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Some notes on the types of pollen aperture in the genus *Crocus* L. (Iridaceae)

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ABSTRACT. *Crocus* L. (Iridaceae) is systematically a very problematic genus due to the lack of clear distinctive features, wide range of habitats and the heterogeneity of morphological features. This genus is also highly heterogeneous from a karyological point of view.

Apart from the most common spiraperturate pollen grains in *Crocus*, the authors frequently mentioned a number of other aperture types for individual species (subspecies, variations, etc.), i.e. polyrugoidate, nonaperturate (inaperturate), polyaperturate, with more or less extensive furrows, with short furrows, etc.

The purpose of this work is to perform a palyno-morphological analysis of pollen aperture types noted in the genus *Crocus*. The reason for the study is a significant disagreement among researchers when describing the types of pollen apertures in the genus *Crocus*. An analysis of the literature, as well as the results of our previous studies, showed that the genus *Crocus* is characterized by inaperturate (nonaperturate), polyaperturoidate, spiraperturate and net-like pollen apertures. The similar net-like apertures were observed for some representatives of the subgenus *Scorpiris* Sach of the genus *Iris* L., in particular, in *Iris atropatana* Grossh. In our opinion, this aperture type can serve as a link between the genus *Crocus* and the subgenus *Scorpiris* of the genus *Iris*.

We suggest, that the spiraperturate pollen type mentioned most often for the representatives of the genus *Crocus* can be considered the basic type within the genus. On the other hand, formless aperture-like areas are genetically unstable transitory variations, which occurred arbitrarily due to mutations. Finally, "polyrugoidate" (or with net-like apertures) pollen type noted in the literature for *C. chrysanthus* subsp. *punctatus* F.Candan et N.Özhatay may be considered to be more advanced in the genus *Crocus*.

KEYWORDS: Iridaceae, *Crocus*, *Iris atropatana*, aperture type, pollen polymorphism

INTRODUCTION

Representatives of the genus *Crocus* L. (Iridaceae) are perennial corm herbaceous plants. There are 85–90 species in the Mediterranean and South-West Asia. *Crocus* flowers are optionally protandric, which is one of the adaptations for cross pollination. The most famous species is an autumn-flowering cultivated perennial *Crocus sativus* L. (Saffron), with no known wild counterpart (Rubio-Moraga et al., 2009). This species is always sterile and probably occurred among cultivated plants as a result of hybridization of several species. The sterility of *C. sativus* is mainly restricted to pollen (Grilli Caiola et al., 2000).

Mathew (1982) has divided the genus *Crocus* into two subgenera: *Crocus* subg. *Crocus* and *Crocus* subg. *Crociris* B.Mathew. The first subgenus includes two sections, *Crocus* and *Nudiscapus*, which are divided into series.

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Species *C. banaticus* J.Gay is the only member of *C.* subg. *Crociris*.

In Armenia, the genus is represented by two species belonging to the section *Nudiscapus*, *Crocus adamii* J.Gay (series *Biflori* B.Mathew) and *C. speciosus* M.Bieb. (series *Osi* B.Mathew) (Mathew, 1982; Gabrielian, 2001). *Crocus adamii* is a polymorphous species in the Caucasus, European Turkey, Macedonia, Bulgaria, Crimea and Iran. Contrary to the fall flowering *C. speciosus*, flowers of *C. adamii* appear in spring. The white flowering population was found on Mount Arteni (Armenia), together with specimens with common purple flowers (Gabrielian, 2001). The distribution of the species *C. speciosus* covers the Caucasus, Anatolia, Crimea and the north of Iran (Gabrielian, 2001). In the territory of the Yerevan Botanical Garden (Armenia), samples with unusually white flowers were also found in a population represented mainly by ordinary purple flowers.

The pollen grains of *Crocus* are spheroidal, exine thin, sometimes discontinuous, with columellae weakly expressed (Knox and Heslop-Harrison, 1971; Kuprianova, 1983), intine thick, often penetrated by radially-oriented tubules (Walker, 1976; Heslop-Harrison, 1977). Exine ornamentation under light microscope (LM) echinate, echinate-granulate, echinate-punctate (Kuprianova, 1948, 1983; Avetisyan et al., 2001), ornamentation under scanning electron microscope (SEM) echinate-granulate-microperforate, echinate (spinulose)-microperforate, spinulose-perforate, echinate, perforate-echinate, etc. (Valdes et al., 1986; Işik and Oybak Dönmez, 2006; Oybak Dönmez and Işik, 2008; Spasova and Todorova, 2012).

