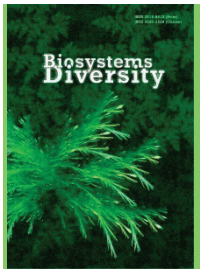

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Palynotaxonomy of the genus *Gladiolus* (Iridaceae) of the flora of Armenia

A. M. Hayrapetyan, A. H. Muradyan, H. H. Sonyan, M. Y. Asatryan, M. E. Oganesian

A. L. Takhtajan Institute of Botany, National Academy of Sciences of the Republic of Armenia, Yerevan, Republic of Armenia

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A. l. Takhtajan Institute of Botany, National Academy of Sciences of the Republic of Armenia, Atcharjan st., 1, Yerevan, 0063, Republic of Armenia. Tel.: +374-93-806-545. E-mail: alla.hayrapetyan.63@gmail.com

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The genus *Gladiolus* L. (Iridaceae) includes about 250–280 species of perennial herbaceous corms, distributed in Africa, Madagascar and Eurasia. The taxonomy of the genus is not simple, since the characteristics of the species are quite confusing. Our article presents the results of a comparative palyno-morphological analysis of all 9 species and 2 subspecies of the genus *Gladiolus* of the Armenian flora. The purpose of the work is to identify diagnostic characteristics of pollen used to distinguish individual taxa. Six morphological characters, namely the length of the polar axis (P), as well as the length of the large and small equatorial diameters (E1 and E2, respectively), exine thickness and the number of echinae and perforations per unit area of the pollen surface were measured using light microscopy (LM) and scanning electron microscopy (SEM). Literature data, as well as the results of our previous studies, showed that the genus is characterized by stenopalynous anasulcate pollen grains with a two-lane operculum. In the presence of significant uniformity in pollen characteristics, our studies revealed that among the species studied, *G. hajastanicus* and *G. kotschyanus* have slightly larger pollen grain sizes, and the pollen of the species *G. tenuis* is characterized by a minimal number of both echinae and perforations per unit surface area of the pollen grain (using SEM). A certain difference has also been established between the subspecies of the species *G. kotschyanus*. In particular, the sizes of pollen grains of *G. kotschyanus* subsp. *kotschyanus* (based on E1) is slightly larger than in *G. kotschyanus* subsp. *distichus*. At the same time, the number of echinae and perforations per unit surface of a pollen grain (at the SEM level) in the subspecies *G. kotschyanus* subsp. *distichus* is approximately twice as large as *G. kotschyanus* subsp. *kotschianus*.

Keywords: palyno-morphological analysis; stenopalynous; light microscopy; scanning electron microscopy.

Introduction

Within the genus *Gladiolus* L. (Iridaceae), about 250–280 species of perennial corms of herbaceous plants, distributed in Africa, Madagascar and Eurasia are noted. For the flora of Armenia, 9 species are given, of which *G. dzhavakheticus* Eristavi is endemic to Transcaucasia, and the species *G. hajastanicus* Gabrielian is endemic to the flora of Armenia (Gabrielyan & Oganesian 2001). The fairly polymorphous *G. kotschyanus* Boiss. is represented in Armenia by two subspecies – *G. kotschyanus* subsp. *kotschyanus* and *G. kotschyanus* subsp. *distichus* Gabrielian.

The name *Gladiolus* had been applied by Tournefort to the European species. Linnaeus placed the diagnosis of the genus in the first edition of Systema naturae (Linnaei, 1935), later in the first volume of Species Plantarum, the author described 6 species (Linnaeus, 1753). One of the first taxonomical treatments of this genus was based on the shape of the tepals, color and consistency of the bracts, where four subgenera within *Gladiolus* namely *Eugladiolus* Bak., *Hebea* Pers., *Schweiggera* E. Meyer and *Homoglosaum* Bak. were presented (Baker, 1878). The author included all the Eurasian species of the genus and most of the species native to Africa in the subgenus *Eugladiolus*, and three other subgenera included the remaining species native to Africa and Madagascar. Also, taking the shape of the seeds as a basis, the subgenus *Eugladiolus* was divided into two groups: the first included species with winged disc-shaped seeds, the second included species with spherical seeds without wings. Subsequently, sectional status was given to the subgenera identified by Baker (Bentham & Hooker, 1883). Considering the pattern of veins in a leaf as diagnostic characters, two main groups were identified: the first has leaves with few veins and the second group – leaves with veins running at an equal distance from each other (Boissier, 1884).

