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Pollen Morphology of Malvaceae in Iran: A Case Study to Complete Pollen Atlas of Iran

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Abstract

The pollen grains of 34 species of eleven genera belonging to three subfamilies (Malvoideae, Grewioideae, Tilioideae) of Malvaceae were studied by scanning electron microscopy (SEM). Pollen grains of the studied taxa were radially symmetrical and principally spheroidal, except *Grewia makranica* Rech.f. & Esfand (prolate), *Tilia cordata* Miller, and *Tilia rubra* Dc. (suboblate). Apertures included tricolporate (*Tilia cordata* and *Tilia rubra*) to pantaporate (*Malvella sherardiana* L., *Malva verticillate* L., *Malvalthaea transcaucasica* (sosn.) Iljinand *Alcea sulphurea* (Boiss. & Hohen). Sculpturing was comprised of echinate, microechinate, baculate, granulate, and perforate types. Some qualitative traits in pollen grains are unique to one or a few genera. The observed variations in pollen characteristics are very useful for the delimitation of subfamilies and in some cases are generic specific but these characters are not functional in separating taxa at a specific level or distinguishing suggested species groups in some genera such as *Alcea* L.. Our results add further support to the current classification of Malvaceae which recognizes the subfamilies Tilioideae, Grewioideae, and Malvoideae but there was no character state in pollen grains to be synapomorphic for Malveae, Hibisceae, and Gossypieae. On the other hand, our results support the separation of *Alcea* from *Althaea*. The PCA analysis represents two clades. The first clade contains both subfamilies Grewioideae and Tilioideae. The second clade contains all genera belonging to the subfamily Malvoideae The resulting study emphasizes that some palynological characteristics represent high systematic value, so can be useful for systematic differentiation of Malvaceae. However, palynological evidence along with other characteristics, can be effective in solving the systematic challenges of this family.

Keywords: Micromorphology, *Alcea*, Phylogeny, Taxonomy, Iran

Introduction

Plants of the Malvaceae family possess morphological plasticity which gives rise to taxonomical discrepancies at both family and genus levels (Alverson et al., 1999; Carvalho-Sobrinho et al., 2016; 2002; Tate et al., 2005). Because of this characteristic, the family is divided into nine

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subfamilies: Brownlowioideae, Bombacoideae, Byttnerioideae, Dombeyoideae, Grewioideae, Helicteroideae, Malvoideae, Tilioideae, and Sterculioideae (Alverson et al., 1999; Bayer et al., 1999; Judd and Manchester, 1997; Xu and Deng 2017).

The Malvaceae sensu lato (sl) (Bayer et al. 1999) includes 244 genera and 4,225 species (Christenhusz and Byng 2016), consisting of nine subfamilies (Bayer et al. 1999): Byttnerioideae, Grewioideae, Tilioideae (with only a single genus *Tilia* L.), Helicteroideae, Sterculioideae, Brownlowioideae, Dombeyoideae, Malvoideae, and Bombacoideae. These ornamental (*Alcea*, *Malva* L., and *Tilia*) and medicinal plants (*Althaea officinalis* L., *Malva sylvestris* L., and *Alcea biemis* Winterl.), as well as the valuable industrial plant taxa (*Gossypium L.* and *Hibiscus*), are widely distributed in tropical to temperate regions of the world (Xu and Deng, 2017). The Malvaceae family comprises herb and shrub forms typically with stellate hairs. The leaves are commonly palmate-lobed and grow alternately on the stem. An epicalyx is regularly present. Plants will usually have five sepals connected below five unfused petals and be merged at the base with the staminal tube. The fruits are mainly schizocarpic and rarely capsule (Davis, 1984). The phenotypic plasticity of Malvaceae presents several challenges in taxonomy and classification (Carvalho-Sobrinho et al., 2016; Tate et al., 2005). Malvaceae are divided into two major clades, namely Byttneriina and Malvadendrina (Alverson et al. 1999, Bayer and Kubitzki 2003, Nyffeler et al. 2005). The Byttneriina clade is divided into two subclades, i.e., the Grewioideae and Byttnerioideae subfamilies. The Malvadendrina clade is divided into six subclades comprising seven subfamilies: Brownlowioideae, Dombeyoideae, Helicteroideae, Bombacoideae, Malvoideae, Tilioideae, and Sterculioideae (Alverson et al. 1999).

The pollen morphology of the family Malvaceae including Tiliaceae has been investigated by Erdtman (1952,1969), Saad (1960), Robyns (1963), Robyns and Nilsson (1975, 1981), Christensen (1986), Culhane and Blackmore (1988), Perveen et al. (1994), Fryxell (1997), Hosni and Araffa (1999), Tahavi (2000), Lakshmi (2003), El Naggar (2004), Perveen et al. (2004), El-Husseini (2006), Perveen and Qaiser (2007), Cabi et al. (2009), Shaheen et al. (2009), Bibi et al. (2010), Li Q et al. (2012).

Three subfamilies (Tilioideae, Grewioideae, and Malvoideae) with thirteen genera of Malvaceae can be found in Iran (Riedl 1976). These nectariferous plants are the main botanical sources of bee pollen in Iran and are valuable to honey production (Refahi and Nemati, 2018). Several melissopalynological studies (Nazarian et al., 1997; Sanei Shariat Panahi, 1974; Ghoraishi and Memariani, 2000; Faghih et al., 2004; Razaghi et al., 2006; Ahmad Abad et al., 2017; Khansaritoreh et al., 2021) have confirmed the presence of Malvaceae in various types of honey produced in Iran. “Cotton” and “linden” are valuable monofloral kinds of honey known to be produced in the Hyrcanian Forest as well as in agricultural bee hives in Iran (Refahi and Alipour, 2017). Today, the illustrated Pollen Atlas remains the foremost scientific database for melissopalynology; thus, preparing an accurate pollen database that includes images and describes distinguishing traits seems necessary for determining the botanical origin of and authenticating different kinds of honey. Despite the many studies conducted worldwide on the palynology of Malvaceae, to date, little attention has been paid to the pollen morphology of Malvaceae in Iran. The current study reports the morphology of pollen in the genera of Malvales using SEM. The main aims of the present study are comprised of verifying all types of Malvaceae pollen grains growing in Iran, evaluating the most important features of pollen grains in terms of systematic significance, particularly in taxonomically challenging genera such as *Alcea*, exploring the molecular and traditional classifications of the pollen grains using the available phylogenetic frameworks of Malvaceae and preparing a pollen data bank for Iran.

