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RESEARCH ARTICLE

Pollen morphology of representatives of the genus *Petrosimonia* (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.) of the flora of Ukraine

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Abstract. Pollen morphology of *Petrosimonia brachiata*, *P. oppositifolia*, and *P. triandra* (*Salsoloideae*, *Chenopodiaceae* s. str. / *Amaranthaceae* s. l.) of the flora of Ukraine was investigated using light and scanning electron microscopy. For *Petrosimonia triandra*, such data are provided here for the first time. The objective of the present study was to obtain data on pollen characteristics of these species and to assess the significance of characters for species-specific identification. Pollen grains in the studied species are pantoporate, spheroidal, circular in outline, slightly undulate or undulate on the edges; small- and medium-sized. Exine sculpture is nanoechinate, tectum is psilate-perforate. Pore membranes are nanoechinate. The exine structure (columellae) of pollen grains of all species was analyzed for the first time in the present study. Significance of pollen grain traits for the taxonomy and pollen analysis in paleopalynology is discussed. UPGMA dendrograms based on palynomorphological data support the differentiation of studied species. Pollen grains of *P. triandra* differ from those of *P. brachiata* and *P. oppositifolia* in their size, distances between pores and between pore centers, as well as the number of pores. Pollen grains in *P. brachiata* have larger size and number of pores, larger nanoechini, and shorter columellae than those in *P. oppositifolia*.

Keywords: light microscopy, palynomorphology, pollen analysis, scanning electron microscopy, sculpture, structure, UPGMA

Introduction

The genus *Petrosimonia* Bunge belongs to the subfamily *Salsoloideae* (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.), and comprises 10 to 12 species (Iljin, 1952; Hernández-Ledesma et al., 2015; POWO, 2025–onward), or up to 15 species (Tzvelev, 1996). Representatives of the genus are annual herbaceous plants occurring from southeastern and eastern Europe to Mongolia and Afghanistan, mainly within the belts of deserts, semi-deserts, and steppes (Kühn et al., 1993; Zhu et al., 2003; Hernández-Ledesma et al., 2015; POWO, 2025–onward). In the flora of Ukraine, the genus is represented by three species, *P. brachiata* (Pall.) Bunge, *P. oppositifolia* (Pall.) Litv., and *P. triandra* (Pall.) Simonk. (Iljin, 1952; Tzvelev, 1996; Mosyakin, Fedoronchuk, 1999). All species are plants of salt marshes and

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partly gypsum-bearing slopes, with the exception of *P. triandra*, which also inhabits solonetzes and solonetzian steppes (Iljin, 1952; Grozeva et al., 2019). There are many publications devoted to the use of halophytes as helpful tools for the restoration of degraded lands and soil protection (Qadir, Oster, 2004; Grozeva et al., 2019). Halophytic plants have a wide range of active components and medicinal properties (De Gregorio et al., 2024). *Petrosimonia* species have high economic value in some Eurasian deserts and semi-deserts as they are good autumn-winter feed for many types of livestock and are harvested in large quantities for this purpose for the winter; and are even recommended for cultivation on the salty soils (Iljin, 1952; Feodorova, Aleksandrov, 2015).

A rather comprehensive taxonomic treatment of the genus *Petrosimonia* in Ukraine was published by Iljin (1952). The author included *Petrosimonia brachiata* in the section *Brachyphyllon* Iljin, *P. oppositifolia* — section *Synandra* Iljin, and *P. triandra* — section *Oligandra* Iljin (Iljin, 1952). Tzvelev (1996), however, placed *P. triandra* in its own newly described section, *Petrosimonia* sect. *Triandra* Tzvelev. Molecular phylogenetic studies of the tribe *Salsoleae* s. l., including three species of *Petrosimonia*, was carried out by Akhani et al. (2007). According to molecular data, *Petrosimonia* and *Ofaiston* Raf. form a clade that, in turn, is sister to the clade containing the genus *Climacoptera* Botsch. The authors noted that *Petrosimonia* and *Ofaiston* are quite distinct morphologically, but *Petrosimonia* was supported as a monophyletic lineage in all analyses (Akhani et al., 2007). Molecular phylogenetic studies of *Salsoleae*, mainly species occurring in China, including six species of *Petrosimonia*, have confirmed the monophyly of this genus (Wen et al., 2010). Molecular phylogenetic studies of ten Eurasian species of *Petrosimonia* were conducted by Fedorova and Aleksandrov (2015). It has been shown that *Petrosimonia* comprises a monophyletic lineage, and sections of the genus were compared with the revealed clades.

The palynomorphological traits are often used as additional diagnostic features in taxonomy and phylogenetic reconstructions (Tsymbalyuk et al., 2022; Borsch, Flores-Olvera, 2025, and references therein), as well as for spore-pollen analysis in paleopalynology (Lu et al., 2019; Marinova et al., 2023; Mudie et al., 2025). The presence of representatives of *Petrosimonia* in fossil palynofloras expands the possibilities of using the results of paleopalynological studies in reconstructing the patterns of distribution of halophytic vegetation in the past in space and time (Bezusko et al., 2006).

Pollen morphology of *Petrosimonia* was studied using light and/or scanning electron microscopy by several authors (Kupriyanova, Alyoshina, 1972; Monoszon, 1973; Tsymbalyuk, 2005, 2008; Grozeva et al., 2019; Sonyan, Hayrapetyan, 2021; Sonyan et al., 2022). Kupriyanova and Alyoshina (1972) investigated pollen grains of *P. oppositifolia*. Monoszon (1973) described pollen grains of *P. brachiata* and *P. oppositifolia.* Grozeva et al. (2019) investigated pollen morphology in two different populations of *P. brachiata*, the only representative of the genus in Bulgaria. The authors did not find significant variability in pollen morphological traits. Sonyan and Hayrapetyan (2021) and Sonyan et al. (2022) investigated pollen grains of *P. brachiata* and *P. glauca* Bunge. The authors also found no significant differences between the two representatives of the genus in any of the four main pollen diagnostic characters used.

Our analysis of literature demonstrated that knowledge about the morphology of pollen grains in *Petrosimonia* still remains rather fragmentary, and, in particular, the exine sculpture and exine structure have not been studied in detail. Pollen grains of *P. oppositifolia* were studied only with a light microscope. Pollen grains of *Petrosimonia triandra* have not been studied previously. The present palynomorphological investigation of *P. brachiata*, *P. oppositifolia*, and *P. triandra* was carried out in order to provide detailed quantitative and qualitative data on their pollen characters and to evaluate the significance of these data for the species-specific identification.