As a whole, the genus *Gladiolus* is well defined within the subfamily Ixoideae by the following main characters: herbaceous bracts, unilateral spike, simple but apically expanded style branches, and seeds with a prominent peripheral wing (Goldblatt, 1971). Investigation, using a scanning electron microscope (SEM), of the leaves and seed surface of four species of *Gladiolus* (*G. imbricatus* L., *G. italicus* Mill., *G. palustris* Gaudin and *G. tenuis* M. Bieb.) of the flora of Ukraine was carried out (Zhygalova et al., 2014).

Information on the pollen morphology of some species of the genus *Gladiolus* at the level of light microscope (LM) and scanning electron microscope (SEM) was given in the works of a number of authors (Beug, 1961; Oybak Dönmez & Işik, 2008; Zhygalova et al., 2014). Characterizing the pollen of the genus, the authors indicate the presence of monosulcate apertures with operculum (Radulescu, 1970a, 1970b; Schulze, 1971; Kupriyanova, 1983). In particular, it was noted that stenopalynous pollen grains of the genus of *Gladiolus* are similar to monosulcate grains of the genus *Iris*, but at the same time differ in the presence of a lanceolate operculum (Kuprianova, 1983). For pollen grains of all species included in the type *Gladiolus italicus* (*G. communis* L., *G. illyricus* W. D. J. Koch, *G. italicus* Mill.), a two-lane operculum, imitating the structure of tricolpate pollen was revealed (Valdes et al., 1987).

The purpose of this study was to conduct a comparative morphological analysis of the pollen of all 9 species and 2 subspecies of the genus *Gladiolus* in Armenia in order to identify the main diagnostic characters that makes it possible to distinguish between individual taxa.

Material and methods

Unopened mature flower buds were obtained from the herbarium of the Institute of Botany after A. Takhtajyan of the NAS of the Republic of Armenia (ERE). The descriptions of pollen grains by light microscopy (LM) for each investigated species are based on acetolyzed material (Avetisyan, 1950) and also on grains stained with basic fuchsine (Smolyaninova & Golubkova, 1950).

1. Method of staining with basic fuchsin (Smolyaninova & Golubkova, 1950). The essence of the method is the alcohol fixation of pollen grains, followed by the addition of a basic fuchsin solution in 96% ethyl

alcohol (the ratio of fuchsin to alcohol is approximately 1: 6000). After staining, without allowing the preparation to dry, the pollen is placed in glycerin gelly.

2. Simplified acetolysis method (Avetisyan, 1950). The treatment of pollen grains with a mixture of acetic anhydride and sulfuric acid (in a ratio of 9:1) is carried out directly on a glass slide, followed by heating until a light brown color appears. After cooling, the pollen is filled with glycerin gelly.

It was found, that after treatment with fuchsin, pollen grains of *Gladiolus* species take on a more rounded shape, and after acetolysis treatment they become oblong, therefore the data obtained on the length of the polar axis (P), large and small equatorial diameters (E1 and E2 accordingly) vary somewhat. One explanation for this phenomenon may be the dehydration of pollen after acetolysis treatment. However, we also noted elongated pollen grains when studying non-acetolyzed pollen at the SEM level. In this regard, we measured the size of pollen grains along the length of the large equatorial diameter (E1) on acetolyzed pollen.

Six morphological characters, namely the length of polar axis (P), as well as the length of large and small equatorial diameters (E1 and E2 accordingly), exine thickness (using LM) and the number of echinae and perforations on a unit area of the pollen surface (on SEM level), were measured (Table 2).

Measurements of the size of pollen grains and exine thickness were taken under light microscopy (AmScope 2000X LED, China, 2015). Pollen shape, size, and the details of exine structure and ornamentation were studied on acetolyzed pollen grains; aperture descriptions were carried out on non-acetolyzed stained pollen grains.

For scanning electron microscopy (SEM), non-acetolysed pollen grains were washed with alcohol and placed on a metal stub and sputter coated with gold (10 nm) using a Jeol Smart Coater (Japan, 2019). Samples were imaged under SEM (JEOL JCM-7000, Japan, 2019), with a 15 kV electron beam. The number of echinae and perforations on 5 μm² was counted in 5 areas of the pollen grain surface (using SEM).

Statistical analysis of all the studied species (with the exception of *G. menitzky* Gabrieljan with one specimen studied) was performed with two indicators: ± SD – standard deviation and CV% – coefficient of variation. Besides, in the case of CV ≤ 10% the sample is weakly variable, with CV from 10% to 20% it is moderately variable, CV ≥ 20% – it is highly variable and with CV ≥ 30%, the highest degree of variability is noted.