Study area

The current study covered the geographical boundaries of Iran, i.e., a total surface area of 1.6 million km^2 at 25°-40° N longitude and 44°-64° E latitude. The main topographical zones of Iran include Zagros, Alborz, and Kopet Dagh as well as some interior mountain chains. These Orogenic massifs form a natural border around the central plateau of Iran, blocking the entry of humidity to this region and shaping diverse rainfall patterns in Iran. Djamali et al. (2011) developed a bioclimatic classification based on Rivas-Martínez et al. (1997, 1999) which included temperate (Northern Iran), Mediterranean (western, northwestern Iran), and tropical (Southern Coast Zones of Persian Gulf and the Gulf of Oman) macro-bioclimates. Annual precipitation averages about 250 mm, which is less than one-third the global rainfall average of 860 mm (Amiri and Eslamian, 2010). Iran also has a vast range of soil features (Dewan and Famouri, 1964), including seven zones comprised of the central plateau, Iranides, Khuzistan plain, the folded zone, the Caspian littoral, the Alborz Mountains, and the Turkeman-Khurasan Mountains.

Material and methods

In the present study, the pollen grains of 34 species of 11 genera belonging to three subfamilies (Malvoideae, Grewioideae, Tilioideae) of Malvaceae were studied by scanning electron microscopy (SEM). Plant materials used in this study were taken from wild populations as well as herbariums. The voucher specimens used in this study are deposited in the Shahid Beheshti University Herbarium (HSBU) and the Herbarium of IRAN (Table 1). Pollen grains were mounted on aluminum stubs with double-sided cellophane tape and covered with gold. The samples (at least twenty pollen grains per species) were then studied with a Phillips × L20 SEM. UTHSCSA (Figures 2-5). Image Tool Version 3.0 was used to perform the required measurements. PAST version 2.17 (Hammer et al., 2001) was used for statistical analyses, including UPGMA and PCA (Fig. 1). Multivariate analysis examined five qualitative and five quantitative palynological features, namely pollen shape (PS), pollen class (PC), equatorial diameter in polar view (ED), tectum sculpture (TS), spine height (SH), spine shape (SS), spine base shape (SBS), spine base distance (SBD), colpus length (CL), and colpus width (CW) (Tab. 2).