Since the middle of the last century, the characteristics of pollen morphology of the genus *Crocus* have been the object of research for a number of authors (Erdtman, 1952; Kuprianova, 1948, 1983; Knox and Heslop-Harrison, 1971; Heslop-Harrison, 1977; Mathew, 1982; Furness, 1985; Valdes et al., 1986; Goldblatt et al., 1991, 2006; Furness and Rudall, 1999; Chichiriccò, 1999; Grilli Caiola et al., 2000; Avetisyan et al., 2001; Işik and Oybak Dönmez, 2006; Oybak Dönmez and Işik, 2008; Spasova and Todorova, 2012; Kerndorff et al., 2016; Mitić et al., 2018; Tabasi and Mehrabian, 2019). At the same time, until now, significant disagreements appeared in the literature concerning the types of pollen apertures in the representatives of this genus. In particular, in addition to the most frequently mentioned spirapertur(oid)ate type, a whole range of different terms have been used when describing the type of apertures, such as: polyrugoidate[1] or nonaperturate (Erdtman, 1952; Mathew, 1982), inaperturate or polyaperturate (Kuprianova, 1983), polycolpate (Heslop-Harrison, 1977), polyrugate (Furness, 1985), "…vary between furrows, colpi, and pores" (Chichiriccò, 1999: 38), pantoaperturate (Grilli Caiola et al., 2000), brevi sulcate (Oybak Dönmez and Işik, 2008), with one spiral groove (Spasova and Todorova, 2012), only papillose without any markings (Kerndorff et al., 2016).

Intraspecific pollen variations were also observed in *Crocus*. Candan et al. (2009) reported that spiral furrows are very obvious on the pollen of *C. flavus* Weston subsp. *dissectus* T.Baytop et Mathew, and *C. flavus* Weston subsp. *flavus* specimens have nonaperturatae pollen type. Candan and Özhatay (2013) indicated 4 aperture types of pollen (spiraperturate, polyrugoidate, polycolpate and nonaperturate)for 7 subspecies and variations of species *C. chrysanthus* sensu lato[2] in Turkey.

The purpose of this work is to perform a palyno-morphological analysis of pollen aperture types available in the genus *Crocus*.

The reason for the study is a significant disagreement among researchers when describing the types of pollen apertures in the genus *Crocus*.

MATERIAL AND METHODS

Unopened mature flower buds were obtained from the herbarium of the Institute of Botany after A. Takhtajyan of NAS of Republic of Armenia (ERE), as well as from living plants in the territory of the Yerevan Botanical Garden (Armenia) (Table 1).

Pollen grains were stained with basic fuchsine (Smolyaninova and Golubkova, 1950), and treated with acetolysis (Avetisyan, 1950). Measurements of the diameter of pollen grains, aperture width, exine

[1] Here and beyond the names of aperture types were given in accordance with the terminology used by each author

[2] According to Mathew (1982) and Candan and Özhatay (2013), in this species the phenotypic variations does not correlate with distribution, habitat, flower and anther colours, chromosome numbers, pollen grains characteristics and seed surface micromorphology

Table 1. List of investigated species and specimens. ERE – Herbarium of the Institute of Botany after A. Takhtajyan, National Academy of Sciences, Yerevan, Armenia

Taxon	Name according to location in The Plant List (http://www.theplantlist.org/)	Herbarium sheet information
Crocus adamii J.Gay	*Crocus biflorus* subsp. *adamii* (J.Gay) K.Richt.	ERE, 143107; ERE, 196495; ERE, 149143, 192728
C. speciosus M.Bieb.	*C. speciosus* M.Bieb.	ERE, 113142; Ijevan Botanical Garden, 04/10/2019 Leg. A. Muradyan (pers. coll.); Yerevan Botanical Garden, 15/10/2020 Leg. A. Muradyan (pers. coll.); Yerevan Botanical Garden, 16/10/2020 Leg. A. Muradyan (pers. coll.); Yerevan Botanical Garden, 26/10/2020 Leg. H. Sonyan (pers. coll.)
Iris atropatana Grossh.	*Iris atropatana* Grossh.	ERE, 143428

Table 2. Palyno-morphological characteristics of the representatives of the species *Crocus adamii* J.Gay. of Armenian flora (Averaged data obtained by measuring 20 pollen grains are presented in the table after the forward slashes)

Specimen	Diameter of pollen grains (μm)	Aperture width (μm)	Exine thickness (μm)	Hyaline thickness (μm)	Exine ornamentation		Height of spinules (μm)	Specimen number
					LM	SEM		
C. adamii (purple-flowered)	53.4–72.4/58.9	1.1–5.0/2.8	0.8–1.2/0.9	0.8–2.6/1.6	spinulose	perforate-spinulose	0.8–1.9/1.2	ERE, 143107; ERE, 192728; ERE, 196495
C. adamii (with white flowers)	57.1–65.8/55.4	1.2–3.0/1.9	0.6–1.0/0.8	1.3–2.4/1.7	spinulose	perforate-spinulose	0.7–1.9/0.9	ERE, 149143

Table 3. Palyno-morphological characteristics of the representatives of the species *Crocus speciosus* M.Bieb. of Armenian flora (Averaged data obtained by measuring 20 pollen grains are presented in the table after the forward slashes)