On the whole, pollen morphological characteristics of 27 samples of 9 species and 2 subspecies of the genus *Gladiolus* of the flora of Armenia were analyzed. For each of the taxa presented below, depending on the amount of available pollen material, one to four specimens were studied. Measurements of individual characteristics for each sample were carried out on 20 pollen grains.

The list of investigated species and specimens are presented in Table 1 and includes also information on synonyms according to their location in The Plant List (www.theplantlist.org) (Table 1).

The morphological terminology used in our study mainly follows Bobrov et al. (1983), Punt et al. (2007) and Halbritter et al. (2018).

Table 1

List of investigated species and specimens (ERE – Herbarium of the A. L.Takhtajan Institute of Botany, National Academy of Sciences, Yerevan, Armenia)

Taxon	Name according to their location in The Plant List (www.theplantlist.org)	Herbarium sheet information
Gladiolus atroviolaceus Boiss.	–//–	ERE, 196844; ERE, 17638; ERE, 148563
G. caucasicus Herb.	–//–	ERE, 125665; ERE, 146062; ERE, 196507
G. dzhavakheticus Eristavi	–//–	ERE, 145045; ERE, 145049; ERE 148570; ERE 78040
G. hajastanicus Gabrielian	–//–	ERE, 151978; ERE, 192829; ERE, 152470; ERE, 151979
G. kotschyanus Boiss.	–//–	ERE, 146831; ERE, 196862; ERE 183064
G. kotschyanus subsp. distichus Gabrielian	*G. kotschyanus* Boiss.	ERE 145305; ERE, 145367
G. italicus Mill.	–//–	ERE, 144940; ERE, 187547
G. menitzky Gabrieljan	–//–	ERE, 128746
G. szovitsii Grossh.	–//–	ERE, 78516; ERE, 119903; ERE, 147178
G. tenuis M. Bieb.	–//–	ERE, 152474; ERE, 145352

Results

Our investigations revealed that in all studied species of the genus *Gladiolus* of the Armenian flora the pollen grains are monosulcate, rounded or elongate boat-shaped, carinate, the carina usually wide, rounded or rounded-angular; in outline from the equator pollen grains flat- or biconvex, from the pole elliptical; polar axis 20.5–65.0 μm; large equatorial diameter (E1) 43.4–81.7 μm; small equatorial diameter (E2) 23.0–67.0 μm. The sulcus in all studied species is long, reaching the ends of the pollen grains, from wide to very wide, with the presence of an operculum, represented by two striae of sculptured exine. The ornamentation of the sulcus membrane irregularly verrucate, verrucae often located in groups (LM, SEM). Exine 0.6–2.4 μm thick, the columella layer clearly defined, columellae thin, long, and evenly spaced. At the LM level, ornamentation of pollen surface and operculum densely finely granular; at the SEM level, ornamentation perforate-echinate, the echinae conical, with pointed, sometimes slightly rounded ends (Tables 2, 3, Fig. 1–3).

Table 2

Palyno-morphological characteristics of the representatives of the genus *Gladiolus* L. of the flora of Armenia (averaged data obtained by measuring 20 pollen grains are presented in the Table after the forward slashes)