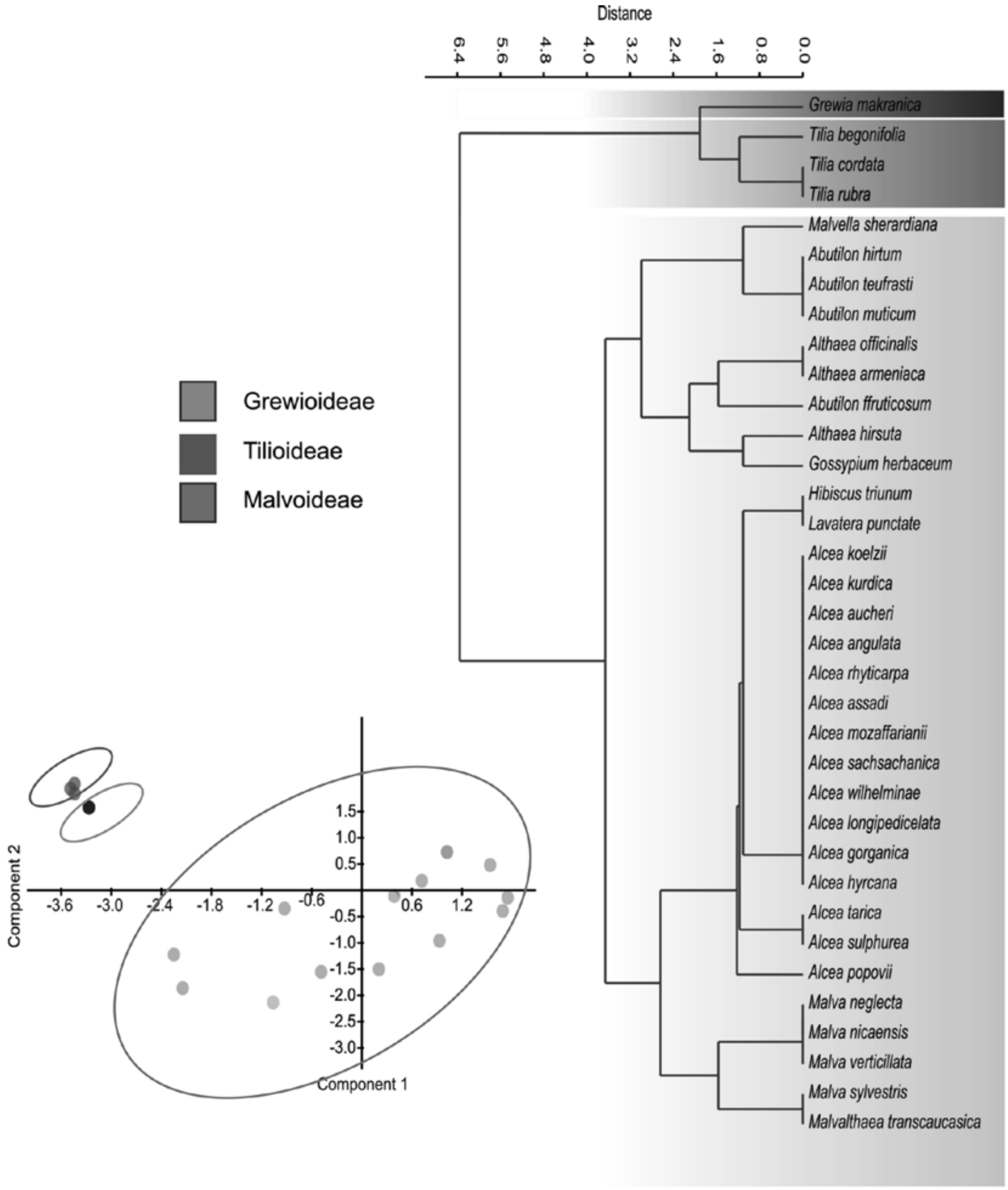

Fig. 1. UPGMA tree and PCA plot of studied taxa based on pollen evidence. ed: equatorial diameter in polar view, sh: spine height, sbd: spines base distance, ss: spine shape, pc: pollen class, ts: tectum sculpture, cl: colpus length, cw: colpus width

Principal components analysis (PCA) was performed among the specimens to determine palynological features useful for separating the species or genera. To group the species, cluster analysis using unweighted paired groups with arithmetic average (UPGMA) methods and PCA ordination plotting using Euclidean methods were performed, and the taxonomic distances among the species were calculated (Podani 2000). The terminology follows Hesse et al. (2009) and Erdtman (1952).

Results

Pollen grains of the studied taxa were radially symmetrical and principally spheroidal, except *Grewia makranica*

Table 1. List of specimens used in palynological investigations

Species	Collection data and herbarium
Abutilon hirtum (Lam.) Sweet.	Prov. Hormozgan, Jazireh Farour, Termeh & Karavar, 25930 (IRAN)
Abutilon muticum (Del.) Boiss.	Prov. West Azerbaijan, 70km Mahabad to Orumieh, Sangari &Tehrani, 67725 (IRAN)
Abutilon theuphrasti Medicus	Prov. Gilan, Langeroud, Sabeti, 30540 (IRAN)
Abutilon fruticosum Guill.& Perr.	Prov. Hormozgan, Baluchestan, Chabahar, Gauba, 30532 (IRAN)
Alcea angulate (Freyn) Iljin.	Prov. Tehran, Damavand, Valian village, M. Arab Ameri & B. Alijanpour, 2019521 (HSBU)
Alcea assadi Pakravan	Prov .Ardabil, Gilvan to Zanjan, M. Arab Ameri & F. Jafari, 2019502 (HSBU)
Alcea aucheri (Boiss.) Alef.	Prov. Kurdistan, Marivan, M. Arab Ameri & B. Alijanpour, 2019510 (HSBU)
Alcea gorganica (Rech. F., Aellen & Esfand.)	Prov. Semnan, Hoseyn Abad, M. Arab Ameri, et al., 2019508 (HSBU)
Alcea hyrcana (Grossh.) Pakravan & Ghahreman	Prov. Mazandaran, Between Chalus and Tonekabon, Ghahreman et al., 10099 (HTU)
Alcea koelzii I.Riedl.	Prov. Kurdistan, Marivan, M. Arab Ameri & B. Alijanpour, 2019510 (HSBU)
Alcea kurdica (schlecht.) Alef.	Prov. Kermanshah, Kangavar to Kermanshah, M. Arab Ameri et al., 2019511 (HSBU)
Alcea longipedicellata I.Riedl.	Prov. Alborz , Chitgar Forest Park, M. Arab Ameri, 2019512 (HSBU)
Alcea mozaffarianii Ghahreman, Pakravan & Assadi	Prov. Ardabil, Kivi, Marand, M. Arab Ameri, et al., 2019525 (HSBU)
Alcea popovii Iljin.	Prov. Gilan, Rostam-Abad, M. Arab Ameri et al., 2019515 (HSBU)
Alcea rhyticarpa (Trautv) Pakravan	Prov. Khorasan, Binalud, M. Arab Ameri, M. Shamsaddini, 2019516 (HSBU)
Alcea sachsachanica Iljin.	Prov. East Azerbaijan, Kaleybar to Aslan-Duz, M. Arab Ameri, et al., 2019517 (HSBU)
Alcea sulphurea (Boiss. & Hohen)	Prov. Tehran, Damavand, M. Arab Ameri, B. Alijanpour, 2019519 (HSBU)
Alcea tarica Pakravan & Ghahreman	Prov. Tehran, Damavand, Valian village, Arab Ameri & B. Alijanpour, 2019521 (HSBU)
Alcea wilhelminae I. Riedl.	Prov. West Azerbaijan, Ghotur valley, M. Arab Ameri et al., 2019523 (HSBU)
Althaea armeniaca Ten.	Prov. West Azarbaijan, Maku, Soltani, 30628 (IRAN)
Althaea hirsuta L.	Prov. East Azarbaijan, Kalibar, Veinagh, Alamlou (Forest), Termeh & Mussavi & Habibi, 67714 (IRAN)
Gossypium herbaceum L.	Prov. Markazi, Saveh, 22 km. E. of Saveh, Akhani, 2141 (IRAN)
Grewia makranica Rech. F. & Esfand.	Prov. Hormozgan, Baluchestan, Chabahar to Negur, Iranshahr & Ershad, 58905 (IRAN)
Hibiscus mutabilis L.	Prov. Mazandaran: 15km Nour, Izad Shahr, Shahrak Akam to Nour, Ashkan, 52647 (IRAN)
Lavatera punctate All.	Prov. Mazandaran, Sari, Sourak, Javanmoghadam, 30666 (IRAN)
Malva neglecta wallr.	Prov. Weast Azarbaijan, 50 km Mahabad to Orumieh, Termeh et al., 52221 (IRAN)
Malva nicaeensis All.	Prov. Golestan, Gorgan, Jangal Golestan, jangar Rah, Termeh & Matin, 67762
Malva sylvestris L.	Prov. Tehran, Velenjak, Iranian Research Institute Plant Protection, Sajedi & Bahramishad, 63776 (IRAN)
Malva verticillata L.	Prov. Bushehr, Jazireh Farsi, Sangari & Tehrani, 25931 (IRAN)
Malvalthaea transcaucasica (sosn.) Iljin.	Prov. Golestan, Azad Shahr, Mirzayans, 30865 (IRAN)
Malvella sherardiana (L.)	Prov. Ardebil, Moghan, Aslandouz, 67792 (IRAN)
Tilia begonifolia Stev.	Prov. Golestan, Jangal Golestan, Jangal Gol Loveh to Jangal Naleyn, Iranshahr & Zargani, 42256 (IRAN)
Tilia cordata Miller	Prov. Tehran, Iranshahr, 42262 (IRAN)
Tilia rubra Dc.	Prov. Golestan, Jangal Golestan, Tangeh Rah to Tangeh Gol, Termeh, 42260 (IRAN)