Materials and Methods

Plant material

Pollen grains of six specimens belonging to *P. brachiata*, *P. oppositifolia* and *P. triandra* species were sampled in the National Herbarium of Ukraine (KW — Herbarium of the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv; the herbarium acronym is given according to Thiers (2025). Abbreviations of taxon author names follow Brummitt and Powell (1992), with additions available from the continuously updated IPNI (2025–onward) and POWO (2025–onward) online databases.

List of specimens investigated

***Petrosimonia brachiata*:** 1. Kherson Region, Novotroitske District [since 2020 included in Henichesk District], Tyubek Peninsula, near Sivash. 8 September 1937. G. Bilyk (KW). 2. [Kherson Region] Arabatska Strilka, Henichesk, salt marsh. 9 September 1936. G. Bilyk (KW).

***Petrosimonia oppositifolia*:** 1. Crimea, Dzhankoy District, Stalne village, the shore of Sivash. 18 August 1996. Ranetskaya (KW093150). 2. Dnipropetrovsk Region [now in Kherson Region], Henichesk District, northern shore of Sivash, Kuyuk-Tuk Island, bottom of the gorge. 15 June 1925. Krivosheev (KW).

***Petrosimonia triandra*:** 1. Crimea, Kerch Peninsula, Mount Opuk, top of the rock. 21 August 1976. O. Dubovyk (KW). 2. [Donetsk Region] Artemivsk [now Bakhmut] District. 13 August 1928. P. Oksiyuk (KW).

Palynomorphological analysis

The methods used in the present study have been described in details earlier (Tsymbalyuk et al., 2023a, 2023b, etc.). For LM (light microscopy) studies (Biolar ×700), the pollen was acetolyzed following Erdtman (1952), mounted on slides with glycerinated gelatin, analyzed, and photomicrographed. Pollen morphometric features of 30 properly developed pollen grains from each specimen were measured, and the measurements included the following parameters: pollen diameter, pore diameter, distance between pores, exine thickness. The distance between pore centers and C/D value (C — distance between pore centers, D — pollen diameter) were calculated (McAndrews, Swanson, 1967). The number of pores was calculated by multiplying the number of pores visible on the surface by two and adding the number of pores at the edge of the pollen grain. For all quantitative characters, descriptive statistics was applied and the range (minimum–maximum), arithmetic mean and standard deviation were calculated using Microsoft Excel software. The slides were deposited in the Palynotheca (KW-P; reference pollen collection) at the National Herbarium of Ukraine.

Acetolyzed as well as dry pollen grains were treated with 96% ethanol, and then the samples were sputter-coated with gold in a vacuum installation and examined using SEM — scanning electron microscopy (JEOL JSM-6060LA) at the Centre of Electron Microscopy of the M.G. Kholodny Institute of Botany. The measurements of the nanoechini and columellae were taken on 6–8 pollen grains from each specimen from SEM micrographs and made using the program AxioVision Rel.4.8.2. The numbers of nanoechini per unit area (4 µm^2) and on pore membranes were determined (Tsymbalyuk et al., 2022, 2023a, 2023b, 2024). Terminology used in descriptions of pollen grains follows the glossaries of Punt et al. (2007) and Halbritter et al. (2018). LO-analysis was used according to Erdtman (1952).

Statistical analysis

The specific quantitative features were assessed for numerical analysis. Thirteen quantitative characters were used to evaluate *Petrosimonia* phenetic similarities: pollen and pore diameter, distance between pores and between pore centres, pore number, C/D value, and exine thickness (Table 1); nanoechini: height, width at the base, number/4 µm^2, number on pore membranes; columellae: height and thickness (Table 2). Cluster analysis was carried out using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA). The Euclidean distance was used as a similarity index in clustering analyses. PAST (PAleontological STatistics) v. 4.08 was used for the analysis (Hammer et al., 2001). The variability of the characters of pollen has been examined by Box plots.

Results

Description of pollen grains

Petrosimonia brachiata (Figs 1A–D; 2A–F; 3G, J).

LM. Pollen grains monads, isopolar, spheroidal, circular in outline, slightly undulate on the edge; small or medium-sized: pollen diameter (D) = 21.28–29.26 µm; pantoporate, with 36–53 pores evenly distributed on the surface. Pores circular, 2.12–3.32 µm in diameter, with distinct or indistinct margins. Distance between pores 2.26–3.72 µm, distance between pore centres (C) = 4.65–7.04 µm. C/D = 0.181–0.278. Exine 2.26–2.66 µm thick (Table 1). Sexine thicker than nexine. Columellae distinct or indistinct. LO-analysis: columellae distinct, circular, densely distributed, nanoechini indistinct or invisible.

SEM. Exine sculpture nanoechinate; nanoechini conic with straight sides and acute apex, 0.05–0.17 µm high, 0.12–0.26 µm wide at base, sparsely or more densely distributed (16–24/4 µm^2); tectum psilate-perforate in areas between nanoechini. Pore membranes with nanoechini (in number 8–19),

Table 1. **Pollen quantitative characters (using LM): the values are presented as Mean ± Standard deviation and Range (minimum–maximum) (all measurements given as μm); 1, 2 — specimen number; G — general specimens' measurements**