Species	Polar axis (P), μm (LM) ± SD (CV%)		Large equatorial diameter (E_1), μm (LM) ± SD (CV%)		Small equatorial diameter (E_2), μm (LM) ± SD (CV%)	
	fuchsin	acetolysis	fuchsin	acetolysis	fuchsin	acetolysis
G. dzhavakheticus	34.0–55.3 /43.6 ± 5.1(11.7)	27.3–49.8 /36.6 ± 2.1(5.7)	43.4–67.6 /58.3 ± 3.4(5.8)	50.2–72.7 /61.5 ± 4.4(7.1)	23.0–56.4 /47.9 ± 2.6(5.4)	33.0–59.6 /44.5 ± 2.7(6.1)
G. caucasicus	31.1–60.0 /45.8 ± 5.7(12.4)	25.5–47.5 /35.1 ± 5.4(15.3)	57.3–74.2 /66.7 ± 2.5(3.7)	53.7–75.8 /64.8 ± 2.6(4.0)	39.7–56.2 /48.3 ± 0.7(1.4)	31.1–58.1 /44.8 ± 7.0(15.6)
G. tenuis	37.0–65.0 /50.9 ± 7.3(14.3)	25.9–53.4 /40.9 ± 6.6(16.1)	56.2–75.5 /66.5 ± 5.7(8.5)	51.4–73.4 /61.5 ± 4.6(7.4)	33.9–64.4 /51.9 ± 2.9(5.5)	28.4–58.8 /44.5 ± 4.9(11.0)
G. kotschyanus subsp. *kotschyanus*	28.9–54.5 /44.8 ± 2.4(5.3)	23.1–50.5 /34.2 ± 2.5(7.4)	52.9–71.2 /61.2 ± 5.4(9.2)	60.6–81.7 /65.7 ± 6.1(9.8)	34.2–52.4 /46.7 ± 4.2(9.5)	33.3–53.9 /41.9 ± 3.9(10.0)
G. kotschyanus subsp. *distichus*	37.7–48.5 /44.9	23.5–42.4 /32.9	46.1–60.9 /55.0	45.2–71.1 /58.2	38.7–48.4 /41.6	28.9–42.7 /35.8
G. hajastanicus	26.0–58.8 /47.2 ± 2.5(5.2)	20.5–50.2 /33.4 ± 1.3(3.9)	51.5–69.3 /60.5 ± 2.9(4.8)	57.9–80.8 /67.7 ± 3.6(5.3)	40.8–54.4 /47.3 ± 1.1(2.1)	32.7–51.8 /41.3 ± 3.9(9.4)
G. italicus	42.6–59.5 /49.1 ± 1.3(2.6)	27.8–56.0 /36.9 ± 6.2(16.7	51.9–75.8 /62.1 ± 5.6(9.0)	58.0–75.4 /63.5 ± 5.2(8.1)	43.8–67.0 /50.3 ± 3.9(7.7)	29.8–52.5 /44.2 ± 3.6(8.1)

Species	Polar axis (P), µm (LM) ± SD (CV%)		Large equatorial diameter (E_1), µm (LM) ± SD (CV%)		Small equatorial diameter (E_2), µm (LM) ± SD (CV%)	
	fuchsin	acetolysis	fuchsin	acetolysis	fuchsin	acetolysis
G. atroviolaceus	36.1–51.1 /44.2 ± 3.2(7.2)	23.8–44.3 /31.9 ± 2.9(9.0)	44.6–67.0 /57.9 ± 6.3(10.8)	50.1–74.7 /60.9 ± 3.3(5.4)	36.4–55.7 /46.2 ± 2.3(4.9)	31.7–48.4 /40.2 ± 1.2(2.9)
G. menitzky	28.8–40.0 /34.4	31.7–45.6 /38.9	54.2–65.5 /59.0	51.8–66.3 /58.4	28.4–43.1 /36.9	33.0–52.1 /46.6
G. szovitsii	32.9–48.0 /44.8 ± 5.8(12.9)	23.9–42.4 /31.2 ± 6.4(20.4)	46.5–65.0 58.5 ± 0.6(1.02)	52.5–77.2 /58.9 ± 2.0(3.4)	42.2–55.0 /46.9 ± 0.4(0.8)	23.0–51.9 /34.3 ± 7.7(23.1)

Notes: LM – light microscopy; SD – standard deviation; CV% – coefficient of variation.