(prolate), *Tilia cordata,* and *Tilia rubra* (suboblate). Apertures included tricolporate (*Tilia cordata* and *Tilia rubra*) to pantaporate (*Malvella sherardiana, Malva verticillate* L.*, Malvalthaea transcaucasica,* and *Alcea sulphurea*). Sculpturing was comprised of echinate, microechinate, baculate, granulate, and perforate types. The equatorial axis explained the variation from 41 to 124 µm in ornamentation, including granulate, perforate, and verrucate.

The UPGMA trees of pollen characters (Fig. 1) showed a relatively high cophenetic correlation (r >0.80). PCA analysis based on palynological variables showed that the first and second components covered about 85% of the total variance (Fig. 1). These characters had the highest correlation value (>0.7) with this axis (Table 2). The UPGMA tree is generally divided into two main clades; PCA analysis shows that pollen shape (prolate or suboblate against spheroidal) differentiates between these two main groups. The first clade contains both subfamilies Grewioideae and Tilioideae (traditionally belonging to the family Tiliaceae) and two separate subclades. The first subclade includes the *Tilia* L. species (subfamily Tilioideae), which have suboblate tricolporate pollen grains with short colpi (brevicolpate) and

Table 2. Qualitative and quantitative palynological features in investigated Malvaceae

