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Pollen typification and palynotaxonomy of subfamily Salsoloideae Ulbr. (Chenopodiaceae Vent.) in the flora of South Transcaucasia

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ABSTRACT. The article presents the results of a comparative palyno-morphological analysis of the representatives of the Salsoloideae subfamily (Chenopodiaceae) in South Transcaucasia. Out of 25 species belonging to 13 genera of Salsoloideae subfamily in South Transcaucasia, pollen morphology of 23 species from 12 genera was investigated, as well as an analysis of the pollen characteristics was conducted. Data on five key features of pollen (on LM level) were statistically analyzed including pollen diameter, pore number, pore diameter, exine thickness, and mesoporium width. The results indicated that within the Salsoloideae subfamily of South Transcaucasian flora the first three features may be considered diagnostic. The application of a scanning electron microscope (SEM) has revealed the fourth diagnostic feature of the pollen within the Salsoloideae subfamily, specifically, the number of spinules on the unit surface of the pollen, which enables, in several cases, to conduct intergeneric or interspecific differentiation.

Based on the obtained data, typification of pollen within the Salsoloideae subfamily of South Transcaucasia was carried out for the first time. As a result, two morphological types and four subtypes combined in two palynogroups were distinguished. The subdivision into palynogroups is based on differences in the size of pollen grains. Only species *Climacoptera crassa* with pollen of average sizes (26–33/29 µm in diameter) is included into the monotypic Palynogroup I, all other investigated species with small pollen grains (10–25 (27)/22 µm in diameter) are joined in Palynogroup II. Allocation of species into two different Types of Palynogroup II is based on the presence of a significant difference in the size of small pollen grains of individual species. In particular, species with relatively large pollen grains (>20 µm in diameter) are included in Type 1, while species with relatively small ones (≤ 20 µm in diameter) are joined in Type 2. And finally, the distribution of species into the subtypes and variations of Palynogroup II is based on differences in pore number and size.

The identified key palyno-morphological features made it possible in some cases to specify the taxonomic boundaries, as well as the relationship between taxa within the subfamily Salsoloideae.

KEYWORDS: Chenopodiaceae, palynotaxonomy, pollen morphology, Salsoloideae, South Transcaucasia, statistical analysis

INTRODUCTION

Chenopodiaceae Vent. family is cosmopolitan including approximately 100 genera and 1300–1600 species of annual and perennial grasses, shrubs, bushes, even small trees (the genus *Haloxylon* Bunge) growing predominantly in eutrophic, halophilic habitats, in areas with arid climate (Cronquist, 1968; Grubov, 1980; Mabberley, 2002; Akopian, 2013; Sukhorukov, 2014). In South Transcaucasia Chenopodiaceae is represented with 30 genera and 90 species, constituting 30% of the generic composition in the world, 85.7% of generic and 80.3% of the species composition in the flora of Caucasus.

The subfamily Salsoloideae is represented with 13 genera and 25 specieis in South Transcaucasia, 2 genera of which – *Halimocnemis*

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C.A.M. (*H. pilifera* Moq.) and *Anabasis* L. (*A. eugeniae* Iljin, *A. aphylla* L.), as well as the species *Caroxylon vermiculatum* (L.) Akhani & E.H. Roalson are met exclusively in Nakhijevan AR (Akopian, 2013).

The genus *Salsola* L. is one of the most widespread ones in the mentioned region, which, according to Botschantsev (1969), arose in South Africa not later than the Miocene, and the *Caroxylon* section is the initial one of the genus. Until the end of the 20th century, 114–117 species were included in this genus (Botschantsev, 1969, 1974, 1980; Kühn et al., 1993; Freitag, 1997).

On the other hand, a trend of fragmentation of phylogenetically heterogeneous and polymorphic genus *Salsola* was indicated in works of Botschantsev (1981), Pratov (1986), Tsvelev (1993), Tzvelev (1996), it was also noted in the results of molecular-genetic analysis (Pyankov et al., 2001; Kadereit et al., 2003; Akhani et al., 2007; Wen et al., 2010; Sukhorukov et al., 2011; Akopian, 2011, 2013).

According to molecular research results of Akhani et al. (2007), some of the genera in the subfamily Salsoloideae, including *Halanthium,* are not monophyletic. The authors wrote that "In some cases, this is due to the misclassification of one or a small number of species [...], whereas other cases, such as the polyphyly and interdigitation of *Halanthium* and *Halimocnemis*, are more difficult" (Akhani et al., 2007: 935).

Palynological investigations of Chenopodiaceae commenced in the mid-19th century (Moquin-Tandon, 1837, 1849a, b). Subsequent studies on the pollen of goosefoot family on the level of light microscope (LM), as well as scanning (SEM) or transmission (TEM) electron microscopes were conducted in the scope of the entire family (Wodehouse, 1935; Monozson-Smolina, 1950; Erdtman, 1952; Kuprianova and Alyoshina, 1972; Monozson, 1973; Tsymbalyuk, 2005, 2008), the separate subfamilies (Dehghani and Akhani, 2009; Dehghani et al., 2020), tribes (Olvera et al., 2006; Zare and Keshavarzi, 2007), genera (Gomez and Pedrol, 1987; Pinar and Inceoglu, 1999; Akhani et al., 2003; Hamdi et al., 2009; Toderich et al., 2010) or separate groups of species (Zaklinskaya, 1950; Tsukada, 1967; Valdes et al., 1987; Angelini et al., 2014; Lu et al., 2018b).

In particular, Monozson (1973) studied the features of the pollen morphology of 117 species of the family Chenopodiaceae. The author noted that in the subfamily Spirolobeae C.A. May. (now including all taxa of the subfamily Salsoloideae) pollen characters differ not only within individual genera, but also within species, as, for example, in the genus *Salsola*. Tsymbalyuk (2005) investigated (on the level of LM and SEM) six species of the genus *Salsola* and classified them within the three types of two different palynogroups. The author also distributed two species of the genus *Climacoptera*, as well as three species of the genus *Caroxylon* (currently considered part of the genus *Salsola* s.l.), within the various types of the same palynogroup. Thus, all these presented data indicate some palynological heterogeneity of all three studied genera.

Toderich et al. (2010) investigated pollen morphology of 27 Asian species of the genus *Salsola* (using SEM) and identified three types of pollen grains. Type I included large pollen grains (17.41–20.76 μm in diameter) with numerous pores (40–58) and the lack of convex mezoporial exine. Type II was characterized by small pollen grains (11.78–16.20 μm in diameter) with sunken pores (16–28) and distinctly convex mesoporial exine. Type III occupied an intermediate position between Types I and II in terms of the number of pores (30–38), as well as extexine spinule/punctate density.

Perveen and Qaiser (2012) studied the pollen morphology of 40 species from 13 genera of the Chenopodiaceae family. Based on the size and number of pores, as well as exine sculpture, authors identified four morphological types of pollen, noting, however, that the Chenopodiaceae family as a whole belonged to stenopalynous taxa. All four species of the genus *Salsola* (*S. tragus* L., *S. richteri* Moq., *S. nitraria* Pall., *S. imbricata* Frossk) were presented in two different types, namely the *Chenopodium album* type (*S. tragus*, *S. nitraria*) and the *Atriplex stocksii* type (*S. richteri*, *S. imbricata*).