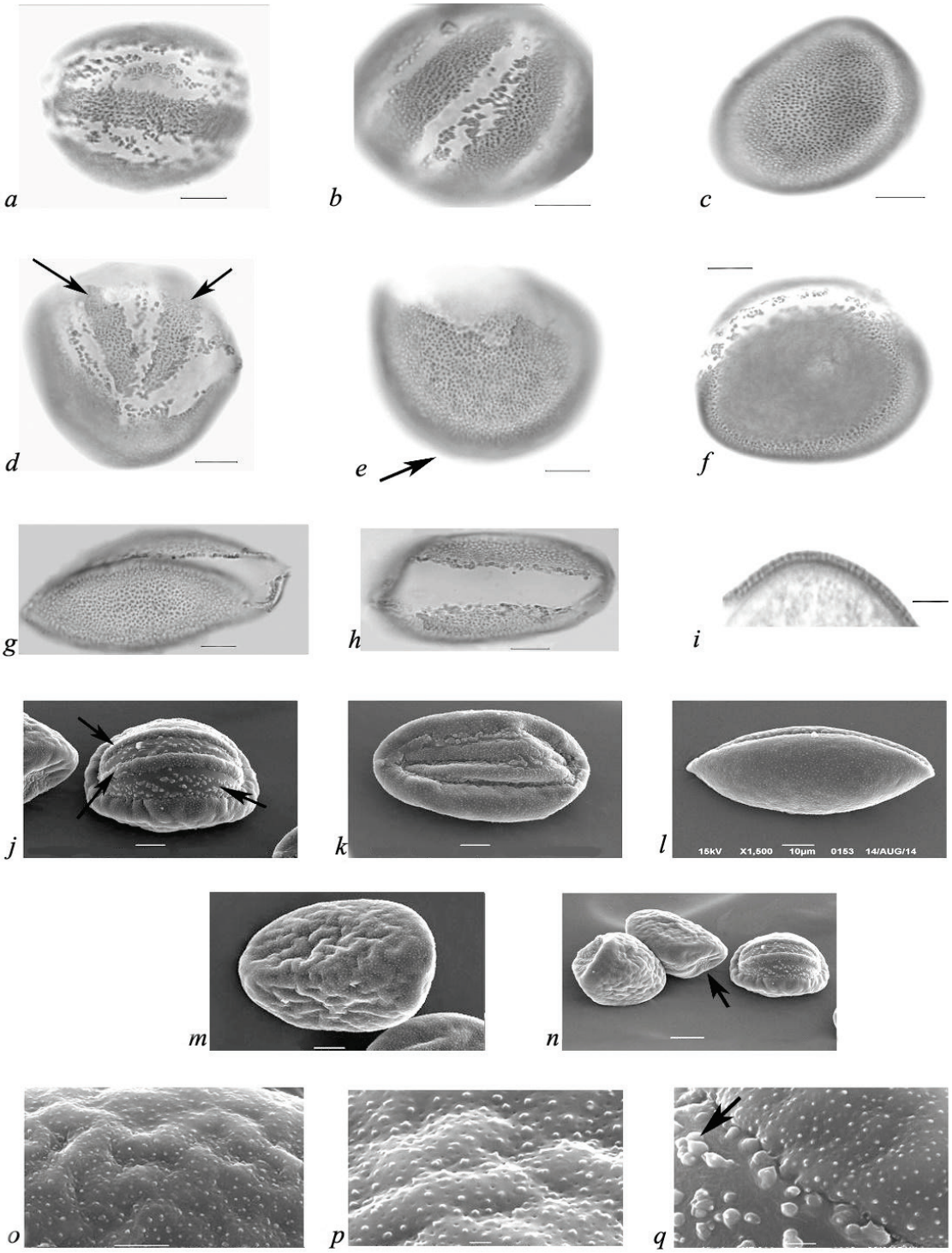

Fig. 1. Pollen grains of *Gladiolus hajastanicus*: *a–i* – LM micrographs: *a–b*– distal pole, sulcus with two-lane operculum, *c* – proximal pole, *d–e* – pollen grains from the small equatorial diameter (E2) (*d* – two-lane operculum, *e* – carina, marked with arrows), *f–g* – pollen grains from the large equatorial diameter (E1), *h* – distal pole, *i* – exine, columellae layer; *j–q* – SEM micrographs: *j–k* – distal pole (*j* – ornamentation of the sulcus membrane and operculum, marked with arrows), *l* – pollen grain from the large equatorial diameter (E1), *m* – proximal pole, *n* – group of pollen grains (small equatorial diameter (E2), marked with arrow), *o–q* – ornamentation of the exine and sulcus membrane (*q* – ornamentation of the sulcus membrane, marked with arrow); scale bar: *a–h*, *j–m* – 10 µm, *n* – 20 µm, *i*, *o* – 5 µm, *p* – 1 µm, *q* – 2 µm