Species	Pollen diameter (D)	Pore diameter	Distance between pores	Distance between pore centres (C)	Pore number	C/D	Exine thickness
Petrosimonia brachiata 1	26.60±1.36 23.94–29.26	2.69±0.23 2.39–3.32	2.92±0.36 2.66–3.72	5.61±0.53 5.05–6.65	46.04±4.43 36–53	0.21±0.01 0.18–0.25	2.58±0.10 2.39–2.66
Petrosimonia brachiata 2	24.80±2.15 21.28–29.26	2.67±0.35 2.12–3.32	2.83±0.41 2.26–3.72	5.51±0.71 4.65–7.04	45.80±3.45 40–52	0.22±0.02 0.19–0.27	2.45±0.14 2.26–2.66
***Petrosimonia brachiata* G**	**25.72±2.00** **21.28–29.26**	**2.68±0.29** **2.12–3.32**	**2.88±0.39** **2.26–3.72**	**5.56±0.63** **4.65–7.04**	**45.92±3.99** **36–53**	**0.21±0.02** **0.18–0.27**	**2.52±0.14** **2.26–2.66**
Petrosimonia oppositifolia 1	23.45±1.10 21.28–25.27	2.80±0.23 2.39–3.32	2.87±0.27 2.39–3.32	5.68±0.40 5.05–6.65	38.04±3.14 34–46	0.24±0.01 0.22–0.27	2.40±0.14 2.12–2.66
Petrosimonia oppositifolia 2	21.28±1.57 18.62–25.27	2.75±0.38 2.26–3.72	2.74±0.27 2.39–3.32	5.49±0.51 4.78–7.04	37.10±2.40 34–42	0.25±0.01 0.23–0.28	2.39±0.17 2.12–2.66
***Petrosimonia oppositifolia* G**	**22.42±1.73** **18.62–25.27**	**2.78±0.31** **2.26–3.72**	**2.81±0.28** **2.39–3.32**	**5.59±0.46** **4.78–7.04**	**37.59±2.85** **34–46**	**0.25±0.01** **0.22–0.28**	**2.39±0.16** **2.12–2.66**
Petrosimonia triandra 1	25.00±1.25 22.61–26.60	2.80±0.40 2.26–3.99	2.07±0.18 1.59–2.39	4.88±0.43 3.99–5.98	64.76±3.55 58–74	0.19±0.01 0.16–0.23	2.47±0.18 1.99–2.66
Petrosimonia triandra 2	23.20±0.98 21.28–25.27	2.62±0.27 2.26–3.32	2.17±0.14 1.99–2.39	4.79±0.35 4.25–5.71	58.30±2.62 54–64	0.20±0.01 0.18–0.23	2.38±0.18 1.99–2.66
***Petrosimonia triandra* G**	**24.28±1.45** **21.28–26.60**	**2.72±0.36** **2.26–3.99**	**2.11±0.17** **1.59–2.39**	**4.84±0.41** **3.99–5.98**	**62.18±4.51** **54–74**	**0.19±0.01** **0.16–0.23**	**2.43±0.19** **1.99–2.66**

Table 2. **Pollen quantitative characters (using SEM): the values are presented as Mean ± Standard deviation and Range (all measurements given as μm); 1, 2 — specimen number; G — general specimens' measurements**

Species	Nanoechini				Columellae	
	Height	Width at the base	Number/4 μm²	Number on pore membranes	Height	Thickness
Petrosimonia brachiata 1	0.10±0.03 0.05–0.17	0.21±0.02 0.16–0.26	20.72±2.04 18–24	15.12±2.84 10–19	0.50±0.20 0.20–0.93	0.22±0.03 0.18–0.28
Petrosimonia brachiata 2	0.11±0.03 0.05–0.16	0.19±0.03 0.12–0.25	19.58±2.66 16–23	12.53±3.24 8–19	0.68±0.19 0.20–0.96	0.21±0.03 0.17–0.28
***Petrosimonia brachiata* G**	**0.10±0.03** **0.05–0.17**	**0.20±0.03** **0.12–0.26**	**20.13±2.45** **16–24**	**13.87±3.30** **8–19**	**0.60±0.21** **0.20–0.96**	**0.22±0.03** **0.17–0.28**
Petrosimonia oppositifolia 1	0.08±0.02 0.05–0.12	0.17±0.02 0.12–0.21	19.25±1.53 17–21	11.35±3.88 6–18	0.53±0.19 0.20–0.84	0.21±0.02 0.18–0.26
Petrosimonia oppositifolia 2	0.09±0.02 0.05–0.14	0.19±0.02 0.12–0.24	19.25±2.58 16–23	12.50±3.67 7–18	0.79±0.33 0.21–1.29	0.21±0.03 0.17–0.27
***Petrosimonia oppositifolia* G**	**0.09±0.02** **0.05–0.14**	**0.18±0.02** **0.12–0.24**	**19.25±1.85** **16–23**	**11.92±3.82** **6–18**	**0.66±0.30** **0.20–1.29**	**0.21±0.02** **0.17–0.27**
Petrosimonia triandra 1	0.07±0.01 0.04–0.10	0.16±0.02 0.13–0.21	20.45±1.87 18–24	10.10±3.08 6–18	0.51±0.14 0.20–0.76	0.21±0.02 0.18–0.28
Petrosimonia triandra 2	0.07±0.02 0.04–0.11	0.14±0.03 0.10–0.21	20.06±2.51 17–25	11.85±3.16 7–18	0.59±0.23 0.23–0.91	0.22±0.03 0.20–0.28
***Petrosimonia triandra* G**	**0.07±0.01** **0.04–0.11**	**0.15±0.03** **0.10–0.21**	**20.22±2.28** **17–25**	**10.97±3.24** **6–18**	**0.52±0.17** **0.20–0.91**	**0.22±0.02** **0.18–0.28**