Specimen	Diameter of pollen grains (μm)	Aperture width (μm)	Exine thickness (μm	Hyaline thickness (μm)	Exine ornamentation		Height of spinules (μm)	Specimen number
					LM	SEM		
C. speciosus (purple-flowered)	72.2–87.9/78.7	1.6–6.6/2.7	0.6–1.8/1.5	1.8–3.7/2.7	spinulose	perforate-spinulose	0.8–2.7/1.1	personal collections (04.10.2019, 16.10.2020, 26.10.2020)
C. speciosus (purple-flowered, collected from Zangezur region)	67.9–79.6/73.6	0.4–2.5/1.6	0.7–1.2/1.0	2.2–3.5/3.0	spinulose	perforate-spinulose	1.1–2.7/1.4	ERE, 113142
C. speciosus (with white flowers)	77.4–89.9/84.8	1.7–3.2/2.5	0.8–1.7/1.3	1.8–3.0/3.0	spinulose	perforate-spinulose	0.9–1.7/0.8	personal collection (15.10.2020)

thickness and the thickness of the hyaline layer of the intine[3] were made using an AmScope light microscope on 20 pollen grains for each specimen. The details of exine structure and ornamentation were studied on acetolysed pollen grains; pollen shape, size and aperture descriptions were carried out on non-acetolysed stained pollen grains. However, it has been observed that, during acetolysis treatment, the coat of pollen grains is partially or completely destroyed[4]. Considering this, the microphotography of the pollen grains of all studied samples was conducted mainly on the material painted with basic fuchsine.

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. Samples were imaged under a Jeol-7000 Scanning Electron Microscope, with a 15 kV electron beam. The height of spinules on the surface of a pollen grain (using SEM) was measured.

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.en.softonic.com/). Besides, in the case of CV ≤ 10%, the sample is weakly variable, with CV from 10% to 20% is moderately variable, CV ≥ 20% – is highly variable and with CV ≥ 30%, the highest degree of variability is noted.

On the whole, the pollen morphological characteristics of 9 samples of 2 species of the genus *Crocus* and one sample of the species *Iris atropatana* Grossh. of the flora of Armenia were analysed.

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

[3] According to Bobrov et al. (1983: 69), the hyaline, or the hyaline layer, is the outer layer of the intine of pollen grains. In representatives of some monocots, including species of the genus *Crocus*, this layer often reaches a significant thickness

[4] Such a phenomenon was also observed by Kuprianova (1983)

List (http://www.theplantlist.org/). The palyno-morphological data (using LM and SEM) for each species are presented in Tables 2 and 3. Data on statistical analysis of pollen characteristics are presented in Table 4.

The morphological terminology used in our study mainly follows that of Erdtman (1952), Kuprianova and Alyoshina (1967), Bobrov et al. (1983), Punt et al. (2007) and Halbritter et al. (2018).

RESULTS AND DISCUSSION

A detailed description of the pollen morphology of the *Crocus adamii* and *C. speciosus* species under a light microscope (LM) and scanning electron microscope (SEM) was presented in an earlier article (Muradyan, 2021). Previously obtained data indicate that both studied species are characterised by the monad, spheroidal pollen grains with spiral apertures (Figs 1, 2). Pollen diameter vary from 55.4–58.9 µm (*C. adamii*) to 73.6–84.8 µm (*C. speciosus*). In the species *C. adamii* spiral apertures are surficial, often interrupted (LM, SEM), in *C. speciosus* M.Bieb. at LM level spiral apertures look like surficial (Fig. 2.2, 2.7, 2.9, 2.10), at SEM level apertures submerged, forming regular spiral rings on the surface of the pollen grain (Fig. 2.4, 2.5, 2.8); the apertures margins are predominantly slightly wavy, the aperture membrane is smooth, very rarely with irregularly located granules; in both species the aperture width is approximately the same (1.9–2.8 µm for *C. adamii* and 1.6–2.7 µm for *C. speciosus*). Exine thickness varies from 0.8–0.9 µm (*C. adamii*) to 1.0–1.5 µm (*C. speciosus*), columellae weakly expressed; the hyaline layer of intine in both species approximately two times thicker than exine (Tables 2, 3). Exine ornamentation for both species spinulose (LM), exine ornamentation perforate-spinulose, occasionally the separate granules were noted between the spinules; the height of spinules on the surface of pollen grains is approximately the same in both species studied (0.8–1.4 µm) (SEM).

For the species *C. adamii*, pollen morphology from white-flowered specimens (ERE, 149143) collected by E. Gabrielyan on Mount Arteni (Armenia) was also investigated. The results showed that the pollen grains in all the samples studied (both with purple and white flowers) are quite similar in size.