Based on the data of the pollen morphology of 18 species from 12 genera of the Chenopodiaceae family (including the species *Salsola passerina* Bunge and *S. collina* Pall.), growing in Mongolia, Punsalpaamuu et al. (2012) noted that all the studied species differ mainly in the size of pollen grains, the thickness of the exine and the number of pores.

Palynological data on the genera *Noaea* and *Girgensohnia* are rather scarce in the literature. Some information on the pollen morphology of the species *Noaea spinosissima* (syn. *N. mucronata*) and *Girgensohnia oppositiflora* was found in the work of Tsymbalyuk (2005), where the author classified these two species in the type *Horaninowia*.

In contrast, the genus *Anabasis* has served as the object of a number of palyno-morphological studies. In particular, Tsymbalyuk (2005) presented three investigated species of this genus in two different subtypes of the same palynogroup. Assadi et al. (2016) studied the pollen morphology of 7 Iranian species of the genus *Anabasis*, including species *A. aphylla* and *A. eugeniae*. As the main diagnostic features, authors consider two variations in the diameter of individual submerged pores, namely, the pore diameter (inner) of holes and pore diameter (outer) of holes, as well as the depth of pore sinking. Based mainly on the above characters, Assadi et al. (2016) identified two types of pollen grains, herewith both Transcaucasian species of the genus *Anabasis* are represented in two different types.

Lu et al. (2018a), based on the data of a hierarchical cluster analysis of pollen morphological features, in particular, the pore number and the type of pore membrane sculpture in 24 species from 13 genera of the Chenopodiaceae family (including three species of the genus *Anabasis*) of the eastern part of Central Asia, distinguished 2 main palynogroups (A and B) and a number of types and subtypes. Herewith the representatives of the genus *Anabasis* were classified in the *Kalidium* type of Palynogroup A with the globally 10–35 pores, pointing to the presence of certain relationships between the genera *Anabasis* and *Kalidium* Moq.

Describing the pollen morphology of five species of the genus *Petrosimonia* (including *P. brachiata*), Monoszon (1973) characterized the genus as morphologically homogeneous with a noticeably wavy contour of the pollen grain surface, thick exine, and up to 50 pores. Grozeva et al. (2019) studied the single representative of the genus *Petrosimonia* (*P. brachiata*) in Bulgaria within two different populations and noted certain karyological and morphological variabilities. However, the authors did not reveal a significant variability in the morphological features of pollen. On the other hand, based on the palyno-morphological data, Tsymbalyuk (2005) classified three investigated species of the genus *Petrosimonia* in two different palynogroups.

Finally, Tsymbalyuk (2005) assigned the species *Halanthium kulpianum* to the type *Halimocnemis*, thus indicating the proximity of the genera *Halanthium* and *Halimocnemis*.

Studies of pollen morphology of Chenopodiaceae family in Armenia were started in the mid-fifties of the last century. A short description of palyno-morphological characteristics of separate genera (using LM) are presented in the second volume of the “Flora of Armenia” (Avetisyan and Manukyan, 1956). Information about the pollen of several representatives of goosefoot family in Armenia using LM and SEM can be found in Akopian and Hayrapetyan (2004, 2009).

The main purpose of our investigation was a comprehensive study of the pollen morphology of the subfamily Salsoloideae in South Transcaucasia using LM and SEM in order to conduct a comparative palyno-morphological analysis of taxa represented in this region.

The reason for the study was the lack of palynological data, which could help in resolving a number of controversial taxonomic issues within the subfamily.

In this research the list of the genera as well as the species within the limits of Salsoloideae subfamily of South Transcaucasia are presented in accordance with Akopian’s data (2013).

MATERIAL AND METHODS

The work presents the results of comparative palyno-morphological analysis of the representatives of Salsoloideae subfamily in South Transcaucasia completed on intergeneric and intrageneric levels. Detailed description of pollen morphology and statistical analysis of 23 representatives (on the level of LM and SEM) were presented in our earlier articles (Hayrapetyan and Sonyan, 2020, 2021a, b; Sonyan, 2020; Sonyan and Hayrapetyan, 2021a, b).

Pollen material was gathered from the herbaria of the Institute of Botany after A. Takhtajyan of NAS of Republic of Armenia (ERE) and Yerevan State University (ERCB), as well as from living plants of the plot “Flora and vegetation of Armenia” of the Institute of Botany and from the suburbs of Eraskhuni village of Armavir District in Armenia (Table 1).

The study of the pollen characteristics using an AmScope light microscope (LM) was carried out on pollen grains stained with basic fuchsine (Smolyaninova and Golubkova, 1950), as well as on acetolyzed material (Avetisyan, 1950), with obligatory fixation of pollen in glycerin gelly. The details of exine structure and ornamentation were studied on acetolyzed pollen grains. Pollen grain shape and size, and also aperture structure, were studied on non-acetolyzed stained pollen grains.

Table 1. List of investigated species and specimens. ERE – Herbarium of the Institute of Botany after A. Takhtajan, National Academy of Sciences, Yerevan, Armenia; ERCB – Herbarium of Yerevan State University, Yerevan, Armenia