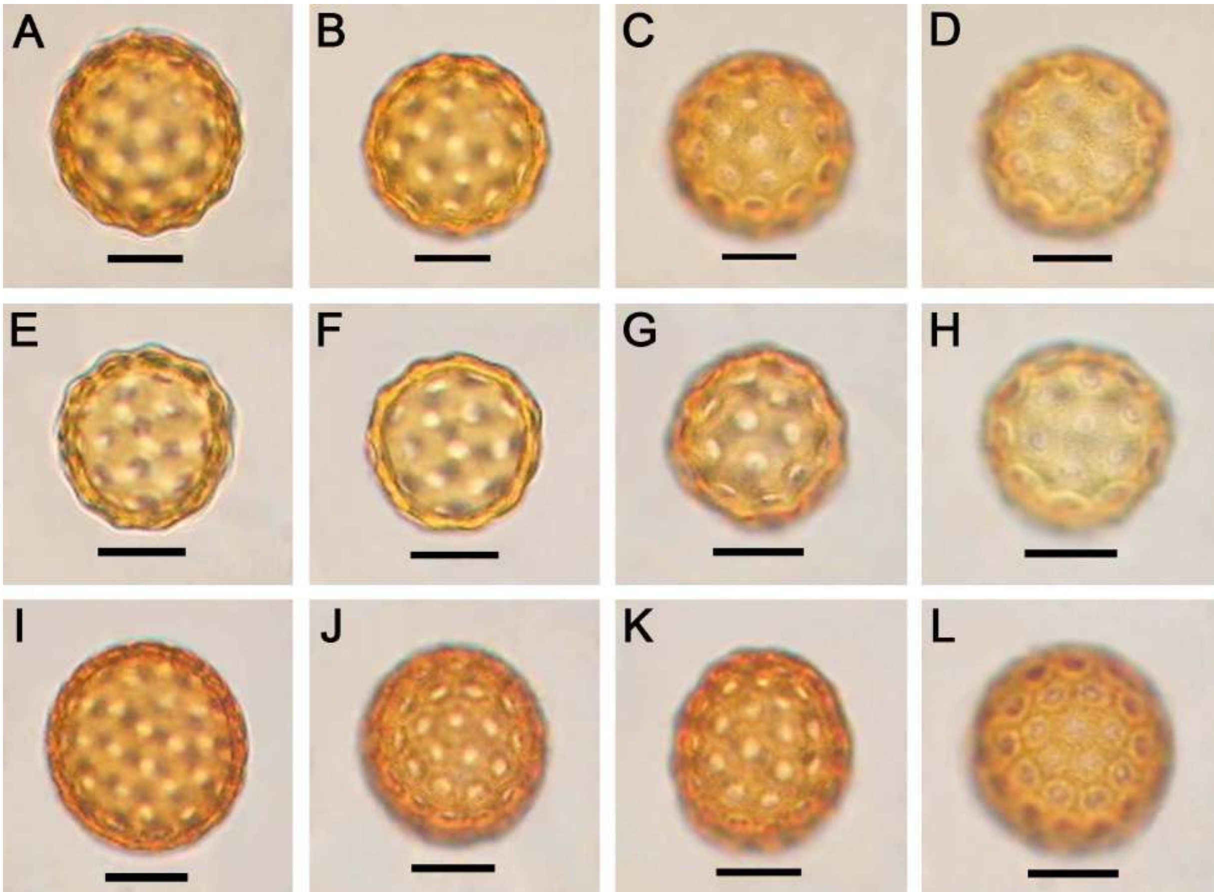

Fig. 1. Pollen grains of *Petrosimonia* (LM). A–D: *P. brachiata* (A — specimen 1; B–D — specimen 2); E–H: *P. oppositifolia* (E–G — specimen 1; H — specimen 2); I–L: *P. triandra* (I, L — specimen 1; J, K — specimen 2). Scale bars: 10 μm

pore margins raised; mesoporia slightly convex. Columellae are continuous from tectum to foot layer; short or long, 0.20–0.96 μm long, 0.17–0.28 μm wide, very densely arranged (Table 2).

Petrosimonia oppositifolia (Figs 1E–H; 2G–L; 3H, K).

LM. Pollen grains monads, isopolar, spheroidal, circular in outline, slightly undulate on the edge; small and medium-sized: pollen diameter (D) = 18.62–25.27 μm; pantoporate, with 34–46 pores evenly distributed on the surface. Pores circular, 2.26–3.72 μm in diameter, with indistinct or distinct margins. Distance between pores 2.39–3.32 μm, distance between pore centres (C) = 4.78–7.04 μm. C/D = 0.221–0.281. Exine 2.12–2.66 μm thick (Table 1). Sexine thicker than nexine. Columellae indistinct or invisible. LO-analysis: columellae indistinct or rarely distinct, circular, densely distributed, nanoechini invisible.

SEM. Exine sculpture nanoechinate; nanoechini conic with straight sides and acute apex, 0.05–0.14 μm high, 0.12–0.24 μm wide at base, sparsely or more densely distributed (16–23/4 μm^2); tectum psilate-perforate in areas between nanoechini. Pore membranes with nanoechini (in number 6–18), pore margins raised; mesoporia slightly convex. Columellae are continuous from tectum to foot layer; short or long, 0.20–1.29 μm long, 0.17–0.27 μm wide, very densely arranged (Table 2).

Petrosimonia triandra (Figs 1I–L; 3A–F, I, L).

LM. Pollen grains monads, isopolar, spheroidal, circular in outline, undulate on the edge; small and medium-sized: pollen diameter (D) = 21.28–26.60 μm; pantoporate, with 54–74 pores evenly distributed on the surface. Pores circular, 2.26–3.99 μm in diameter, with indistinct or distinct margins. Distance between pores 1.59–2.39 μm,