For the species *C. speciosus*, pollen grains from the sample collected from the Zangezur floristic region (Armenia) (ERE, 113142) were also observed. It has been found, that at LM level pollen grains are characterized by rather narrow, sometimes discontinuous spiral apertures. However, at SEM level the submerged apertures typical for the species *C. speciosus* have been revealed (Fig. 2.8).

Palynological investigations of the white-flowered sample of *C. speciosus* from the territory of the Yerevan Botanical Garden (personal collection, 15/10/2020) detected that pollen grains are slightly larger than those of typical purple flower samples, but are within the boundaries of the size of this species (Table 3, Fig 2.9–2.11). In our opinion, because of the small number of white-flowered samples (2–3%), the presence of albino specimens in this population may be considered.

Thus, the comparative palyno-morphological analysis of two species of the Armenian representatives of the genus *Crocus* revealed the uniformity both in the unit of pollen dispersion (monads) and in the general shape of pollen grains (spheroidal), as well as the type of apertures (spiraperturate, with varying degrees of submergence). Analysis of the few other key features, such as diameter of pollen grains, aperture width, exine thickness, thickness of the hyaline layer of intine and the height of spinules on the surface of pollen grains, showed that the the diameter of pollen grains can be considered the main diagnostic feature. At the same time, despite the noted differences in the degrees of submergence of spiral apertures, thickness of the exine and the hyaline layer of the intine also, we consider the last three characters as secondary

Table 4. Data on the statistical analysis of pollen characteristics of the representatives of the genus *Crocus* L. of Armenian flora

Species	Diameter of pollen grains (µm)		Exine thickness (µm)		Hyaline thickness (µm)	
	± SD	CV%	± SD	CV%	± SD	CV%
Crocus adamii	58.97 ± 1.9	3.2%	0.91 ± 0.02	2.1%	1.63 ± 0.1	6.1%
Crocus speciosus	77.44 ± 5.7	7.3%	1.2 ± 0.08	6.6%	2.72 ± 0.2	7.3%
Variation intervals ± SD and CV%	± 1.9–5.7	3.2–7.3%	± 0.02–0.08	2.1–6.6%	± 0.1–0.2	6.1–7.3%