Species		Specimens
Currently accepted name (according to J. Akopian, 2013)	Name according to their location in ERE herbarium	
Anabasis aphylla L.	*Anabasis aphylla* L.	ERE, 1857; ERE, 1852; ERE, 72308
A. eugeniae Iljin	*A. eugeniae* Iljin	ERE, 146060; ERE, 77574
Caroxylon dendroides (Pall.) Tzvelev	*Salsola dendroides* Pall.	ERE, 76089; ERE, 86593; ERE, 82553; ERE, 76081
C. ericoides (M. Bieb.) Akhani et E.H. Roalson	*Salsola ericoides* M. Bieb.	ERE, 72306; ERE, 76067; ERE, 7065
C. gemmascens (Pall.) Tzvelev	*Salsola gemmascens* Pall.	ERE, 171291; ERE, 171293; ERE, 171290; ERE, 168976
C. nitrarium (Pall.) Akhani et E.H. Roalson	*Salsola macera* Litv.	ERE, 28401; ERE, 87469
C. nitrarium (Pall.) Akhani et E.H. Roalson	–	personal collection (Armenia, Institute of Botany of NAS RA, plot of "Flora and Vegetation of Armenia". 02.08.2017. Leg. J. Akopian)
C. nitrarium (Pall.) Akhani et E.H. Roalson	*Salsola nitraria* Pall.	ERE, 171294
C. nodulosum Moq.	*Salsola nodulosa* (Mog.) Iljin	ERE, 76102; ERE, 2203
C. nodulosum Moq.	*Salsola verrucosa* M. Bieb.	ERE, 128802; ERE, 168561
Climacoptera crassa (M.B.) Botsch.	*Salsola crassa* M. Bieb.	ERE, 147798
C. crassa (M.B.) Botsch.	*C. crassa* (M.B.) Botsch.	ERE, 172359
Girgensohnia oppositiflora (Pall.) Fenzl	*Girgensohnia oppositiflora* (Pall.) Fenzl	ERE, 136814; ERE, 64726; ERE, 1990; ERE, 1991
Halanthium kulpianum (K. Koch) Bunge	*Halanthium kulpianum* (K. Koch) Bunge	ERE, 76036; ERE, 73310; ERE, 73309; ERE, 106924
H. rarifolium K. Koch	*H. rarifolium* K. Koch	ERE, 172394; ERE, 172383; personal collection (Armenia, Armavir province (marz), village Yeraskhaun, 17.06.19. Leg. H. Sonyan, J. Akopian; 23.09.2018. Leg. H. Sonyan, J. Akopian)
Halothamnus glaucus M. Bieb. Botsch.	*Salsola glauca* Bieb.	ERE, 70326; ERE, 137448; ERE, 104791; ERE, 35058
Kali tragus (L.) Scop.	*Salsola australis* R. Br.	ERE, 76071; ERE, 27970; ERE, 47055; ERE, 82901; ERE, 76076; ERE, 39622; ERE, 172511
K. tragus (L.) Scop.	–	personal collection (Armenia, Institute of Botany of NAS RA, plot of "Flora and Vegetation of Armenia") 20.09.2017. Leg. H. Sonyan)
K. collina (Pall.) Akhani et E.H. Roalson	*Salsola collina* Pall.	ERE, 82258
K. tamamschjanae (Iljin) Akhani et E.H. Roalson	*Salsola tamamschjanae* Iljin	ERE, 3157; ERE, 150915
Kaviria cana (K. Koch) Akhani	*Salsola cana* K. Koch	ERE, 12181; ERE, 103595; ERE, 71593; ERE, 19874; ERE, 73537
K. cana subsp. *futilis* (Iljin) Akopian	*Salsola cana* K. Koch	ERE, 82904; ERE, 70310
K. cana subsp. *futilis* (Iljin) Akopian	*Salsola futilis* Iljin	ERE, 82755
K. tomentosa (Moq.) Akhani et E.H. Roalson	*Salsola tomentosa* (Moq.) Spach	ERE, 82903; ERE, 171311; ERE, 128801; ERE, 172544
Noaea minuta Boiss. et Bal.	*Noaea minuta* Boiss. et Bal.	ERE, 171245; ERE, 172476; ERE, 56045; ERE, 172478
N. mucronata (Forsk.) Asch. et Schweinf	*N. mucronata* (Forsk.) Asch. et Schweinf	ERE, 170531; ERE, 172473; ERE, 85851; personal collection, Armenia, Gegharkunik province (marz), near Shorzha, 19.08.2019. J. Akopian)
N. mucronata subsp. *leptoclada* (Woron.) Assadi	*N. leptoclados* (Wor.) Iljin	ERE, 7926
Petrosimonia glauca (Pall.) Bunge	*Petrosimonia glauca* (Pall.) Bunge	ERE, 172490; ERE, 146036; ERE, 123431; ERE, 169751
P. brachiata (Pall.) Bunge	*P. brachiata* (Pall.) Bunge	ERE, 136806
Salsola soda L.	–	ER*CB*, 12263
Seidlitzia florida (Bieb.) Bunge ex Boiss.	*Seidlitzia florida* (Bieb.) Bunge ex Boiss.	ERE, 106912; ERE, 75977; ERE, 91692; personal collection (Armenia, Institute of Botany of NAS RA, plot of "Flora and vegetation of Armenia" 02.08.2017. Leg. J. Akopian)

For scanning electron microscope (SEM), non-acetolyzed dry pollen grains were placed in a drop of alcohol and then mounted on aluminium stubs and sputter-coated with gold. For SEM a Jeol JSM-6390 and JEOL-7000 scanning electron microscopes were run at 15kV.

Five morphological characters, namely diameter of pollen grains, number and diameter of pores, exine thickness, mesoporium width (using LM), and the number of spinules on a unit area (1 μm^2) of the surface of a pollen grain, or mesoporium (on SEM level), were measured.

Pores of each research sample were counted according to the method of Angelini et al. (2014).

Twenty pollen grains were examined and measured for each investigated specimen.

Statistical analysis of all the studied species was performed using Microsoft Excel 2016 with two indicators: SD – standard deviation and CV% – coefficient of variation (https: microsoft-excel-2016.ru.softonic.com).

On the whole, pollen morphological characteristics of 84 samples from 23 species and 4 subspecies from 12 (out of 13 available) genera of subfamily Salsoloideae (Chenopodiaceae) in South Transcaucasia were analyzed.

The list of species analysed in this study includes information on synonyms according to their locaion in the Herbarium of the Institute of Botany after A. Takhtajan, National Academy of Sciences, Yerevan, Armenia (ERE) (Table1).

The morphological terminology used in our study mainly follows Erdtman (1952), Kuprianova and Alyoshina (1972), and Punt et al. (2007).

The summarized palyno-morphological data are presented in Table 2, the data of statistical analysis are presented in Table 3.

RESULTS AND DISCUSSION

Our investigation confirms palynological uniformity both in the general shape of pollen grains and in the type of apertures typical for the representatives of the Chenopodiaceae family on the whole.

On the other hand, preliminary analysis (using LM) of five key morphological features, namely, diameter of pollen grains, number and diameter of pores, exine thickness, mesoporium width in the genus *Salsola* s.l. indicates that only the first three features can be used for diagnostic purposes (Sonyan, 2018). Later, the given assumption was proven for the representatives of the entire Salsoloideae subfamily in South Transcaucasia in general (Hayrapetyan and Sonyan, 2021a, b; Sonyan and Hayrapetyan, 2021b). It was also established that in some cases, the number of spinules in the unit area (1 μm^2) of a pollen grain surface, or mesoporium (on SEM level), may vary, which can also be used in pollen typification (Table 2).

Extended statistical analysis on three pollen features, namely the diameter of pollen grains, and the number and diameter of pores, conducted for the representatives of 11 genera of Salsoloideae subfamily of South Transcaucasian flora revealed that the highest variability (CV = 0–10.0%) was noted in pore number, whereas the coefficient of variation of pollen diameter (CV = 0.5–16.6%) and the diameter of pores (CV = 0.4–20.0%) have average variability. Nevertheless, the results obtained do not exceed the limits of data reliability (Table 3).

On the other hand, the statistical analysis of the variation of exine thickness and width of mesoporium did not reveal any significant differences, therefore the mentioned characteristics were not included in the scope of our further research.

Comparative palyno-morphological analysis has revealed that among 13 investigated species of the genus *Salsola* s.l., species *Climacoptera crassa* (M.B.) Botsch. has the largest size of pollen grains (26.3–33.1/29.4 μm in diameter), while in other species, the size of pollen grains varies between 12.0 and 26.4/18.5 μm in diameter.