Species	Ed[1] (µm)	Sh[2] (µm)	Sbd[3] (µm)	Cl[4] (µm)	CW[5] (µm)	Sbs[6]	Ss[7]	Ps[8]	Pc[9]	Ts[10]
Abutilon fruticosum	50.2–56.6 (52.8)	6.1–11.4 (8.5)	5–8.5 (6.5)	–	–	Bolbous	Flask shape	Spheroidal	3-Zonoporate	Echinate, granulate
Abutilon hirtum	43.8–54.4 (49.2)	4.5–5.8 (5.2)	4.6–10 (6.2)	–		Bolbous	Flask shape	Spheroidal	3-Zonoporate	Echinate, perforate
Abutilon muticum	47.3–60.4 (52.1)	3.3–5.9 (5)	5.9–8.2 (7.3)	–	–	Bolbous	Flask shape	Spheroidal	3-Zonoporate	Echinate, granulate, perforate-
Abutilon teufrasti	41–48.5 (44.9)	4.1–6.2 (5)	6.4–12.6 (8.3)	–	–	Bolbous	Flask shape	Spheroidal	3-Zonoporate	Echinate, microechinate, granulate
Alcea angulata	95.4–106.5 (102.7)	8.3–12.5 (10.2)	12.1–17.2 (14.5)	–	–	Flat	Conical with rounded apices	Spheroidal	Pantoporate	Echinate, baculate, granulate
Alcea assadi	100.9–108.5 (105.2)	7.5–11.4 (9.4)	9.1–16.4 (12.7)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate
Alcea aucheri	103.4–123.3 (113.8)	7.8–13.2 (10.1)	8.5–21.4 (14.7)	–	–	Flat	Conical with rounded apices	Spheroidal	Pantoporate	Echinate
Alcea gorganica	100.6–111.9 (104.7)	9.5–14.8 (12.3)	10.7–22.4 (14.8)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate
Alcea hyrcana	91.7–117.7 (104.9)	7.7–12.7 (9.4)	9.6–19.8 (13.7)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, baculate
	(79)	(10)	(8.6)							
Althaea hirsuta	97.7–120.4 (108.3)	9.3–12.2 (10.7)	5.1–11.5 (9.1)	–	–	Bolbous	Flask shape	Spheroidal	Pantoporate	Echinate
Gossypium herbaceum	76.8–95.2 (88.0)	7.9–11.4 (9.8)	10.6–17.8 (13.7)	–	–	Bolbous	Flask shape	Spheroidal	Pantoporate	Echinate, granulate, perforate
Grewia makranica	45.2–48.1 (46.65)	–	–	10.1–10.4 (10.2)	2.3–2.5 (2.4)	–	–	Prolate	Tricolporate	Reticulate, perforate
Hibiscus mutabilis	88.5–110.9 (102.9)	5.3–13.5 (10.3)	7.3–14.5 (10.3)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, microechinata
Lavatera punctate	95.4–117 (106.7)	8.1–13 (10.2)	7.2–15.3 (10.7)	–	–	Flat	Conical with rounded apices	Spheroidal	Pantoporate	Echinate, microechinata
Malva neglecta	58.2–68.8 (64)	3.6–7.6 (5.4)	3.2–8 (5.1)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, microechinata
Malva nicaensis	72.3–80.6 (75.5)	3.9–8.1 (5.9)	4.2–10.6 (6.7)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, microechinata
Malva sylvestris	77.1–87.6 (84.2)	4.5–9.8 (6.8)	6.1–11.9 (9)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate
Malva verticellata	56.8–62.3 (59.5)	3.8–6 (4.6)	4.8–9.6 (6.5)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, microechinata
Malvalthaea transcaucasica	86.7–108.7 (94.6)	2.6–11.1 (7.4)	5.2–12.1 (7.9)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, verrucate
	(79)	(10)	(8.6)							
Althaea hirsuta	97.7–120.4 (108.3)	9.3–12.2 (10.7)	5.1–11.5 (9.1)	–	–	Bolbous	Flask shape	Spheroidal	Pantoporate	Echinate
Gossypium herbaceum	76.8–95.2 (88.0)	7.9–11.4 (9.8)	10.6–17.8 (13.7)	–	–	Bolbous	Flask shape	Spheroidal	Pantoporate	Echinate, granulate, perforate
Grewia makranica	45.2–48.1 (46.65)	–	–	10.1–10.4 (10.2)	2.3–2.5 (2.4)	–	–	Prolate	Tricolporate	Reticulate, perforate
Hibiscus mutabilis	88.5–110.9 (102.9)	5.3–13.5 (10.3)	7.3–14.5 (10.3)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, microechinata
Lavatera punctate	95.4–117 (106.7)	8.1–13 (10.2)	7.2–15.3 (10.7)	–	–	Flat	Conical with rounded apices	Spheroidal	Pantoporate	Echinate, microechinata
Malva neglecta	58.2–68.8 (64)	3.6–7.6 (5.4)	3.2–8 (5.1)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, microechinata
Malva nicaensis	72.3–80.6 (75.5)	3.9–8.1 (5.9)	4.2–10.6 (6.7)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, microechinata
Malva sylvestris	77.1–87.6 (84.2)	4.5–9.8 (6.8)	6.1–11.9 (9)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate
Malva verticellata	56.8–62.3 (59.5)	3.8–6 (4.6)	4.8–9.6 (6.5)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, microechinata
Malvalthaea transcaucasica	86.7–108.7 (94.6)	2.6–11.1 (7.4)	5.2–12.1 (7.9)	–	–	Flat	Conical with acuminate apices	Spheroidal	Pantoporate	Echinate, verrucate
Malvella sherardiana	36.1–53.7 (42.1)	3.5–5.2 (4.4)	5.6–9.3 (7.4)	–	–	Bolbous	Flask shape	Spheroidal	Pantoporate	Echinate, granulate
Tilia begonifolia	36–38.4 (36.9)	–	–	8.1–8.4 (8.2)	2–2.6 (2.3)	–	–	Suboblate	Tricolporate	Reticulate, perforate
Tilia cordata	35–38 (36.3)	–	–	9.7–12 (10.6)	3.6–5.6 (4.8)	–	–	Suboblate	tricolporate	Reticulate, perforate
Tilia rubra	38.1–43.9 (40.68)	–	–	8.3–8.4 (8.4)	5.3–6.5 (5.8)	–	–	Suboblate	Tricolporate	Reticulate, perforate

1: equatorial diameter in polar view, 2: spine height, 3: spine base distance, 4: colpus length, 5: colpus width, 6: spine base shape, 7: spine shape, 8: pollen Shape, 9: pollen class, 10: tectum sculpture reticulate-perforate sculpturing (Fig. 2 a-l). The second subclade contains *Grewia* L. species (subfamily Grewioideae), which have prolate tricolporate pollen grains with long colpi and reticulate-perforate sculpturing (Fig. 2 m-p).

The second clade contains all genera belonging to the subfamily Malvoideae. Pollen grains in this group are spherical-globular, and the tectum sculpture is variable; it was echinate in all genera, microechinate in a few genera (e.g., *Abutilon* mill (Fig. 3 b, j), and *Malva* (Fig. 3 r), baculate only in *Alcea* species (Fig. 4 n, t), sometimes granulate (Fig. 3 f, h), and also perforate (Fig. 3 d). The spines were evenly distributed on the entire pollen surface and varied in height, base, and interspinal distance.

The subfamily Malvoideae is also clustered in two separate subclades. PCA analysis showed that these two groups emerge based on the presence (Fig. 3 b, d, f, h; Fig. 4 B, j) or absence (Fig. 4 d, f, h; Fig. 5 a-t) of the subglobose pattern at the base of echinae.

The largest and smallest pollen grains were seen in *Alcea* (133.6 µm) and *Malvella* (36 µm), respectively. The highest spines were present in *Alcea* and *Hibiscus* with an average of 10.35 µm, and the shortest one was seen in *Malvella* (4.4 µm). Maximum spine base distances were found in *Gossypium* (17.8 µm) and *Alcea* (25.4 µm), with *Malva* displaying the shortest (3.2 µm).

Moreover, there are three general spine types; flask-shaped in pollen grains, in *Abutilon*, *Gossypium*, *Althaea* and *Malvella* (Fig. 3 a-l; Fig. 4 a-b and i-j), Conical with a rounded end in *Lavatera* and some species of *Alcea* (Fig. 4 f, p) and Conical with a pointed end in *Malva*, *Hibiscus*, *Malvalthaea* Iljin, and some other species of *Alcea* (Fig. 4 d, h; Fig. 5 F, r). The spines are conical with straight sides in most cases and curved in fewer cases (Figs. 3-l and 5-l). Curved spines are not unique to one genus or species; they may be seen mixed with other spines in different species or pollen grains.