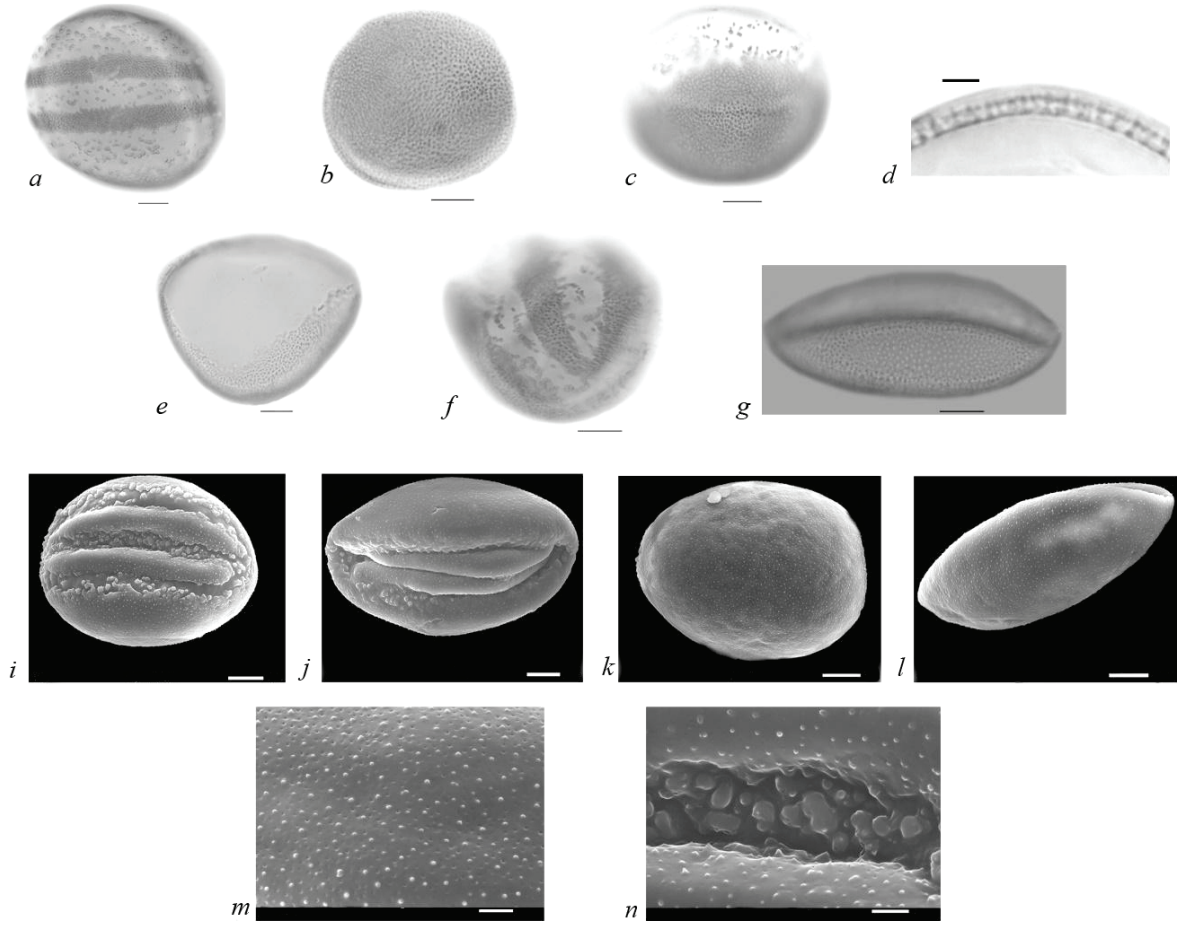

Fig. 2. Pollen grains of *Gladiolus italicus*: *a–g* – LM micrographs: *a* – distal pole (sulcus with two-lane operculum), *b* – proximal pole, *c*, *g* – pollen grains from the large equatorial diameter (E1), *d* – exine, columellae layer, *e–f* – pollen grains from the small equatorial diameter (E2) (*f* – sulcus with two-lane operculum); *i–n* – SEM micrographs: *i–j* – distal pole, *k* – proximal pole, *l* – pollen grain from the large equatorial diameter (E1), *m* – exine ornamentation, *n* – ornamentation of the sulcus membrane and operculum (SEM); scale bar: *a–c*, *e–g*, *i–l* – 10 μm, *d* – 3 μm, *m–n* – 2 μm

Discussion

Morphological characteristics of pollen are of significant importance in the classification of related groups of plants, and for assessing the evolutionary significance of changes in characteristics in the morphogenesis of these groups. In particular, considering the two-lane operculum in the pollen of *Gladiolus* as the most specialized trait, it has been suggested that the origin of the operculum and its possible variations can be considered in connection with the taxonomy of the subfamily Ixioideae (Goldblatt, 1990).

Despite the significant number of species and wide range that make up the genus *Gladiolus*, literary data on the pollen morphology of the genus are rather scarce. Among the latest studies, one should note the studies of *Gladiolus* species of the Ukrainian flora (Zhygalova et al., 2014). The authors wrote that pollen grains characteristics are not diagnostic for distinguishing species, but they could be important at the genus level.

A detailed description of pollen morphology of the genus *Gladiolus* of Armenian flora on the whole using LM (Avetisyan et al., 2001), as well as the separate species using LM and SEM was previously presented by some of the authors of this article. In particular, data on pollen morphology of a rare endemic species of the flora of Armenia, namely *G. hajastanicus* Gabrielian, were revealed for the first time (Muradyan, 2021). Afterwards, the palynomorphological investigation of the remaining eight species of the genus *Gladiolus* of the Armenian flora was carried out (Hayrapetyan & Muradyan, 2021, 2022; Muradyan & Hayrapetyan, 2022).