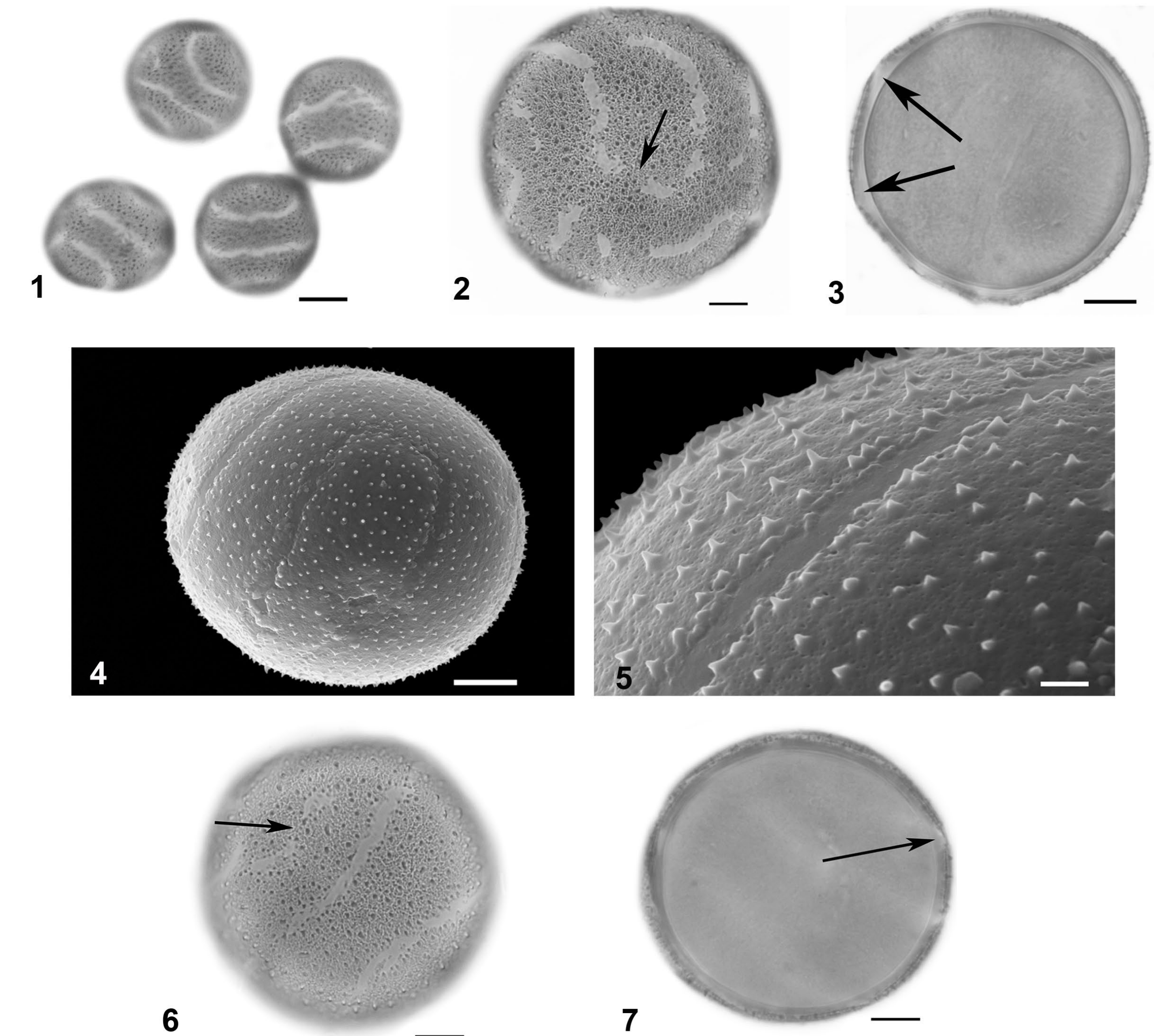

Figure 1. Pollen grains of the species *Crocus adamii* J.Gay. **1–5**. Purple-flowered specimen (ERE, 192728), **1–3**. LM micrographs, **1**. general view, **2**. surficial, often interrupted aperture (marked with arrow), **3**. hyaline thickening under spiral aperture (marked with arrows), **4**, **5**. SEM micrograph, **4**. general view, **5**. fragment of spiral aperture and exine ornamentation; **6**, **7**. Specimen with white flowers (ERE, 149143), LM micrographs: **6**. general view with discontinuous spiral aperture (marked with arrow), **7**. hyaline thickening under spiral aperture (marked with arrow). 1–3, 6, 7 stained with fuchsine. Scale bars = 20 µm in 1; 10 µm in 2–4, 6, 7; 2 µm in 5

diagnostic, due to the presence of a clear difference in the size of pollen grains.

Extended statistical analysis on three pollen features, namely the diameter of pollen grains and the thickness of both the exine and hyaline layers, conducted for the representatives of the two species of the genus *Crocus* of the flora Armenia, revealed the weakly variability (CV ≤ 10%) for all three above mentioned parameters (Table 4). On the other hand, the statistical analysis of the aperture width and the height of spinules on the surface of pollen grains did not reveal any significant differences, therefore, these characteristics were not included in our ongoing investigation.

Considering the origin of monocotyledons and citing a number of authors (Cronquist, 1981; Daghlian, 1981; Muller, 1981), Zawada (1983: 371) wrote that "...monocots are thought to be derived from dicotyledonous-like (ranalean) ancestors that diverged from dicots early in the evolutionary history of angiosperms...". In this regard, taking as a basis the principle of the evolution of apertures in the pollen of primitive angiosperms, presented earlier by Walker (1974: fig. 12), the author also contemplates the inaperturate type in monocots as a derivative of the more primitive anasulcate one. However, unlike Walker (1974), Zawada considers the inaperturate type not