Detailed pollen morphological features of the investigated taxa are summarized in Table 2 and a general description of each genus is as follows.

Abutilon

Spheroidal; 3-zonoporate, tectum sculpture echinate, microechinate, granulate, perforate; Equatorial diameter in polar view 41–60.4 µm, spine height 3.3–11.4 (5.9) µm; spine base bulbous; spines base distance 4.6 –12.6 (7.7) µm

Althaea

Spheroidal; pantoporate, tectum sculpture echinate, equatorial diameter in polar view 71.7–120.4 µm, spine height 7.6–12.2 µm, spine base bulbous, spines base distance is 5.1–12.9 (8.9) µm.

Gossypium

Spheroidal; pantoporate; tectum sculpture echinate, granulate, perforate, equatorial diameter in polar view 76.8–95.2 (88) µm, spine height 7.9–11.4 (9.8) µm, spine base bulbous; spine base distance is 10.6–17.8 (13.7) µm.

Hibiscus

Spheroidal; pantoporate; tectum sculpture echinate, microechinate; equatorial diameter in polar view 88.5–110.9 (102.9) µm, spine height 5.3–13.5 (10.3) µm, spine base flat; Spines base distance 7.3–14.5 (10.3).

Lavatera

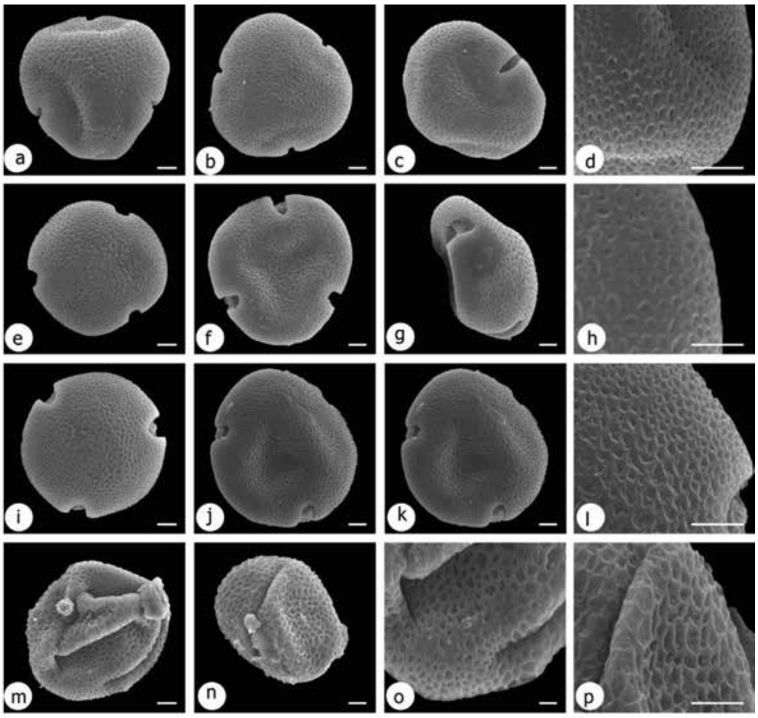

Fig. 2. SEM micrographs of pollen grains, a-b: *Tilia begonifolia*, c-d: *Tilia cordata*, e-f: *Tilia rubra*, g-h: *Grewia makranica*. Scale bar 20 µm

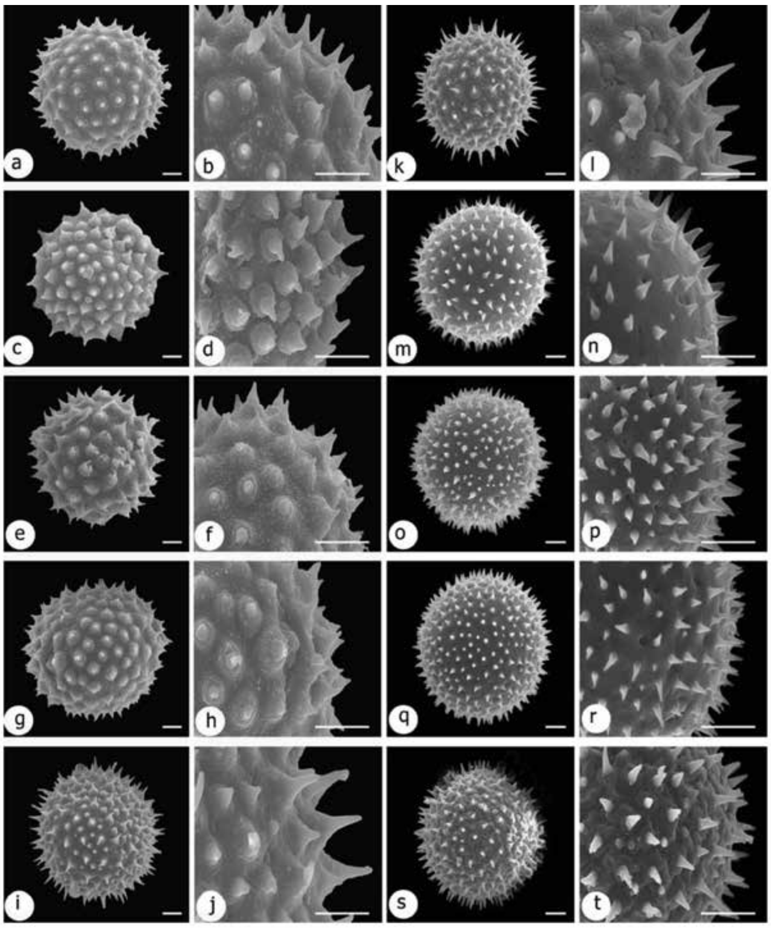

Fig. 3. SEM micrographs of pollen grains, a-b: *Abutilon fruticosum*, c-d: *Abutilon hirtum*, e-f: *Abutilon theuphrasti*, g-h: *Abutilon muticum*, i-j: *Althaea armeniaca*, k-l: *Althaea officinalis*, m-n: *Malva neglecta*, o-p: *Malva nicaensis*, q-r: *Malva sylvestrs*, s-t: *Malva verticillata*. Scale bar 20 µm