Analysis of the data obtained indicate that in the species *G. hajastanicus* and *G. kotschyanus*, pollen grains have slightly larger sizes according to E1 (57.9–80.8 and 60.6–81.7 μm appropriately), while in other species the sizes of pollen grains vary from 50.1–66.3 μm (Table 2). On the other hand, comparative analysis on the size of pollen grains with the data presented by a number of other researchers (Valdes et al., 1986; Oybak Dönmez & Işik, 2008) for the species *G. italicus*, *G. kotschyanus* and *G. atroviolaceus* revealed that the pollen grains of these species growing in Armenia are somewhat smaller in size.

Based on SEM data, it was revealed that pollen of the species *G. tenuis* is characterized by a minimum number of both echinae and perforations per unit surface area (9–20/14 and 15–28/23 respectively).

Our research has also established a certain difference between the subspecies of the species *G. kotschyanus*. In particular, the size of pollen grains *G. kotschyanus* subsp. *kotschyanus* (based on E1) is slightly larger than that of *G. kotschyanus* subsp. *distichus* (60.6–81.7/65.7 μm and 45.2–71.1/58.2 μm accordingly). At the same time, the number of echinae and perforations per unit surface area of a pollen grain (at the SEM level) in the subspecies *G. kotschyanus* subsp. *distichus* are approximately twice as large as *G. kotschyanus* subsp. *kotschyanus* (12–25/18 and 17–49/33 vs 20–29/24 and 25–77/51 respectively).

The data obtained served as the basis for creating a key to the genus *Gladiolus* of the flora of Armenia, based on the pollen morphological characteristics.

1. Large equatorial diameter (E1) on average 67.7 μm …… ……..…….. *G. hajastanicus* (Fig. 1)
– Large equatorial diameter (E1) on average 58.2–64.8 μm …… 2
2. Number of perforations per unit surface area (5 μm²) on average ≤ 23 …..……..……..…….. *G. tenuis*
– Number of perforations per unit surface area (5 μm²) on average > 23 ……..……..……..……..…..... 3
3. Number of perforations per unit surface area (5 μm²) on average 32–43……*G. caucasicus*, *G. atroviolaceus* (Fig. 3),
G. kotschyanus subsp. *kotschyanus*, *G. dzhavakheticus*, *G. szovitsii*
– Number of perforations per unit surface area (5 μm²) on average 48–51 …… *G. menitzky*, *G. italicus* (Fig. 2), *G. kotschyanus* subsp. *distichus*

Table 3
Palyno-morphological characteristics of the representatives of the genus *Gladiolus* of the flora of Armenia
(averaged data obtained by measuring 20 pollen grains are presented in the Table after the forward slashes)

Species	Exine thickness, μm (LM) ± SD (CV%)	Number of echinae on 5 μm² (SEM)	Number of perforations on 5 μm² (SEM)
G. dzhavakheticus	1.0–1.3 / 1.3 ± 0.05(4.7)	11–24/16	32–47/36
G. caucasicus	0.8–1.6 / 1.2 ± 0.02(1.6)	14–29/22	24–50/32
G. tenuis	0.8–1.8 / 1.2 ± 0.1(8.1)	9–20/14	15–28/23
G. kotschyanus subsp. *kotschyanus*	1.1–2.4 / 1.7 ± 0.3(7.6)	12–25/18	17–49/33
G. kotschyanus subsp. *distichus*	0.6–1.6 / 1.1	25–43/34	25–77/51
G. hajastanicus	1.6–1.9 / 1.8 ± 0.2(1.2)	20–29/24	34–48/41
G. italicus	0.9–1.6 / 1.2 ± 0.1(8.0)	8–34/23	42–56/48
G. atroviolaceus	0.9–1.8 / 1.3 ± 0.1(7.4)	10–23/15	23–45/33
G. menitzky	0.8–1.3 / 1.1	19–42/26	41–70/28
G. szovitsii	1.2–1.6 / 1.4 ± 0.1(5.9)	16–34/25	24–62/43

Notes: see Table 2.