The largest pores were noted in pollen grains of the species *Kaviria cana* (K. Koch) Akhani (2.3–5.3/3.5 μm in diameter), while for example, the size of pores in the species *Caroxylon nitrarium* (Pall.) Akhani et E.H. Roalson does not exceed 2.3/1.6 μm in diameter (Pl. 1, fig. 12 and Pl. 1, fig. 6 respectively). The species *Kaviria cana* also stands out with a minimal number of pores (7–16/10 pores), while the total number of pores in the other species varies between 16 and 38/27.

It was revealed that the number of the spinules on the unit surface of the pollen grains (at the level of SEM) varies also considerably in certain species. Based on this fact, the averaged data were obtained for another additional diagnostic feature. It was found, that in most species of the genus *Salsola* s.l. the number of spinules varies between 4 and 9 on 1 μm^2, except for *Caroxylon gemmascens* (Pall.) Tzvelev*, Kali tragus* (L.) Scop.*, Climacoptera crassa, Halothamnus glaucus* (M.B.) Botsch.*, Salsola soda*, where it does not exceed 4.

Comparative analysis of the four abovementioned key pollen morphological features within the whole *Salsoloideae* subfamily in

Table 2. Distribution and palyno-morphological characteristics of the representatives of the subfamily Salsoloideae in South Transcaucasia[1]

Species	Distribution		Pollen diameter (μm)	Pore number	Pore diameter (μm)	Exine thickness (μm)	Mesoporium width (μm)	Number of spines on 1 μm²
	Armenia	Nakhijevan AR						
Caroxylon gemmascens	+	+	(12.3)14.3–21.4/17.8	16–22/19	(0.9)2.7–4.1/3.2	0.7–1.2/0.9	1.7–2.7/2.2	2–4/3
C. nodulosum	+	+	14.7–20.8/17.6	25–35/30	1.7–2.7/2.0	1.0–1.5/1.22	2.2–3.0/2.6	5–6/5
C. ericoides	+	+	17.3–26.4/20.6	27–38/32	1.3–2.8/2.2	1.0–1.9/1.4	1.8–2.6/2.1	5–9/7
C. nitrarium	+	+	14.8–21.9/17.7	24–36/30	0.8–2.3/1.6	0.9–1.2/1.0	1.7–2.0/1.8	5–8/6
C. dendroides	+	+	14.4–21.9/16.7	24–38/28	1.1–2.7/1.7	0.8–1.2/1.0	1.5–2.0/1.7	4–8/5
Climacoptera crassa	+	+	26.3–33.1/29.4	28–36/31	3.1–5.0/4.0	2.0–3.1/2.5	2.5–3.7/3.0	2–4/3
Halothamnus glaucus	+	+	18.7–23.2/21.4	(16)20–28/25	2.5–4.6/3.7	1.6–2.5/2.1	2.4–3.9/3.0	2–4/2
Kali tragus	+	+	17.1–25.1/20.8	22–34/28	1.2–3.0/1.8	1.6–2.2/1.8	1.6–2.3/1.9	2–4/3
K. tamamschjanae	+	+	18.5–22.5/20.6	27–32/30	1.6–2.8/2.2	1.2–2.0/1.5	1.2–2.6/2.2	4–6/5
K. collina	(adventive)	(adventive)	18.9–24.5/21.9	32–38/35	1.2–2.9/2.2	1.3–1.9/1.6	1.9–2.9/2.3	–
Kaviria cana	+	+	14.9–21.7/18.7	7–16/10	2.3–5.3/3.5	1.3–1.9/1.6	3.5–4.9/4.2	4–7/5
K. tomentosa	+	+	14.2–16.9/15.7	12–17/13	1.9–3.8/2.6	1.1–1.4/1.2	2.1–3.0/2.5	4–5/5
Salsola soda	+	+	12.0–14.0/13.0	20–22/20	2.0–2.5/2.2	–	2.0–2.3/2.1	3–5/4
Seidlitzia florida	+	+	10.1–15.1/13.0	7–11 (14)/9	2.2–4.2/2.9	0.5–1.2/0.9	2.1–3.9/2.8	2–3/2
Noaea minuta	+	–	17.0–22.1/19.6	20–26/22	2.4–3.9/3.2	1.1–1.9/1.4	2.0–3.4/2.5	2–4/3
N. mucronata subsp. *mucronata*	+	+	12.2–15.6/14.0	10–14/13	2.1–3.6/2.7	0.7–1.2/0.9	2.1–3.6/2.6	2–4/3
N. mucronata subsp. *leptoclada*	+	+	14.0–15.2/14.6	14–17/15	3.0–3.9/3.3	1.0–1.4/1.2	1.9–2.5/2.2	2–4/3
Girgensohnia oppositiflora	+	+	11.0–14.7/13.0	10–15/12	2.2–3.9/2.9	0.8–1.3/1.0	2.0–3.5/2.5	2–4/3
Anabasis aphylla	–	+	12.0–17.0/14.4	14–20/17	2.1–3.8/2.6	0.6–1.2/0.9	2.0–3.2/2.6	3–5/4
A. eugeniae	–	+	17.0–20.8/19.0	18–24/21	2.0–3.1/2.6	1.0–1.4/1.2	2.2–3.2/2.8	3–4/3
Petrosimonia glauca	+	+	15.1–19.5/16.8	28–38/34	1.3–2.3/1.7	0.8–1.8/1.2	1.1–2.1/1.7	3–7/5
P. brachiata	+	+	18.0–21.2/20.0	34–36/35	1.6–2.1/1.8	0.9–1.5/1.2	1.7–2.4/2.1	4–6/5
Halanthium kulpianum	+	+	17.7–27.5/22.3	20–26/23	2.6–4.0/3.4	1.1–1.9/1.3	2.1–3.2/2.5	1–3/3
H. rarifolium	+	+	16.3–20.0 (25.0)/17.4	14–18/16	2.9–3.8 (5.9)/3.3	0.9–1.5/1.1	2.7–4.0/3.2	1–3/2

[1] Averaged data obtained by measuring 20 pollen grains are presented in the table after the forward slashes

Table 3. Data on statistical analysis of pollen characteristics of Salsoloideae Ulbr. subfamily in South Transcaucasia