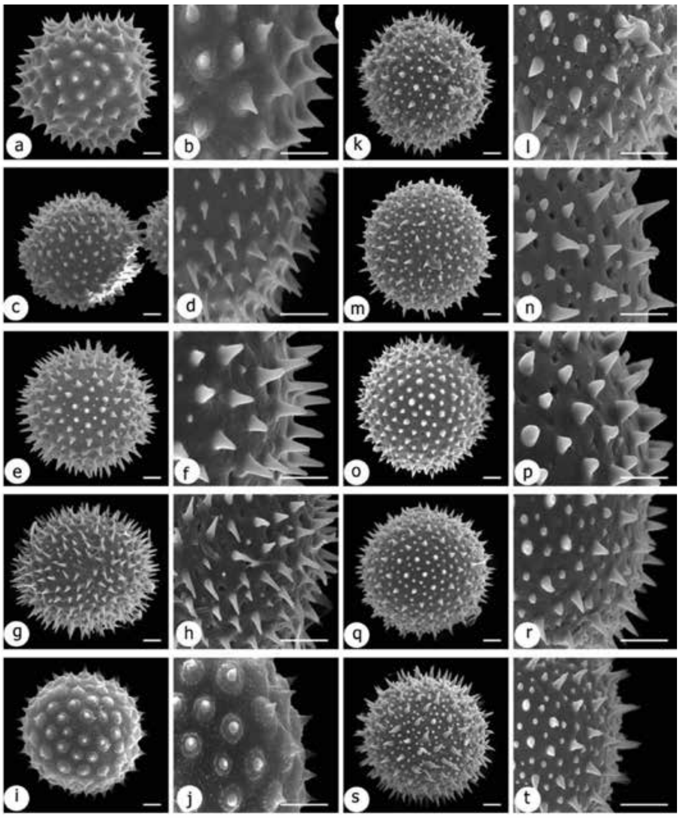

Fig. 4. SEM micrographs of pollen grains, a-b: *Gossypium herbaceum*, c-d: *Hibiscus mutabilis*, e-f: *Lavatera punctate*, g-h: *Malvathaea transcaucasica*, i-j: *Malvella sherardiana*, k-l: *Alcea angulata*, m-n: *Alcea assadi*, o-p: *Alcea aucheri*, q-r: *Alcea popovii*, s-t: *Alcea gorganica*. Scale bar 20 µm

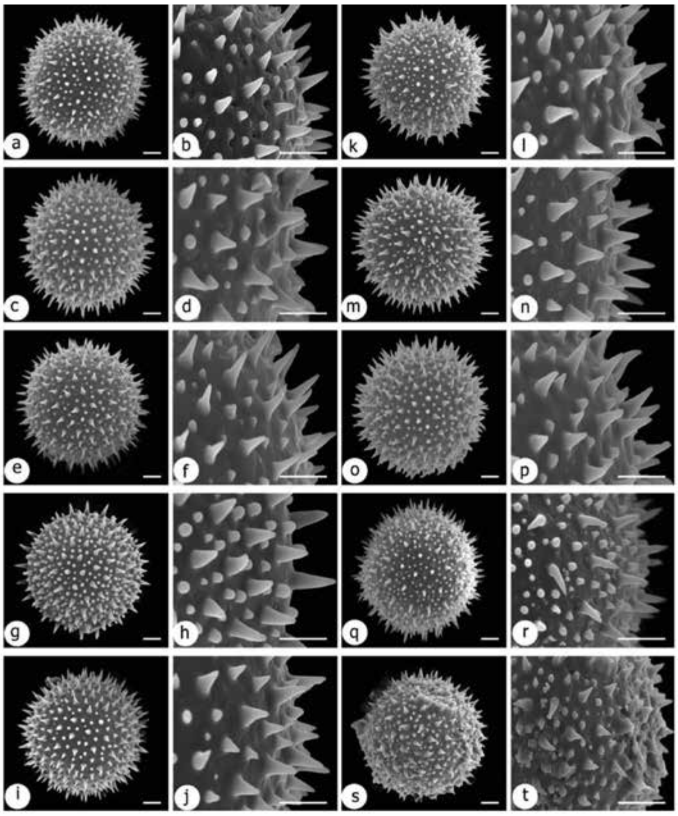

Fig. 5. SEM micrographs of Pollen grains, a-b: *Alcea koelzii*, c-d: *Alcea mozaffarianii*, e-f: *Alcea sachsachanica*, g-h: *Alcea sulphurea*, i-j: *Alcea kurdica*, k-l: *Alcea wilhelminae*, m-n: *Alcea longipedicellata*, o-p: *Alcea rhyticarpa*, q-r: *Alcea tarica*, s-t: *Alcea hyrcana*. Scale bar 20 µm

Spheroidal; pantoporate, tectum sculpture echinate, microechinate, equatorial diameter in polar view 95.4–117 (106.7) µm, spine height 8.1–13 (10.2) µm; spine base flat; spines base distance 7.2–15.3 (10.7) µm.

Malva

Spheroidal; pntoporate; tectum sculpture echinate, microechinate, equatorial diameter in polar view 56.8–87.6 (70.8) µm, spine height 3.6–9.8 (5.6) µm, spine base flat; spines base distance is 3.2–11.9 (6.8) µm.

Malvalthaea

Spheroidal; pantoporate, tectum sculpture echinate, equatorial diameter in polar view 86.7–108.7 (94.6) µm, spine height 2.6–11.1 (7.4) µm, spine base flat, spines base distance is 5.2–12.1 (7.9) µm.