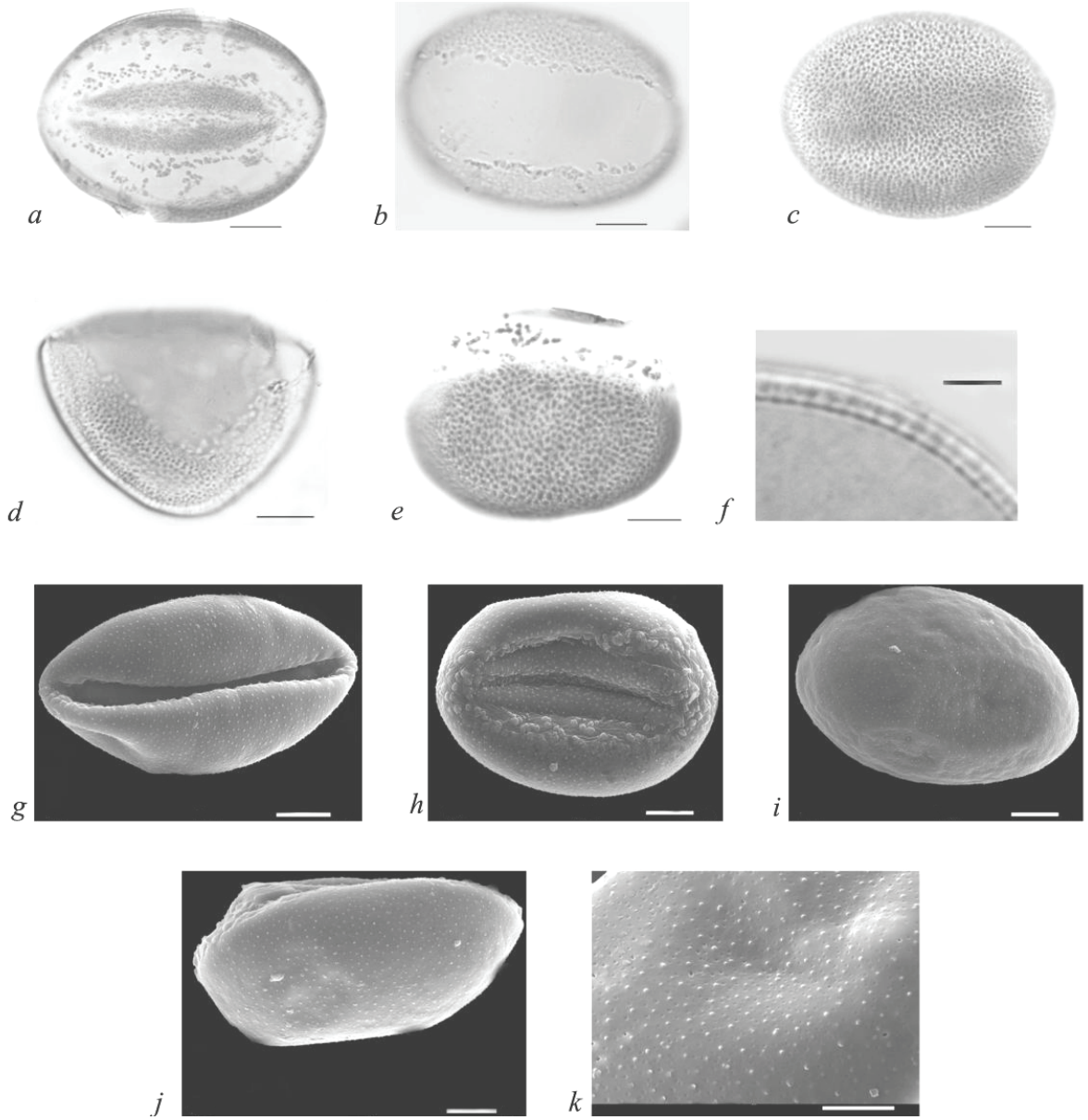

Fig. 3. Pollen grains of *Gladiolus atroviolaceus*: *a–f* – LM micrographs: *a–b* – distal pole (*a* – sulcus with two-lane operculum), *c* – proximal pole, *d* – pollen grain from the small equatorial diameter (E2), *e* – pollen grain from the large equatorial diameter (E1), *f* – exine, columellae layer; *g–k* – SEM micrographs: *g–h* – distal pole, *i* – proximal pole, *j* – pollen grain from the large equatorial diameter (E1), *k* – exine ornamentation; scale bar: *a–e*, *g–j* – 10 μm, *f* – 3 μm, *k* – 5 μm

Conclusion

According to Goldblatt (1971), the uniformity of the genus *Gladiolus* is probably due to its monophyletic nature, as well as to the same basic chromosomal number (x = 15). The closely related relationships of the taxa in the genus *Gladiolus* are also confirmed by serological studies (Shneyer, 1990).

At the same time, the comparative morphological analysis of pollen features showed that in the presence of significant uniformity of pollen grains in the studied species of the genus *Gladiolus* in Armenian flora, the

length of the large equatorial diameter (E1), as well as the number of echinae and perforations per unit surface area of the pollen, can be considered as diagnostic.

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