Species	Diameter of pollen grains (μm)		Number of pores		Diameter of pores (μm)	
	± SD	CV%	± SD	CV%	± SD	CV%
Caroxylon gemmascens	17.8 ±2.7	16.6	19 ±1.5	7.8	3.2 ±0.1(±1.1)	3.1 (42.3)
C. nodulosum	17.6 ±1.8	10.3	30 ±2.1	7.0	2.0 ±0.1	5.0
C. ericoides	20.6 ±3.1	15.0	32 ±1.1	3.4	2.2 ±0.4	18.2
C. nitrarium	17.7 ±1.2	6.8	30 ±0.8	2.6	1.6 ±0.3	18.7
C. dendroides	16.7 ±2.5	14.9	28 ±2.2	7.8	1.7 ±0.3	17.6
Climacoptera crassa	29.4 ±0.5	1.7	31 ±0.7	2.3	4.0 ±0.1	2.5
Halothamnus glaucus	21.4 ±1.5	7.0	25 ±2.1 (±4.0)	8.4 (18.1)	3.7 ±0.6	16.2
Kali tragus	20.8 ±1.8	8.6	28 ±0.9	3.2	1.8 ±0.3	16.6
K. tamamschjanae	20.6 ±0.1	0.5	30 ±2.1	7.0	2.2 ±0.3	13.6
K. collina	21.9 ±1.5	6.8	35 ±1.8	5.1	2.2 ±0.4	0.4
Kaviria cana	18.7 ±1.5	8.0	10 ±0.9	9.0	3.5 ±0.7	20.0
K. tomentosa	15.7 ±0.7	4.4	13 ±1.3	10.0	2.6 ±0.3	11.5
Seidlitzia florida	13.0 ±1.4	10.8	9 ±0.6 (1.7)	6.6 (18.8)	2.9 ±0.4	13.7
Noaea minuta	19.6 ±1.2	6.1	22 ±0.5	2.3	3.2 ±0.3	9.3
N. mucronata subsp. *mucronata*	14.0 ±0.9	6.4	13 ±0.5	3.8	2.7 ±0.1	3.7
N. mucronata subsp. *leptoclada*	14.6 ±0.4	2.7	15 ±1.0	6.7	3.3 ±0.3	9.1
Girgensohnia oppositiflora	13.0 ±0.6	4.6	12 ±0	0	2.9 ±0.09	3.1
Anabasis aphylla	14.4 ±1.2	8.3	17 ±1.5	9.0	2.6 ±0.4	15.3
A. eugeniae	19.0 ±0.3	1.6	21±1.4	6.6	2.6 ±0.07	2.7
Petrosimonia glauca	16.8 ±0.9	5.3	34 ±1.2	3.5	1.7 ±0.2	11.8
P. brachiata	20.0 ±0.9	4.5	35 ±1.3	3.7	1.8 ±0.1	5.5
Halanthium kulpianum	22.3 ±2.6	11.6	23 ±1.7	7.4	3.4 ±0.3	8.8
H. rarifolium	17.4 ±0.5(3.4)	2.8 (17.9)	16 ±0.6	3.7	3.3 ±0.1(1.1)	3.0 (28.2)
Variation intervals ± SD and CV%	±0.1–3.1	0.5–16.6	±0–2.2	0–10.0	±0.07–0.7	0.4–20.0

South Transcaucasia revealed that the species *Seidlitzia florida* (Bieb.) Bunge ex Boiss. and *Girgensohnia oppositiflora* are significantly close regarding the size of pollen grains (10.1–15.1 μm in diameter), as well as regarding the number (7–15) and diameter of pores (2.2–4.2 μm in diameter). Based on the data obtained with SEM, no considerable variability was revealed in the number of spinules on the surface of mesoporiums (2–4).

Palyno-morphological analysis of two species of the genus *Noaea* has revealed a correlation between the size of pollen grains and the number of pores. In particular, the largest pollen was observed in species *N. minuta* (17.0–22.1 μm in diameter), and also the highest number of pores (20–26) was noted in relation to the above species, whereas pollen grains of the species *N. mucronata* are noticeably small (12.2–15.6 μm in diameter) with the number of pores does not exceed 10–17 (Pl. 2, fig. 4 and Pl. 2, fig. 9 respectively). Our data confirm the data of Avetisyan and Manukyan (1956), who used the number of pores as a diagnostic feature for the identification of two species of the given genus.

Our research has also defined a certain difference in the number of pores in the pollen of different subspecies of *N. mucronata.* In particular, the number of pores in subspecies *N. mucronata* does not exceed 14, whereas in *N. mucronata* subsp. *leptoclada* it varies within 14–17.

A similar correlation between pollen size and pore number has been revealed in two species of the genus *Anabasis.* The largest pollen sizes were observed in the species *A. eugeniae* (17.0–20.8 μm in diameter), it was also characterized by the greatest number of pores (18–24), whereas in the species *A. aphylla* pollen grains were much smaller (12.0–17.0 μm in diameter) and the number of pores did not exceed 14–20 (Pl. 3, fig. 9 and Pl. 3, fig. 4, respectively).

Our study did not find significant differences in any of the four key diagnostic characteristics of pollen between two representatives of the genus *Petrosimonia*, therefore it is necessary to search for new features which will enable the distinction between the species.