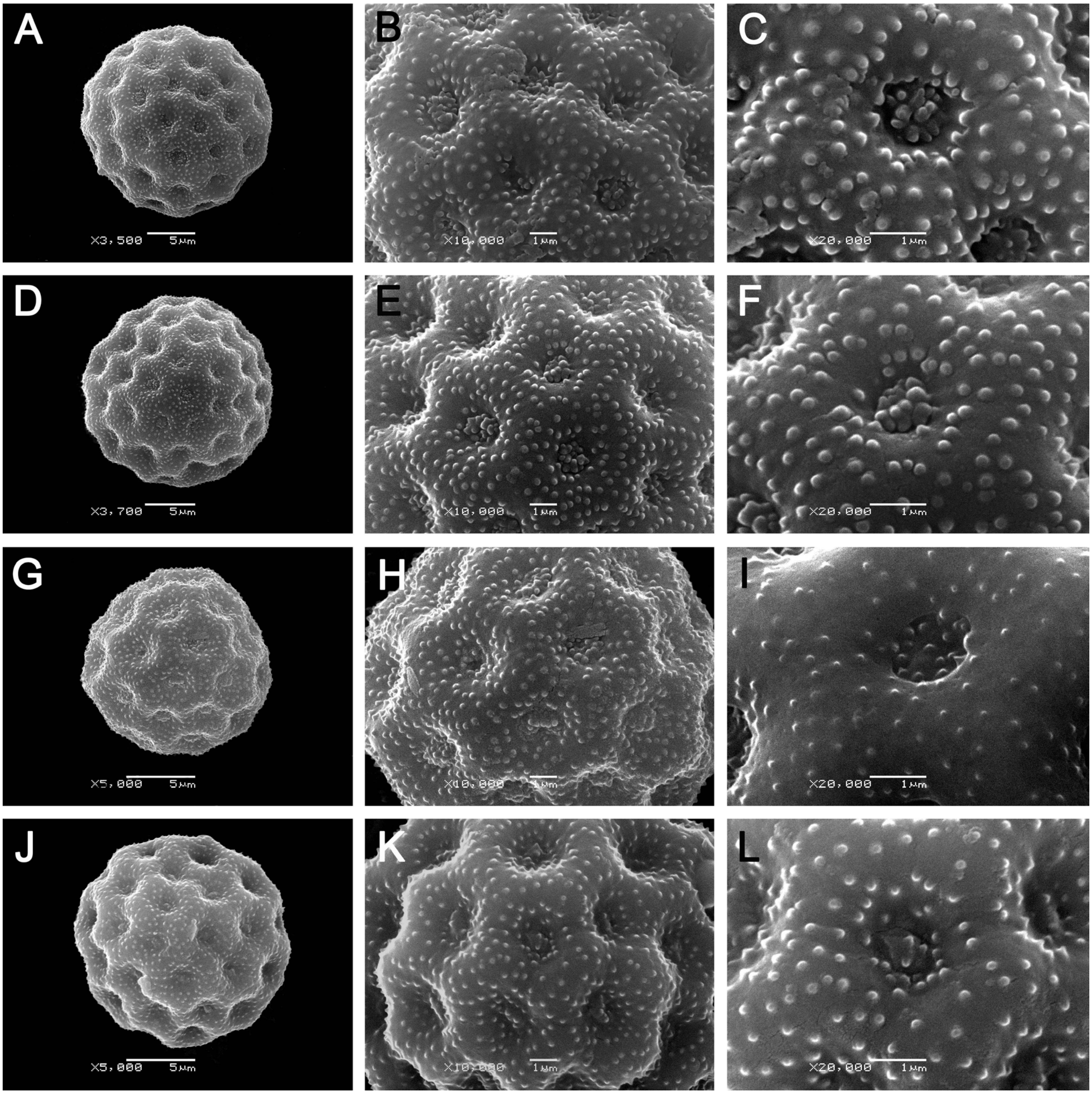

Fig. 2. Pollen grains of *Petrosimonia* (SEM). A–F: *P. brachiata* (A–C — specimen 1, D–F — specimen 2); G–L: *P. oppositifolia* (G–I — specimen 1, J–L — specimen 2). A, D, G, J: general view; B, E, H, K: nanoechinate exine sculpture; C, F, I, L: pores. A–L: dry pollen

distance between pore centres (C) = 3.99–5.98 μm. C/D = 0.165–0.238. Exine 1.99–2.66 μm thick (Table 1). Sexine thicker than nexine. Columellae indistinct or invisible. LO-analysis: columellae indistinct or rarely distinct, circular, densely distributed, nanoechini invisible.

SEM. Exine sculpture nanoechinate; nanoechini conic with straight sides and acute apex, 0.04–0.11 μm high, 0.10–0.21 μm wide at base, sparsely or more densely distributed (17–25/4μm^2); tectum psilate-perforate in areas between nanoechini. Pore membranes with nanoechini (in number 6–18), pore margins sunken; mesoporia convex. Columellae are continuous from tectum to foot layer; short or long, 0.20–0.91 μm long, 0.18–0.28 μm wide, densely arranged (Table 2).

