as a well-developed perianth of Early Cretaceous Platanaceae have been cited to support this idea (e.g., Crane, Friis, & Pedersen, 1986, 1993; Friis et al., 1988; Hu, Dilcher, Jarzen, & Taylor, 2008; Wang, 2008). There are glandular trichomes that might have produced secretion on the apices of carpels of *Friisicarpus sarbaensis*. Secretion could have attracted insects and made pollen grains stick together. Secretion (probably, mucilage) was noticed also for *Friisicarpus* sp. 1 (Wang, 2008) and for *F. kubaensis* (Maslova et al., 2011); the latter species is also

characterized by trichomes on carpels. Trichomes on the axes with adhering pollen grains were also described for *F. sarbaensis* and *F. kubaensis*. Additional indirect evidence for entomophily of these two *Friisicarpus* species is the discovery of damaged carpel apices. The damage is identical in both species and has not been described before. They are probably galls of unknown origin (Maslova and Vassilenko, in preparation). The galls could have been caused by arthropods (e.g. induced by small mites) or by bacteria or viruses. In the last case insects as vectors can also have been involved. The identity of the damage in both species (from different localities) may also imply that certain co-evolutionary relationships existed between the plants and arthropods. Other *Friisicarpus* species lack trichomes, secretions or such damage.

Pollen characters do not add much information for determining mode of pollination. Few works discuss whether and how pollen morphology and structure can be connected to the pollination mode (e.g., Whitehead, 1969; Hesse, 1979, 1980; Zavada, 1984; Friedman & Barrett, 2009; Wragg & Johnson, 2011). Pollen size is often discussed in the context of pollination (e.g., Whitehead, 1969; Niklas, 1985; Friis et al., 1988). Friedman and Barrett (2009) gave a short review on pollen size in both pollination modes. They stated that there is less variation in size range in wind-pollinated plants though the average can be similar in both wind- and insect-pollinated groups. The size of the pollen grains under study is somewhat smaller than is usually observed in wind-pollinated taxa.

There is a detailed discussion of such data concerning reticulate pollen in Zavialova and Gomankov (2009) but on the whole there is no clear understanding as to how a reticulate exine pattern could be related to a particular pollination mode. On the one hand, pollen grains with a smoother surface and without echini or other well-expressed ornamentation are considered more characteristic of wind-pollinated plants; on the other hand, a reticulum and spaced columellae could serve as a container for substances involved in insect pollination. As this sculpture pattern is widespread and is known both for wind- and insect-pollinated plants it seems impossible to use this pollen character alone to reveal the pollination mode of fossil platanoids.

The presence of pollenkitt is thought to be a character of entomophilous plants though it is known to occur in wind-pollinated species too (Hesse, 1979, 1980). Wragg and Johnson (2011) found low levels of wind pollination in their modern putatively insect-pollinated species, and suggested that the presence of pollenkitt might limit the amount of pollen transfer by wind, facilitate pollen clumping and adherence to the insects and in ambophilous species it can mediate the amount of pollen transferred by insects and wind. Hesse (1979) found that in some cases the pollenkitt becomes dry after some hours, and becomes whitish, and the pollination mode may shift towards anemophily. Friis et al. (1988) reported pollenkitt on their fossil dispersed platanoid stamens and some pollen in other platanoid taxa appeared to be covered with something resembling pollenkitt. So, this can serve as an additional character to consider when inferring the possible pollination mode.

It is important to consider which pollen grains, how many of them, and how exactly they were found on plant remains (e.g., different pollen grains on the same species, pollen found individually or in clumps, pollen in seeds and pollen chambers or on the surface of plant structures). This might provide additional information on the pollination mode. The studied pollen grains were found as single grains (pollen types 5–9) and in clumps (types 2–4). Pollen type 1 occurs both individually and in clumps.

Considering the common idea that early angiosperms were probably insect pollinated, this seems consistent with the entomophily of early platanoid members too, particularly the parent plant of *Friisicarpus sarbaensis*. The next question is whether the

pollination was specialized, as suggested by Wang (2008). In our case, this does not seem so, as different pollen types were found on the infructescence surface of the same species. On the other hand, they are of a similar morphology, so some specialization can be supposed, but not to a particular plant species. If we consider that early Platanaceae were at least partly entomophilous then it is appropriate to ask what could have been the reason to shift to wind pollination. Was it because of environmental conditions or extinction of most family members? This is an interesting aspect to keep in mind when looking into the phylogeny of Platanaceae. Some of the species could have been ambophilous plants as has been shown for some modern angiosperm taxa (Culley, Weller, & Sakai, 2002). It is difficult to be absolutely sure about the pollination mode of fossil plants; we can only rely on comparison with modern plants and the traits they show. For example, Wragg and Johnson (2011) studied the transition from wind pollination to insect pollination in sedges and Friedman and Barrett (2009) explicitly discussed the evolution of wind pollination. As Friedman (2011, p. 912) pointed out: “the morphological similarity of the insect- and wind-pollinated species suggests that, under the appropriate ecological conditions, small changes might be sufficient to achieve pollination transitions.” This also implies that this shift can be realized by changes in some plant parts while others retain their original structure. Pollen grains of Platanaceae probably reflect this situation as there is little change in their pollen morphology and ultrastructure from the Early Cretaceous until today.

## 5. Conclusions

Diverse pollen grains were found adhering to the platanaceous infructescences of *Friisicarpus sarbaensis* from the Cenomanian–Turonian of western Kazakhstan. At least nine morphological types have been distinguished among 250 studied pollen grains. They occur in clumps and as individual pollen grains. Three quantitatively prevailing types (1–3) belong to platanoid taxa. The remaining types belong to other angiosperm families. Pollen type 1 is dominant, similar to other pollen found on different *Friisicarpus* species, and was thus most likely produced by the plant with infructescences of *F. sarbaensis*. This pollen type has not been described *in situ* from any anthers so far, so we cannot associate the infructescences with a particular staminate platanaceous reproductive organ. Pollen type 2 is identical to pollen of *Sarbaya radiata*, staminate inflorescences described from the same locality. The diversity and abundance of different pollen types found on the infructescences of *F. sarbaensis* favour entomophily of this plant but challenge any specific plant–insect specialization.

## Acknowledgements

We are grateful to Prof. J.A. Doyle, Dr P. Herendeen, and Dr Natalia Zavialova for valuable comments and linguistic corrections. Dr. David Batten and an anonymous reviewer are thanked for their useful comments. The work was carried out at the User Facilities Center of M.V. Lomonosov Moscow State University under financial support of the Ministry of Education and Science of the Russian Federation and at the User Facilities Center of the A.A. Borissiak Paleontological Institute, Russian Academy of Sciences. The work was supported by a grant of President RF MK-3156.2014.4 for MT and by the Russian Foundation for Basic Research 14-04-00800 for NM.

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