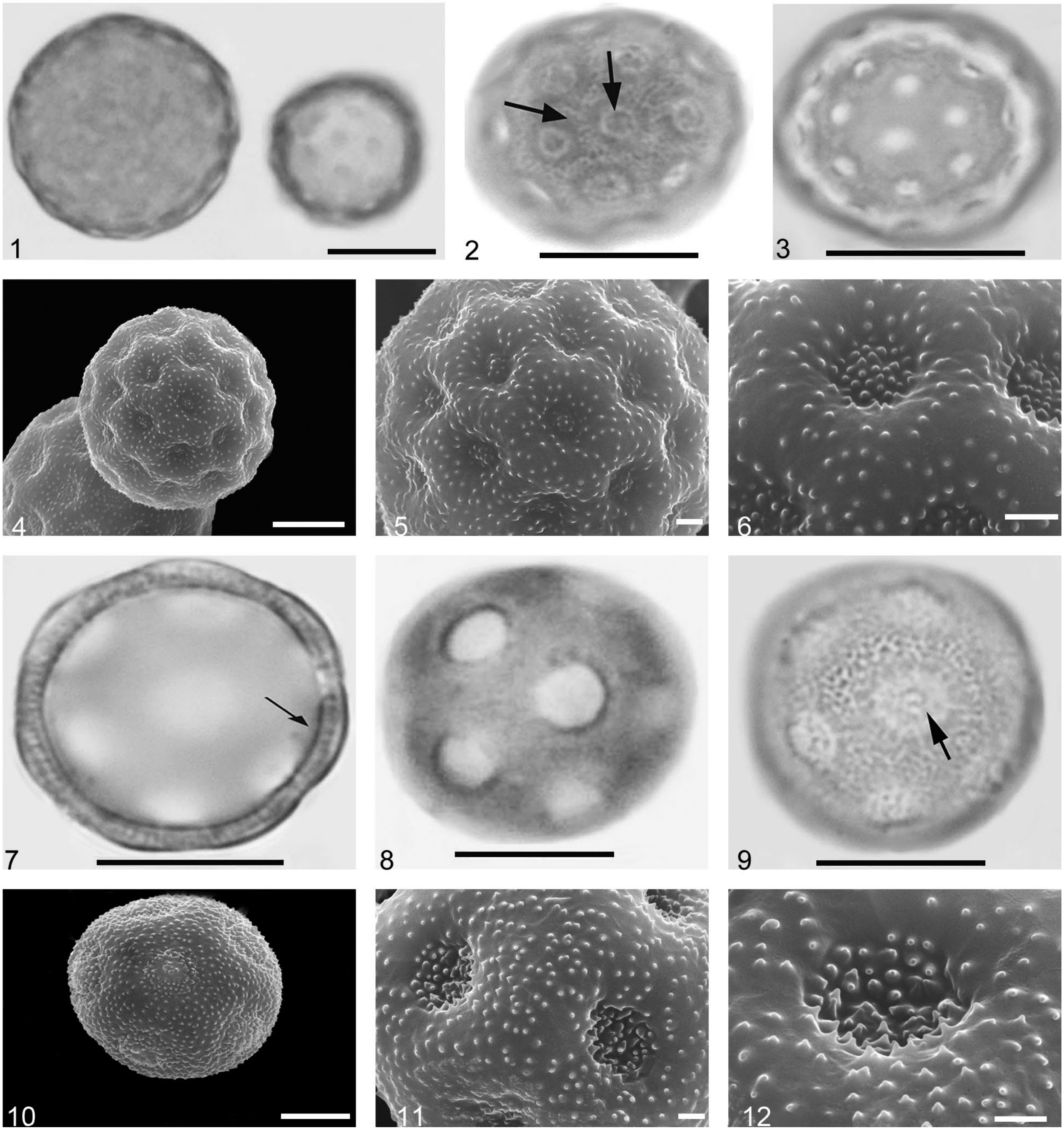

Plate 1. Pollen grains of *Caroxylon nitrarium* and *Kaviria cana*. **1–6**. *Caroxylon nitrarium* (specimen ERE, 171294); **1–3**. LM micrographs: **1**, **3** – general view and pollen size variability, **2** – mesoporium and pore membrane ornamentation (marked with arrows); **4–6**. SEM micrographs: **4** – general view, **5** – pollen surface fragment, **6** – mesoporium and pore membrane ornamentation (1, 2 stained with fuchsine, 3 acetolyzed); **7–12**. *Kaviria cana* (specimen ERE, 71593); **7–9**. LM micrographs: **7** – columellae (marked with arrow), **8**, **9** – general view, mesoporium and pore membrane ornamentation (marked with arrow); **10–12**. SEM micrographs: **10** – general view, **11** – pollen surface fragment, **12** – mesoporium and pore membrane ornamentation (7, 8 acetolyzed, 9 stained with fuchsine). Scale bar = 10 µm in 1–3 and 7–9; 5 µm in 4 and 10; 1 µm in 5, 6, 11, 12

Finally, within the genus *Halanthium* we found a certain difference in the number of pores. Particularly, in the species *H. kulpianum* the number of pores varies within 20–26, while in *H. rarifolium* it does not exceed 18. On the other hand, significant differences in the size of pollen grains and the diameter of pores between the two species were not observed.

Thereby, the palyno-morphological analysis in Salsoloideae subfamily has revealed that within the genus *Salsola* s.l., as well as subfamily Salsoloideae in South Transcaucasia in general the genus *Climacoptera* (*C. crassa*) is characterized with the largest pollen size (26.3–33.1 µm in diameter), and the smallest pollen was noted in species *Salsola soda* (12.0–14.0 µm in diameter). The species *Kali collina* (Pall.) Akhani

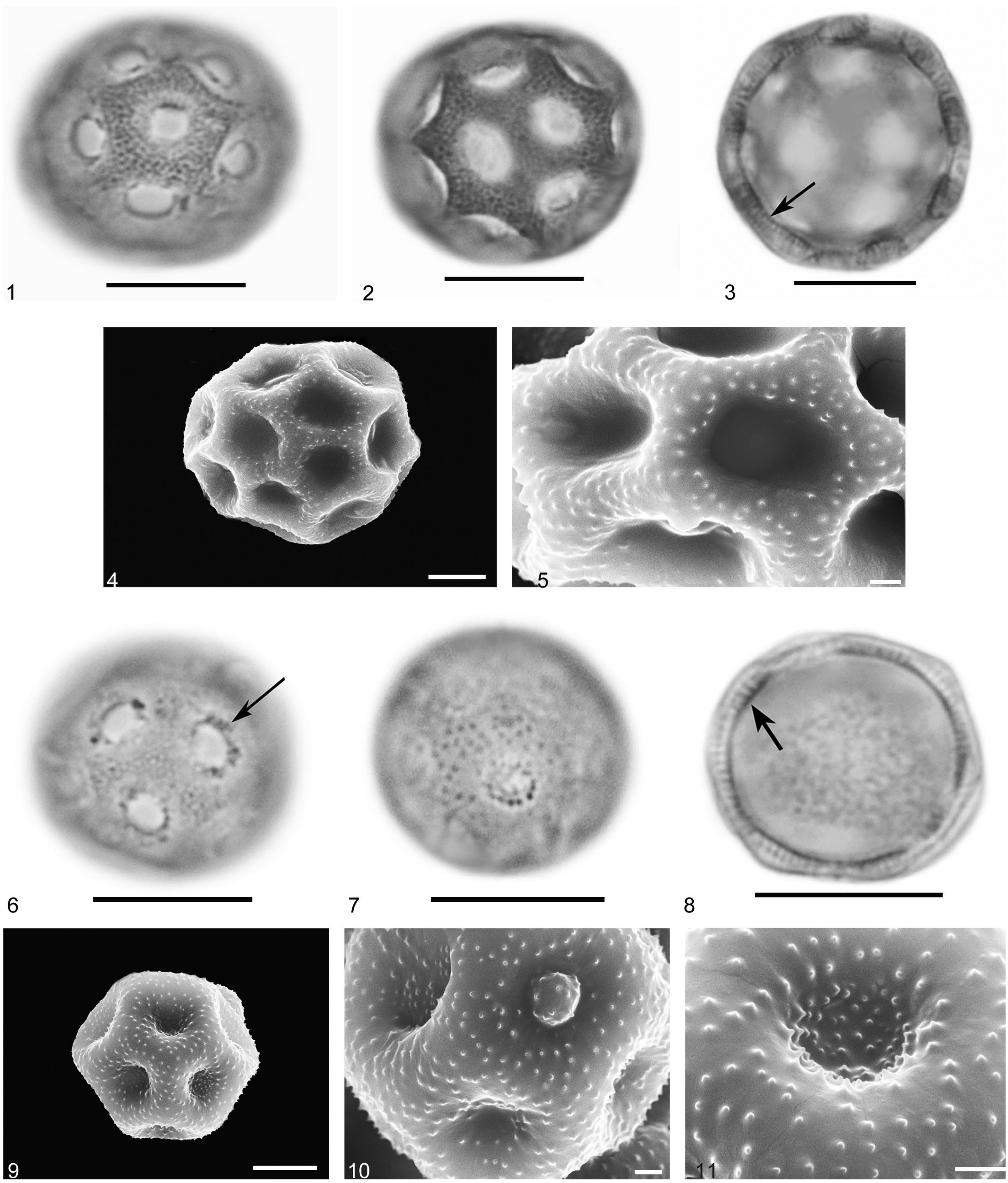

Plate 2. Pollen grains of the genus *Noaea*. **1–5**. *N. minuta* (specimen ERE, 56045); **1–3**. LM micrographs: **1**, **2** – general view, pore shape and mesoporium ornamentation, **3** – columellae (marked with arrow); **4**, **5**. SEM micrographs: **4** – general view, **5** – pollen surface fragment (1, 2 stained with fuchsine, 3 acetolyzed); **6–11**. *N. mucronata* (specimen ERE, 170531); **6–8**. LM micrographs: **6**, **7** – general view, pore shape and mesoporium ornamentation (6 – pore "edging", marked with arrow), **8** – columellae (marked with arrow), (6, 7 stained with fuchsine, 8 acetolyzed); **9–11**. SEM micrographs: **9** – general view, **10** – pollen surface fragment, **11** – mesoporium and pore membrane ornamentation. Scale bar = 10 µm in 1–3 and 6–8; 5 µm in 4 and 9; 1 µm in 5, 10, 11