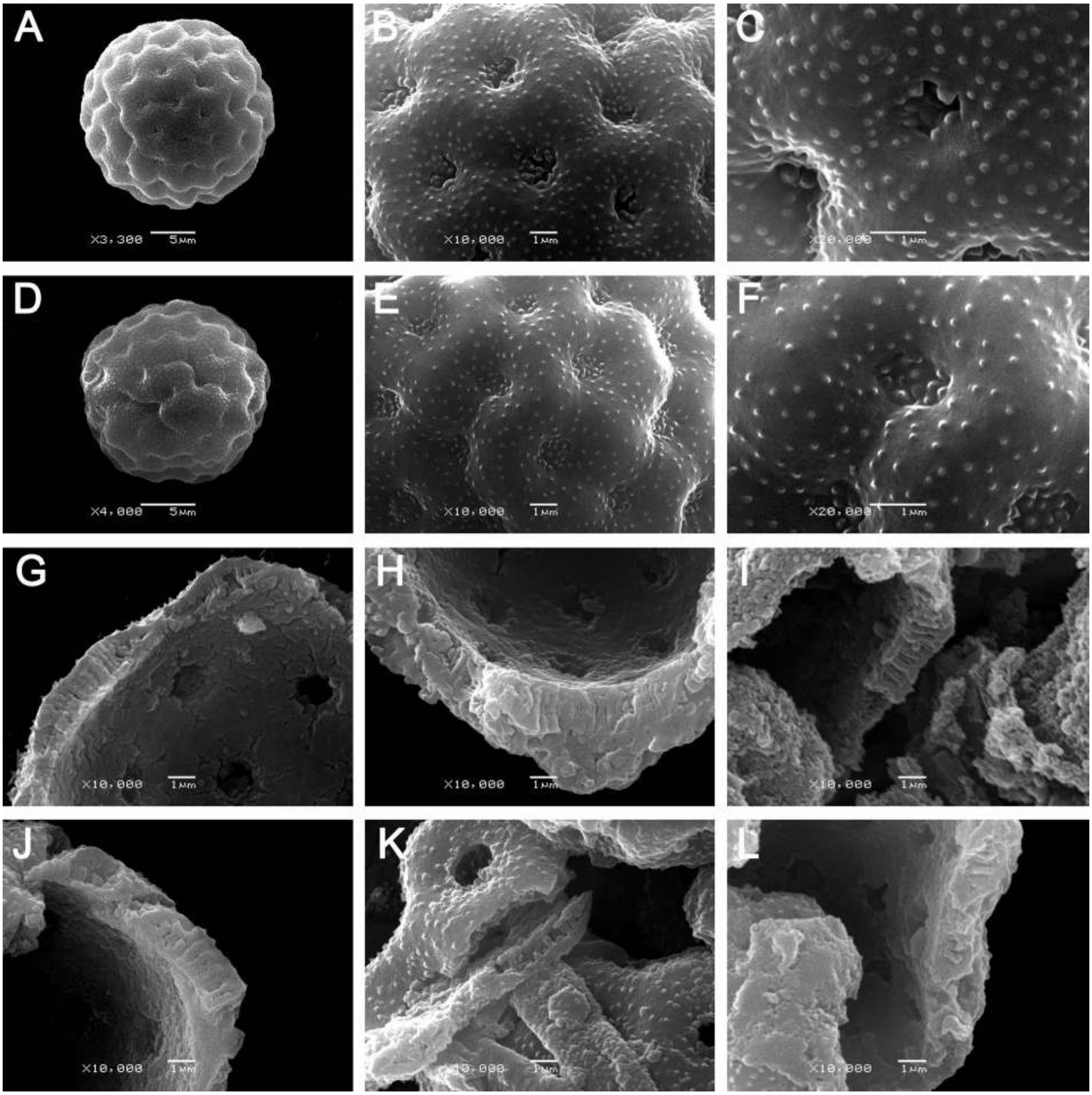

Fig. 3. Pollen grains and exine structure of *Petrosimonia* (SEM). A–F, I, L: *P. triandra* (A–C, I — specimen 1, D–F, L — specimen 2); G, J: *P. brachiata* (G — specimen 1, J — specimen 2); H, K: *P. oppositifolia* (H — specimen 1, K — specimen 2). A, D: general view; B, E: nanoechinate exine sculpture; C, F: pores, G–L: exine structure. A–F: dry pollen; G–L: acetolysed pollen

Numerical analysis of the palynomorphological characters states

Cluster analysis of all six studied specimens clearly distinguished the three clades corresponding to three species of *Petrosimonia* (Tables 1 and 2; Fig. 4A). Specimens with comparable average measurements of pollen grain features, belonging to *P. brachiata* and *P. oppositifolia*, are grouped together and placed in a separate cluster (Fig. 4A). On the other hand, *P. triandra* specimens with the different measurements of pollen grain features are placed in another cluster (Fig. 4A). In general, the variation ranges in the characters of pollen grains between different specimens of *P. brachiata* and *P.*

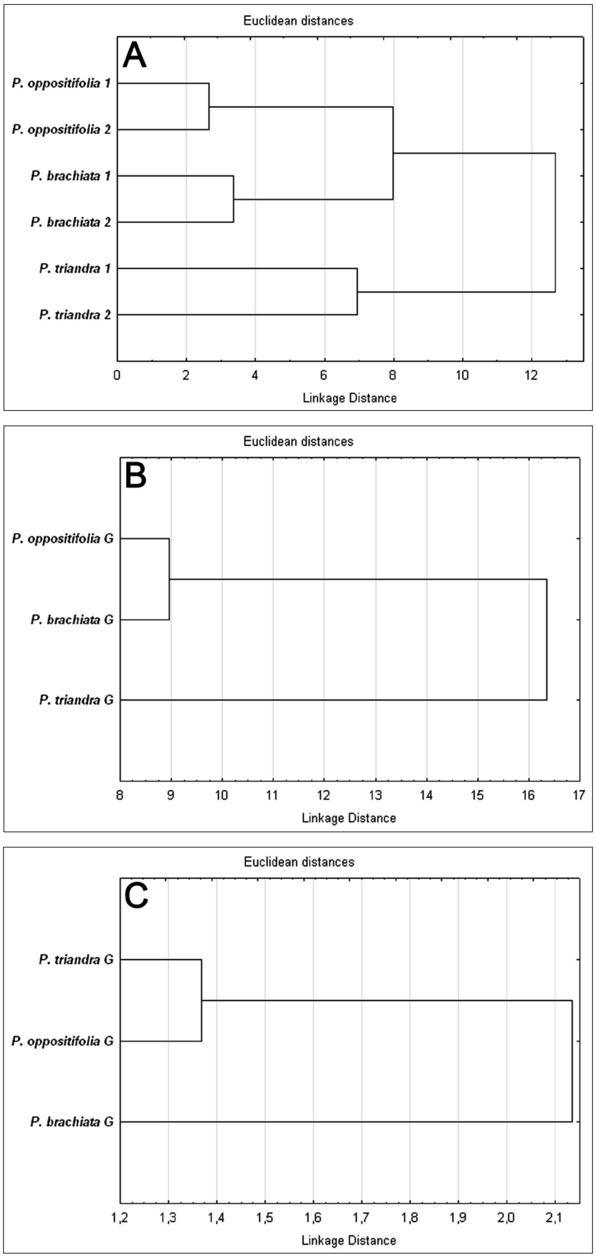

Fig. 4. UPGMA dendrograms showing the relationships of pollen grains of *P. brachiata*, *P. oppositifolia* and *P. triandra* species. A: quantitative characters (see Tables 1 and 2); B: quantitative characters (see Table 1, general specimens' measurements); C: quantitative characters (see Table 2, general specimens' measurements)

oppositifolia were small (Fig. 5); we did not observe significant discontinuity within species. However, the two samples of *P. triandra* have differences in the number of pores (Fig. 5E). But in general, the number of pores in *P. triandra* was greater than that in *P. brachiata* and *P. oppositifolia*. The average value of the pore diameter in the *P. triandra* pollen samples is the same, while the measurements at the range differ (Fig. 5B).

As seen in the UPGMA dendrogram based on total pollen characters (Table 1), *P. triandra* has distinctive pollen morphometric features and is placed in a separate cluster (Fig. 4B). *Petrosimonia brachiata* and *P. oppositifolia* are grouped together and placed in their separate cluster. Based on the nanoechini and columellae characters (Table 2), *P. brachiata* is distinct and forms a separate cluster, whereas *P. oppositifolia* and *P. triandra* are grouped together in their separate cluster (Fig. 4C).

Discussion

The obtained data showed that some characters of pollen grains of representatives of *Petrosimonia* are significant for their taxonomy and for spore-pollen analysis. The pollen grains are mostly small and rarely medium-sized. The pollen size generally overlaps in all species, but on average the pollen grains are smallest in *P. oppositifolia*, and the larger dimensions are characteristic of *P. brachiata* (Table 1). The pollen size for *P. oppositifolia* was given by Kupriyanova and Alyoshina (1972) as 21.6–24.0 µm, and by Monoszon (1973) as 18.0–23.0 µm. These data are similar to those for *P. oppositifolia* obtained in the present study (Table 1). The pollen size range for *P. brachiata* was given by Monoszon (1973) as 21.3–26.0 µm, and by Sonyan et al. (2022) as 18.0–21.2 µm. Their data are close to our pollen diameter measurements, although the range in our study is slightly wider.