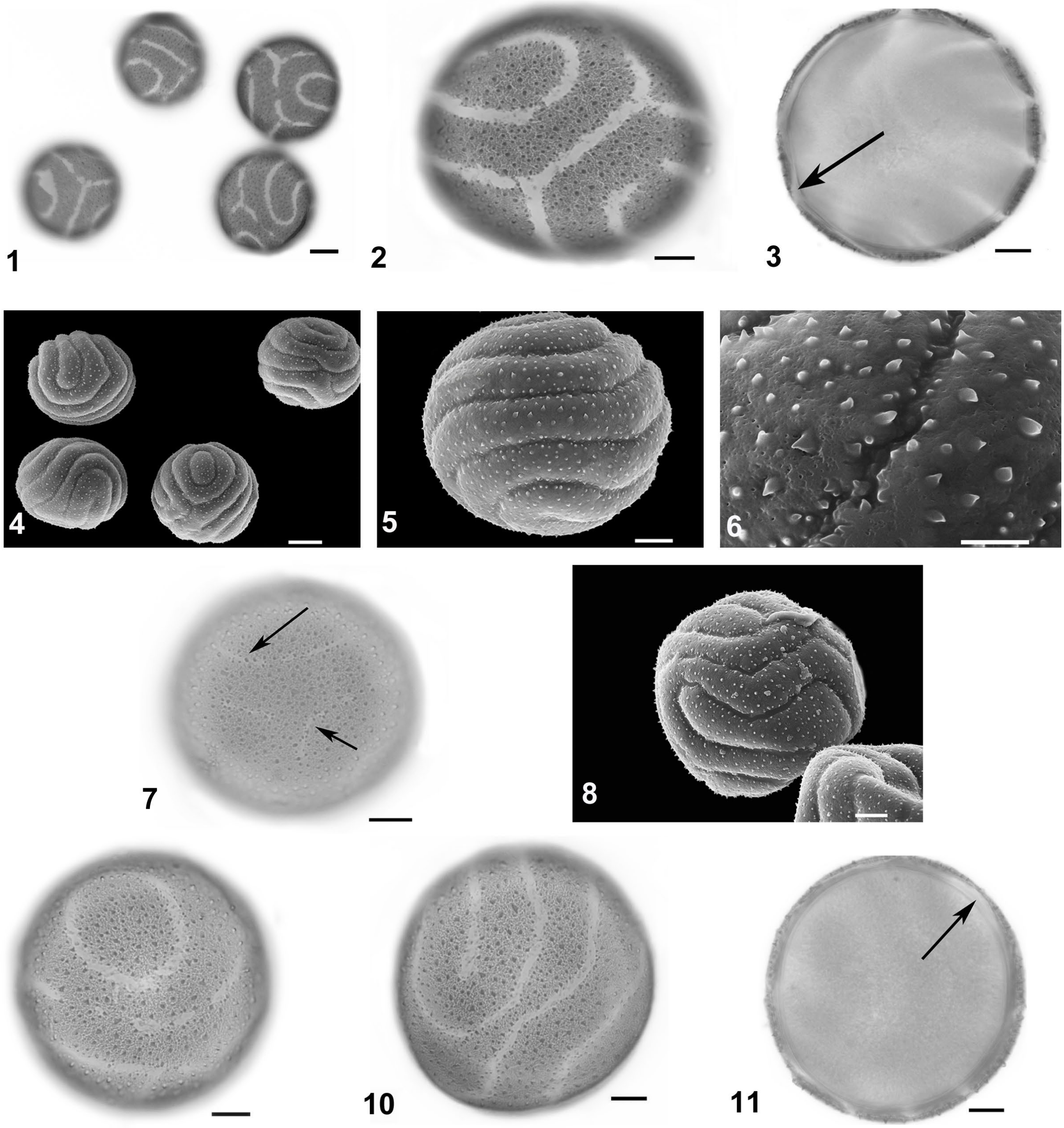

Figure 2. Pollen grains of the species *Crocus speciosus* M.Bieb. **1–6**. Purple-flowered specimen (personal collection, 16/10/2020), **1–3**. LM micrographs: **1**, **2**. general view, **3**. hyaline thickening under spiral aperture (marked with arrow), **4–6**. SEM micrographs: **4**, **5**. general view, **6**. fragment of spiral aperture and exine ornamentation; **7**, **8**. Specimen from Zangezur floristic region (ERE, 113142): **7**. LM micrograph, general view with narrow spiral aperture (marked with arrows), **8**. SEM micrograph, general view with submerged spiral aperture; **9–11**. Specimen with white flowers (personal collection, 15/10/2020), LM micrographs, **9**, **10**. general view, **11**. hyaline thickening under spiral aperture (marked with arrow). 1–3, 7, 9–11 stained with fuchsine. Scale bars = 20 µm in 1, 4; 10 µm in 2, 3, 5, 7–11; 5 µm in 6

as a transitional stage from anasulcate to other aperture types (in the case of Walker (1974), colpate and porate ones), but, along with the multiaperturate type with indistinct defined deckle-edged apertures, as the final stages of pollen aperture evolution in monocots (Walker, 1974: fig. 56). On the other hand, Zawada (1983), characterizing the pollen of the family Iridaceae, noted only monosulcate and inaperturate aperture types for the representatives of this family.

According to Erdtman (1952), the term "spiraperturate" has been used to describe the pollen grains with one or several spiral apertures. Furness (1985) reported, that spiraperturate pollen occurs in a few families of angiosperms (both dicots and monocots) and appears to be polyphyletic. In dicots this aperture