& E.H. Roalson is characterized by the highest number of pores (32–38), while the number of pores in *Seidlitzia florida* does not exceed 11. Both in the genus *Salsola* s.l. and the subfamily Salsoloideae in general, the largest pores were observed in the pollen of the species *Kaviria cana* (2.3–5.3 µm in diameter), and the smallest ones were found in the species *Petrosimonia brachiata* (1.6–2.1 µm in diameter).

The maximum number of spinules (5–9) per unit surface of the pollen grains was revealed in the species *Caroxylon ericoides*, and the

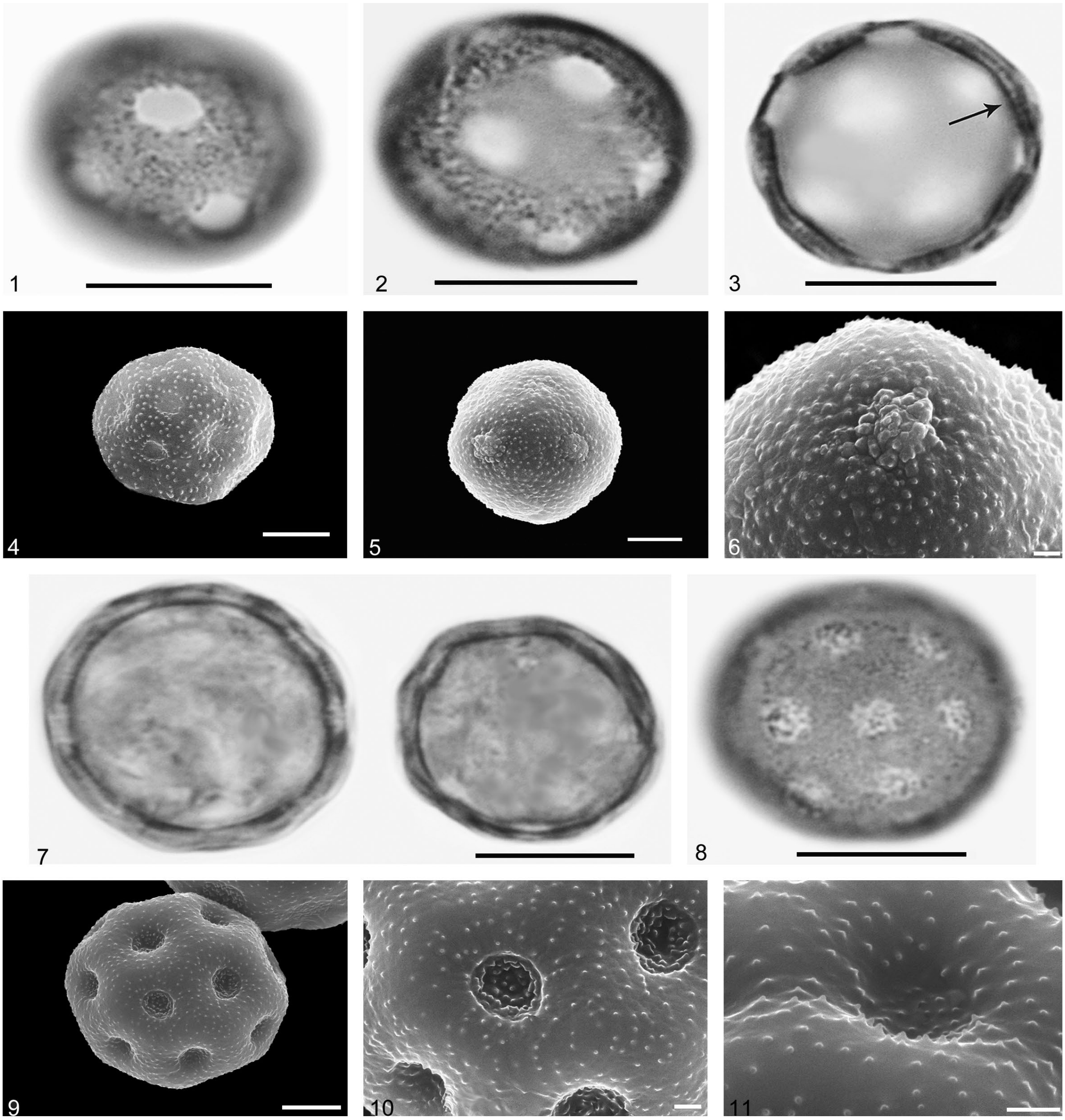

Plate 3. Pollen grains of the genus *Anabasis*. **1–6**. *A. aphylla* (specimen ERE, 1857); **1–3**. LM micrographs: **1**, **2** – general view, pore shape and mesoporium ornamentation, **3** – columellae (marked with arrow); **4–6**. SEM micrographs: **4**, **5** – general view (5 – operculate pores), **6** – mesoporium ornamentation and operculate pore (1, 2 stained with fuchsine, 3 acetolyzed); **7–11**. *A. eugeniae* (specimen ERE, 146060); **7**, **8**. LM micrographs: **7** – pollen size variability, **8** – general view, pore shape, pore and mesoporium ornamentation; **9–11**. SEM micrographs: **9** – general view, **10** – pollen surface fragment, **11** – mesoporium and pore membrane ornamentation (7, 8 stained with fuchsine). Scale bar = 10 μm in 1–3, 7, 8; 5 μm in 4, 5, 9; 1 μm in 6, 10, 11

lowest number (1–3) in the representatives of the genus *Halanthium*.

POLLEN TYPFICATION OF THE SUBFAMILY SALSOLOIDEAE OF SOUTH TRANSCAUCASIA

Two morphological types and four subtypes united in two palynogroups were differentiated in the subfamily Salsoloideae of South Transcaucasia using the four key palyno-morphological features, namely the size of the pollen grains, the size and number of pores (using LM) and the number of spinules on 1 μm^2 surface of mesoporium (using SEM) (see below).

The difference between the overall size of pollen grains has been accepted as the basic criterion in distinguishing palynogroups.