Pollen grains of all species have similar pore diameters (Table 1, Fig. 5B). Monoszon (1973) and Sonyan et al. (2022) described pore diameters in *P. brachiata* (2.2–3.0 µm and 1.6–2.8 µm, respectively), which are in general consistent with our data. Kupriyanova and Alyoshina (1972) and Monoszon (1973) reported pore diameters in *P. oppositifolia* (1.2–2.4 µm and 2.5–3.3 µm, respectively), in which the diameter of pores is comparable to those of *P. oppositifolia* revealed in the present study (Table 1).

The data obtained show that shortest distances between pores are characteristic for *P. triandra* (Fig. 5C), the largest distances between pores are characteristic for *P. brachiata* and *P. oppositifolia* (Fig. 5C). Sonyan et al. (2022) reported *P. brachiata*

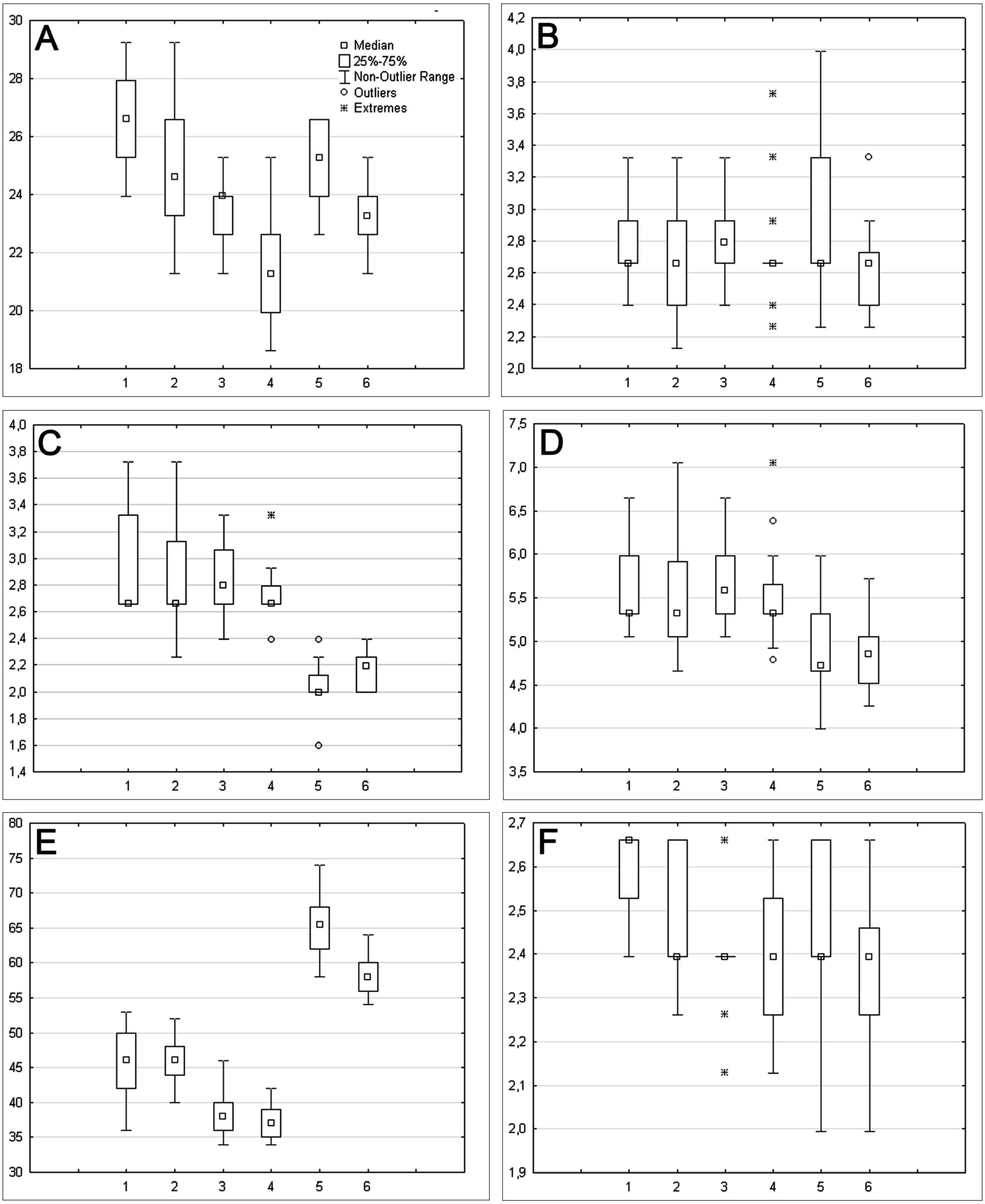

Fig. 5. Box plots of variation of *Petrosimonia* pollen grains. A: pollen diameter; B: pore diameter; C: distance between pore; D: distance between pore centers; E: pore number; F: exine thickness. 1, 2 — *P. brachiata*; 3, 4 — *P. oppositifolia*; 5, 6 — *P. triandra*

pollen grains that have distances between pores of 1.7–2.4 μm, which is not consistent with the values obtained in this study. Kupriyanova and Alyoshina (1972) recorded pollen grains of *P. oppositifolia* with the distances between pores (2.4–3.0 μm) comparable to those of *P. oppositifolia* in the present study (Table 1). The shortest distances between centers of pores are characteristic for *P. triandra*, and the largest ones in *P. brachiata* and *P. oppositifolia* (Table 1, Fig. 5D). Monoszon (1973) described pollen grains with distances between centers of pores in *P. brachiata* (4.7–5.4 μm) and in *P. oppositifolia* (4.9–6.3 μm), which is consistent with our data (Table 1).

Pollen grains in all species are pantoporate. The smallest number of pores is characteristic of *P. oppositifolia*, while the largest number of pores is characteristic of *P. triandra* (Fig. 5E). The data obtained show that pollen grains with many pores are characterized by a low mean C/D ratio (0.19 in *P. triandra*), and pollen with a fewer pores has a high mean C/D ratio (0.21 in *P. brachiata*, and 0.25 in *P. oppositifolia*). The number of pores for *P. oppositifolia* was given by Kupriyanova and Alyoshina (1972) as 40–50, and Monoszon (1973) as 30–36. Monoszon (1973) also reported pollen grains of *P. brachiata* with 38–53 pores, which is consistent with our data (Table 1).