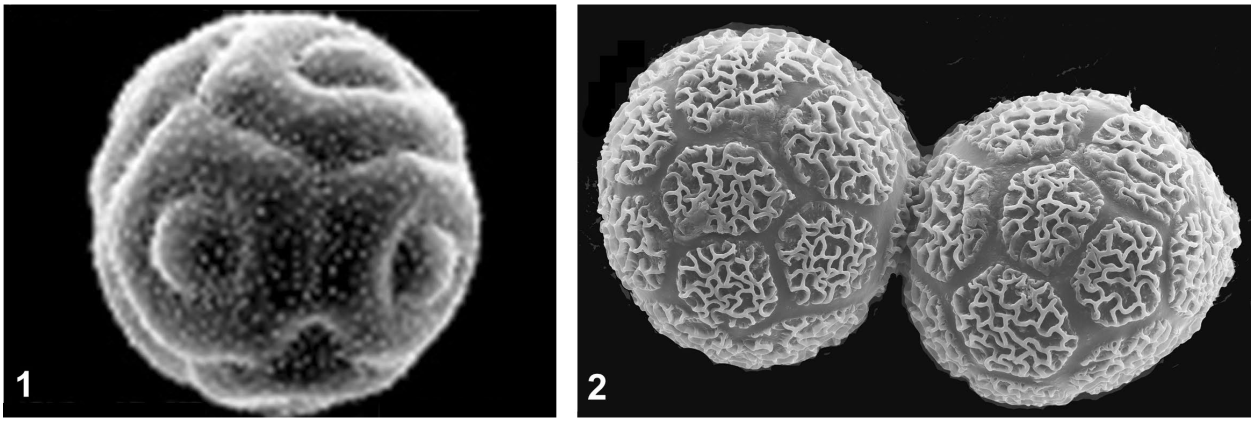

Figure 3. Pollen grains of some representatives of the family Iridaceae. **1**. *Crocus chrysanthus* subsp. *punctatus* F.Candan et N.Özhatay with "polyrugoidate" (netaperturate) apertures (from Candan and Özhatay, 2013); **2**. *Iris atropatana* Grossh. with net-like apertures

type was mentioned, for example, in Acanthaceae (Al-Hakimi et al., 2015), Berberidaceae (Kosenko, 1980; Nowicke and Skvarla, 1981), Bignoniaceae (Mitra, 1968; Gentry and Tomb, 1979), Lentibulariaceae (Beretta et al., 2014), Podostemaceae (Rutishauser, 1997; Osborn et al., 2000), Ranunculaceae (Blackmore et al., 1995), Scrophulariaceae (Argue, 1981) and others. In monocots, it can be found in Araceae (Ueno, 1980), Arecaceae (Nair and Sharma, 1963), Costaceae (Ueno, 1980; Stone et al., 1981; Furness, 1985), Eriocaulaceae (Ueno, 1980; Furness, 1985), Iridaceae (Furness, 1985), Liliaceae (Díaz Lifante et al., 1990), Xanthorrhoeaceae (Chanda and Ghosh, 1976), Zingiberaceae (Punt, 1968; Liang, 1988).

As a rule, the type of apertures is a relatively constant feature and is considered to be a diagnostic feature, particularly at the level of individual genera. Moreover, according to literature data, the spiraperturate pollen type sometimes occurs in the same taxa in combination with other aperture types, namely trichotomocolpate and l-porate (Nair and Sharma, 1963), trisulcate (Le Thomas et al., 2000), tricolpate (Osborn et al., 2000), 2-zonasulcate (Giulietti et al., 2012), colporate (Beretta et al., 2014).

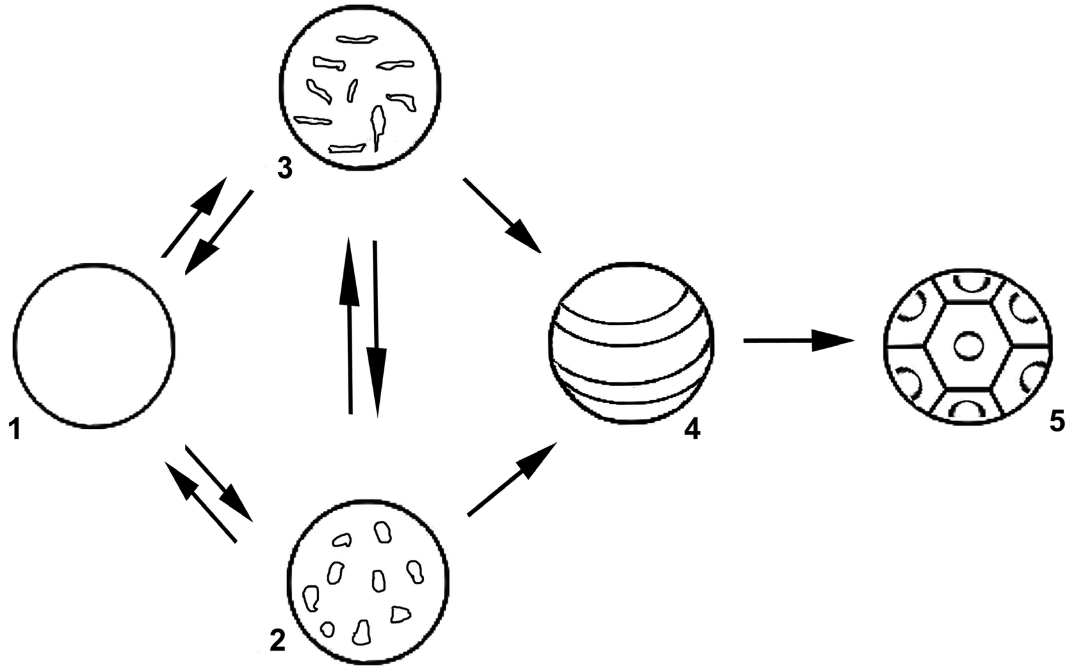

Figure 4. Types and variations of pollen apertures, their potential connections and possible directions of evolutionary development in the genus *Crocus*. **1**. Inaperturate (nonaperturate); **2**. Polyaperturoidate (poroidate-like exine discontinuities); **3**. Polyaperturoidate (rugoidate-like exine discontinuities); **4**. Spiraperturate; **5**. "Polyrugoidate" (or net-like apertures) (Candan and Özhatay, 2013)