Palynogroup I is monotypic and covers a single genus *Climacoptera*, from *Salsola* s.l. and represented in South Transcaucasia by the species *C. crassa.* In contrast to other studied taxa, pollen grains in *C. crassa* are of average size (according to the classification of Erdtman (1952)) and vary between 26.3 and 33.1/29.4 µm in diameter. All the other investigated taxa are characterized by small pollen grains, from 10.1 to 25.1(27.5)/22.3 µm in diameter and are included in Palynogroup II.

Classification of species in two different types in Palynogroup II is based on the presence of a significant difference in the size of *small* pollen grains of individual species. In particular, species with relatively large pollen grains (>20 µm in diameter) are included in Type 1, while species with relatively small grains (≤ 20 µm in diameter) are classified in Type 2. And finally, the distribution of species into the differnt subtypes and variations in Palynogroup II is based on the differences in size and pore number of pollen grains.

PALYNOGROUP I. Pollen grains have average sizes (26–33/29 µm in diameter)[1] . . . ***Climacoptera crassa***

PALYNOGROUP II. Pollen grains are small (10–25 (27) /22 µm in diameter)

- **Type 1**. Relatively large pollen grains (>20 µm in diameter)
  - **Subtype 1**. relatively large pores (>2.0 µm in diameter)
    - Many pores (>30) ***Caroxylon ericoides***, ***Kali collina***
    - Few pores (≤ 30) . . . . ***Kali tamamschjanae***, ***Halothamnus glaucus***, ***Halanthium kulpianum***
  - **Subtype 2**. relatively small pores (<2.0 µm in diameter), few (≤ 30) . . . . ***Kali tragus***
- **Type 2**. Relatively small pollen grains (≤ 20 µm in diameter)
  - **Subtype 1**. relatively large pores (>2.0 µm in diameter), few (≤ 30)
    - Number of spinules on 1 µm² >4 . . . . ***Kaviria cana***, ***K. tomentosa***
    - Number of spinules on 1 µm² ≤ 4 . . . . ***Caroxylon gemmascens***, ***Seidlitzia florida***, ***Salsola soda***, ***Anabasis aphylla***, ***A. eugeniae***, ***Noaea minuta***, ***N. mucronata* subsp. *mucronata***, ***N. mucronata* subsp. *leptoclada***, ***Girgensohnia oppositiflora***, ***Halanthium rarifolium***
  - **Subtype 2**. relatively small pores (≤ 2.0 µm in diameter), number of spinules on 1 µm² >4
    - Many pores (>30). . . . . ***Petrosimonia glauca***, ***P. brachiata***
    - Few pores (≤ 30) . . . . ***Caroxylon nodulosum***, ***C. nitrarium***, ***C. dendroides***

[1] According to Erdman's (1952) classification of pollen size, the small ones range from 10 to 25 µm in diameter, the average ones range from 25 to 50 µm in diameter

CONCLUSION

Despite the existing palynological uniformity both in the general shape of pollen grains and in the type of apertures in the Chenopodiaceae family as a whole, our study succeeded in finding a few key palyno-morphological features which made it possible in some cases to specify the taxonomic boundaries, as well as the relationship between taxa within the subfamily Salsoloideae.

Our data revealed some separation of the genera *Climacoptera* (Palynogroup I) and *Kaviria* (Palynogroup II) within the limits of *Salsola* s.l., thus confirming the previously existing opinion about the independence of the mentioned genera (Botschantsev, 1956; Akhani et al., 2007; Wen et al., 2010; Akopian, 2011). Separation of the species *Climacoptera crassa* was mentioned also by Tsymbalyuk (2005).

Based on the results, two of the three investigated species of the genus *Kali* (*K. tamamschjanae* and *K. collina*) were classified in different variations of Subtype 1 (Type 1, Palynogroup II). At the same time, the species *Kali tragus,* thanks to the presence of pollen grains with relatively small size (< 2.0 µm in diameter) and few pores (up to 30), was classified into Subtype 2.

It should also be noted that the analysis of palyno-morphological characteristics within the entire *Salsoloideae* subfamily has confirmed once again, the alterity of the representatives of the genera *Climacoptera, Kaviria,* as well as the species *Kali tragus.*

Our investigations have also revealed palyno-morphological heterogeneity of the genus *Caroxylon* and the presence of quite close relations of the latter with the genus *Kali*, as well as a number of taxa outside the genus *Salsola* s.l. The data obtained are consistent with the results of Botschantsev (1969) who considers the section *Caroxylon* the original one in the genus *Salsola*. Heterogeneity of the genus *Caroxylon* was confirmed by the results of Tsymbalyuk (2005) as well.

Based on a number of morphological features of pollen, we revealed significant similarities between the species *Caroxylon gemmascens* and the genus *Salsola* s. str., represented in South Transcaucasia only by the species *S. soda*. It was also revealed that these two taxa are closely related to the genus *Kaviria.*

The number of spinules on the pollen grain surface is the main difference between them.

Thus, the data obtained indicate a significant heterogeneity of the genus *Salsola* s.l., since the species of this genus are represented in almost all types and subtypes of both palynogroups. Palynological heterogeneity of the genus *Salsola* was also confirmed by morpho-anatomical studies of the structural features of stems, particularly the structure of epicuticular wax, trichomes, and the relief of the surface (Ghazali et al., 2016), as well as the molecular research of Akhani et al. (2007).

Analysis of pollen-morphological characteristics within the subfamily Salsoloideae has confirmed uniformity, as well as some alterity among the representatives of the genus *Petrosimonia* due to the presence of relatively small pollen grains with small and multiple pores, not noticed in any other representatives of the given subfamily. On the other hand, we did not find any key pollen diagnostic characters that could allow us to distinguish species.

Homogeneity of the genus *Petrosimonia* is confirmed also by palyno-morphological research of Monoszon (1973). Grozeva et al. (2019) mention a definite karyological and morphological variability in *P. brachiaa* within two different populations, however, they could not reveal essential variability of morphological features of the pollen.

Species of the genus *Halanthium* are presented in Palynogroup II in two different types, which indicates its palynological heterogeneity. This view is also supported by molecular studies by Akhani et al. (2007), who point to a significant difficulty in explaining the presence of this kind of polyphilia.

Due to the relatively large pollen grains, as well as the presence of large, but few pores, the genus *Halothamnus* (represented in South Transcaucasia only by the species *H. glaucus*) together with species *Kali tamamschjanae* and *Halanthium kulpianum*, was separated in Palynogrup II to a distinct variation of Subtype 1 (Type 1). This points to the possible relatedness of the mentioned species (by the pollen features).

It is also important to mention that the wide spectrum of species, as well as subspecies presented in the given variational group indicates the presence of close relationships between the genera *Seidlitzia*, *Anabasis*, *Noaea*, *Girgensohnia,* and *Halanthium.* On the other hand, selected pollen diagnostic features in some cases enabled us to draw a demarcation not only on the interspecific (*Anabasis*) but also intraspecific (*Noaea*) levels.

And, finally, comparative palyno-morphological analysis made it possible to identify the monotypic groups in the subfamily Salsoloideae, which are represented in one case by a separate species (*Kali tragus*), and in three other cases by separate genera (*Climacoptera, Kaviria, Petrosimonia*).

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