The thickness of the exine generally overlaps in all species, but on average the exine is thicker in *P. brachiata* pollen, while it is thinner in *P. oppositifolia* and *P. triandra* (Table 1). Kupriyanova and Alyoshina (1972) recorded pollen grains of *P. oppositifolia* that had slightly thinner exine (1.2–2.4 μm) than the values measured in this study. The exine of the pollen grains of *P. brachiata* (0.9–1.5 μm), reported by Sonyan et al. (2022), is generally thinner than the exine of *P. brachiata* measured in our study (Table 1). Monoszon (1973) described pollen grains of *P. oppositifolia* (2.5–3.5 μm) and *P. brachiata* (2.4–3.5 μm) that had thicker exine, than the values measured in this study. In general, our data are in agreement with the results of previous LM studies (Kupriyanova, Alyoshina, 1972; Monoszon, 1973; Sonyan et al., 2022).

The obtained data show that among the studied species, *P. triandra* differs in some pollen characters, in particular the distances between pores and between pore centers, nanoechini bases and columellae height (Tables 1 and 2). According to recent molecular phylogenetic data (Fedorova, Aleksandrov, 2015), *P. triandra* forms a separate clade that is rather phylogenetically distant from other clades, which is in good agreement with the inclusion of this species in the section *Oligandra*. The pollen features obtained in the present investigation are consistent with these conclusions (Figs 4A, B; 5C– E).

Pollen grains of *P. brachiata* and *P. oppositifolia* are similar in some pollen characters, in particular the distances between pores and between pore centers, nanoechini bases and columellae height (Fig. 4A, B), but differ in other characters. Pollen in *P. brachiata* has a larger size and pore number, larger nanoechini and shorter columellae, and the species is thus placed in a separate branch (Fig. 4C). This is also supported by the box plots (Fig. 5A, E). Molecular phylogenetic data placed these species in different clades (Fedorova, Aleksandrov, 2015), which correspond to sections *Brachyphyllon* and *Synandra*, respectively.

There are several palynomorphological characters that overlap. For example, pollen grains in *P. brachiata* and *P. oppositifolia* have only slightly undulate edges, and in *P. triandra* they are undulate on the edge. According to the mesoporial exine level, pores in *P. brachiata* and *P. oppositifolia* are sunken or raised, while in *P. triandra* they are sunken. Pollen grains in *P. brachiata* and *P. oppositifolia* have slightly convex mesoporia, while in *P. triandra* they are convex (Figs 2 and 3). Since these characters are similar in all species, their usefulness for distinguishing of the species is limited. Thus, diagnostic features for the purposes of taxonomy are the following: size, distances between pores and between pore centers, pore number, nanoechini size, nanoechini bases size and columellae height.

Our study improves the knowledge of *Petrosimonia* species and provides the refined diagnostic characters for the identification of their pollen grains. *Petrosimonia brachiata* is similar to *P. oppositifolia* in LM that they are difficult to properly separate using palynological data. In case of good preservation of pollen grains of *Petrosimonia*, we propose to use a set of features: size, distances between pores and between pore centers, and pore number. With pollen analysis we can identify pollen of *P. triandra*. The smaller distances between pores and between centers of pores were characteristic for *P. triandra* while larger ones were observed in *P. brachiata* and *P. oppositifolia* (Fig. 5C, D). *Petrosimonia brachiata* and *P. oppositifolia* have fewer pores, while *P. triandra* have bigger pore numbers (Fig. 5E). Identification of these species is an important criterion for reconstructing the distribution pattern of halophytic vegetation in the recent past (Pleistocene–Holocene).

Conclusions

Pollen morphology proved to be an important source of additional information for the species-specific identification of the genus *Petrosimonia*. A detailed description of the pollen grains of *P. triandra* is provided for the first time in this study using LM and SEM. This study presents the first detailed description of pollen grains of *P. oppositifolia* using SEM. The exine structure of pollen grains of all species was also studied for the first time using SEM. The diagnostic features of the studied species included the pollen sizes, distances between pores and between pore centers, pore numbers, and features of nanoechini and columellae. The presented characteristics of pollen grains and their photomicrographs can be used for pollen identification in the spore-pollen analysis. The species *P. brachiata* and *P. oppositifolia* are quite similar in their pollen grain characters. When identifying pollen grains, it is possible to use a complex of features of *P. brachiata* / *P. oppositifolia*. The pollen characteristics described here may also be used in future studies aiming at expanding the knowledge on taxa of *Salsoloideae* and *Chenopodiaceae* / *Amaranthaceae* in general.

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ETHICS DECLARATION

The authors declare no conflict of interest.

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Морфологія пилкових зерен представників роду *Petrosimonia*
(*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.) флори України

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Реферат. Морфологію пилкових зерен *Petrosimonia brachiata*, *P. oppositifolia* та *P. triandra* (*Salsoloideae*, *Chenopodiaceae* s. str. / *Amaranthaceae* s. l.) флори України досліджено за допомогою світлової та сканувальної електронної мікроскопії, пилкові зерна *P. triandra* було досліджено вперше. Метою роботи було отримати характеристики пилкових зерен цих видів та оцінити значення ознак для видоспецифічної ідентифікації. Пилкові зерна досліджених видів багатопорові, сфероїдальні, округлі, злегка хвилясті або хвилясті по краях; дрібного та середнього розміру. Скульптура екзини наношипикувата, покрив гладенько-перфорований. Порові мембрани наношипикуваті. Вперше вивчено і проаналізовано структуру екзини (стовпчики) пилкових зерен усіх видів. Обговорюється значення особливостей пилкових зерен для таксономії та пилкового аналізу в палеопалінології. Дендрограми UPGMA, засновані на паліноморфологічних даних, підтверджують диференціацію досліджених видів. Пилкові зерна *P. triandra* чітко відрізняються від пилкових зерен *P. brachiata* та *P. oppositifolia* за розміром, відстанями між порами та між центрами пор, а також кількістю пор. Пилкові зерна *P. brachiata* мають більший розмір та кількість пор, більші наношипики та коротші стовпчики порівняно з такими у *P. oppositifolia*.

Ключові слова: паліноморфологія, пилковий аналіз, світлова мікроскопія, сканувальна електронна мікроскопія, скульптура, структура, UPGMA