The genus *Crocus* is systematically very problematic genus due to the lack of clear distinctive features, the wide range of habitats and the heterogeneity of morphological features (Brighton et al., 1973; Yilmaz and Yeltekin, 2022). Mathew (1982) wrote that it is also highly heterogeneous from a karyological point of view. The chromosome number within the genus varies from 2n = 6 to 2n = 70 (Brighton et al., 1973; Uslu et al., 2012; Harpke et al., 2013). Furthermore, closely related species often show intermediate signs due to introgression following hybridization (Rubio-Moraga et al., 2009; Harrison and Larson, 2014; Kerndorff et al., 2016; Yılmaz, 2021).

The analysis of the palynological literature, together with the results of our surveys, have shown that in general, the following types (or variations) of pollen aperture have been observed within the boundaries of the genus *Crocus* (Fig. 4):

– inaperturate (nonaperturate) (Fig. 4.1);

– polyaperturoidate – represented by poroidate-like or rugoidate-like exine discontinuities irregularly distributed over the surface of pollen grains (Fig. 4.2 and 4.3 accordingly);

– spiraperturate –- spirally arranged band-shaped apertures (sometimes partially fragmented, discontinuous) (Fig. 4.4);

– “polyrugoidate” (Candan and Özhatay, 2013) – *C. chrysanthus* subsp. *punctatus* (Fig. 4.5).

As for the last subspecies, the surface of the pollen grains here is divided into several regular and well-defined pentagonal fragments resembling shields on the pollen surface. The similar net-like pollen apertures were observed for some representatives of the genus *Iris* (subgenus *Scorpiris* Sach) (Fig. 3), that certain authors (Pinar and Oybak Dönmez, 2000; Oybak Dönmez and Pinar, 2001; Oybak Dönmez and Işik, 2008) described as inaperturate (clypeate).

In our opinion, such a regular arrangement of apertures indicates a higher degree of pollen specialization in *C. chrysanthus* subsp. *punctatus*. We assume also, that the pollen of the representatives of the subgenus *Scorpiris* (genus *Iris*) is not inaperturate, since on the surface of the pollen grains the net-like thinned exine areas have been noted. By analogy with the term spiraperturate, the aperture type in the pollen grains of the *Crocus chrysanthus* subsp. *punctatus*, as well as in those of the representatives of the subgenus *Scorpiris* (genus *Iris*) can be characterized as netaperturate (i.e. with net-like apertures).

CONCLUSION

From a palynological point of view, the simultaneous occurrence of different types of pollen aperture both within one genus and within the same species reflects active ongoing evolutionary processes. In the case of the genus *Crocus*, the strongly pronounced pollen polymorphism may be a direct reflection on the genetic instability, as well as on the lack of clear boundaries between individual intraspecific taxa.

In our opinion, the spiraperturate pollen type is the most often mentioned for the representatives of the genus *Crocus*, so can be considered the basic type within the genus. Furthermore, exineless, formless plots, irregularly placed on the surface of the pollen grain (noted in some taxa of the genus *Crocus*), can hardly be regarded as true apertures, such as colpus, pore, ruga, etc. And the fact that the totally sterile species *C. sativus* is also characterized by the lack of well-defined apertures, indicates the primitivity of inaperturate pollen type in the genus *Crocus*. Most likely, formless aperture-like areas are genetically unstable transitory variations from the inaperturate type to the spiraperturate one, which occurred arbitrarily due to mutations (Fig. 4). This hypothesis can be supported by the presence in *Crocus chrysanthus* s. lato (Candan and Özhatay, 2013) of almost all pollen aperture types and variations that have been cited in the literature for representatives of the entire *Crocus* genus. This assumption is consistent with the view of Furness and Rudall (1999), noted that the development mechanisms controlling aperture form are particularly labile in the early branched monocotyledonous groups.

The scheme of the relationships between pollen aperture variations and types within the genus *Crocus*, as well as possible ways of their further development (Fig. 4), in our opinion, can serve a logical continuation of the main evolutionary trends of apertures in monocots presented by Zawada (1983). We suggest that the key point for the genus *Crocus* was the appearance of spiral apertures with clearly defined edges, and, in the case of

C. chrysanthus subsp. *punctatus*, previously unmarked net-like apertures.

Finally, the "polyrugoidate" (netaperturate) pollen type noted in *C. chrysanthus* subsp. *punctatus* (Candan and Özhatay, 2013) may be considered to be more advanced in the genus *Crocus*. On the other hand, this aperture type can serve as a link between the genus *Crocus* and the subgenus *Scorpiris* of the genus *Iris*.

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