Malvella

Spheroidal; pantoporate, tectum sculpture echinate, granulate, equatorial diameter in polar view 36.1–53.7 (42.1) µm, spine height 3.5–5.2 (4.4) µm, spine base bulbous; spines base distance is 5.6–9.3 (7.4) µm.

Alcea

Spheroidal; pantoporate; tectum sculpture echinate, microechinate, baculate, granulate, Equatorial diameter in polar view 91.7–124 (100.2) µm, spine height 3.4–15.4 (10.35) µm, spine base flat, spines base distance 6.6–25.4)13.5) µm.

Tilia

Pollen grains are tricolporate with short colpi (brevicolpate), sculpturing is reticulate–perforate, equatorial diameter in polar view 35–43.9 (37.9) µm, colpus length 8.1–12 (9) µm, colpus width 2.2–6.5(4.3) µm.

Grewia

Pollen grains are prolate and tricolporate with long colpi, sculpturing is reticulate–perforate. equatorial diameter in polar view is 41.8–45.2 (46.6) µm, and pollen width is 38.3–45.9 (42.1) µm.

A diagnostic key for pollen of Malvaceae in a scale of Iran

1-Pollen grains reticulate-perforate, sub-oblate..*Tilia*

2-Pollen grains micro-echinate, echinate, accurate, granulate, perforate, spheroidal...3

3-spine shape flask shape, spine base bulbous...4

-spine conical with rounded apices, spine base flat.........................*Alcea, Gossypium, Hibiscus, lavatera, Malva, Malvalthaea*

4- zonoporate, spheroidal.............. *Abutilon*

-pantaporate,tricolporate............................5

5-pantaporate, spheroidal..............*Malvella, Lavatera, Althaea*

-tricolporate, prolate.........................*Grewia*

Discussion

The current investigation presents the most comprehensive palynological study on Iranian Malvoides. It placed greater focus on *Alcea* as the largest genera of this family with many endemic species in Iran. Unlike previous studies that have palynologically considered Malvaceae to be a stenopalynous family with uniform pollen characteristics (Tahavi, 2000), the current study regards the new definition of the family comprising Malvoideae, Tilioideae, and Grewioideae and considers it to be a relatively eurypalynous family. The current results confirm those of previous studies that found Malvoideae pollen grains to be spheroidal with echinate sculpture, tricolporate pollen grains with short colpi present in Tilioideae, and tricolporate pollen grains with long colpi present in the Grewioideae subfamily (Erdtman, 1952; Perveen et al., 1994; El Naggar, 2004; Bibi, 2010; Bibi, 2010; Shaheen, 2010). The monophyly of the core Malvaceae was supported by several features (Judd and Manchester, 2016). Tribe Malveae includes eight genera (*Alcea*, *Althaea*, *Sida* L., *Abutilon*, *Malvella* Jauband Spach, *Lavatera*, *Malva*, and *Malvalthaea*) and displays the majority of the morphological and taxonomic diversity among Malvaceae in Iran. This tribe is a geographically, chromosomally, and morphologically diverse clade (Bates, 1968; Bates and Blanchard, 1970). Several of the morphological characters traditionally used in this tribe, in particular features of the epicalyx and life form, are hampered by extensive homoplasy, which creates many taxonomic problems in this tribe (Escobar Garcia et al., 2009).

Researchers disagree about the importance of palynological characters in determining taxonomic boundaries. Some consider them to be distinctive characters utilizable in generic delimitation in the family Malvaceae (Saad, 1960), while others believe that these characters do not benefit by distinguishing between the genera in this family (Christensen 1986). The current results have revealed that variations in pollen characters are the most useful features for the delimitation of subfamilies, although some characters show efficiency in generic and specific levels. Moreover, such differentiation is supported by cladistic analyses (Eumalvoideae of Baum et al. 2004, Alverson et al. 1998, Bayer et al. 1999, Bayer & Kubitzki, 2003, Baum et al. 2004, Judd and Manchester, 2016).

Some qualitative traits in pollen grains are unique to one or a few genera, for example, *Abutilon* has distinct pollen grains that are 3–4 zonoporate in contrast with all other investigated genera which have pantoporate pollen grains (Christensen, 1986). The baculate structure is present only in *Alcea,* and the subglobose pattern at the base of echinae is present in *Abutilon*, *Althaea,* and *Malvella* (Cabi 2009). Following the study of El Naggar (2004) on Egyptian Malvaceae members, spines show reliable variations in size, shape, and surface distribution, providing useful traits at different taxonomic levels. Spine length may be monomorphic, as in most species of tribes Hibiscieae, or it may vary on the same grain, giving a dimorphic pattern as in species of the tribe Malveae. Conical spines with rounded ends are found in *Lavatera* and some species of *Alcea,* whereas those with pointed ends are present in *Malva*, *Hibiscus*, *Malvalthaea,* and some other species of *Alcea*.

In contrast with El Naggar (2004), who stated that spine base distances vary from species to species, the current results showed a relatively constant trait within genera; nonetheless, it is a changing trait among different genera. For example, it ranges from 7.3 to 14.5 µm in *Hibiscus* but is found in smaller amounts in *Malva* and *Abutilon* (3.2–11.9 µm).

Our results showed that there is relatively high uniformity in terms of palynology in several genera of this family which follows Bibi et al. (2010), and Tahavi (2000). and

Aiman Ahmad Juhari et al. (2021). Saad (1960) studied the pollen morphology of 35 species of Malvaceae. He emphasized the importance of the aperture and spine characteristics, as well as exine stratification, to distinguish between different taxa Based on Saad (1960), there is a correlation between pollen size and chromosome number. Accordingly, Christensen (1986) believes that small pollen size is an underived trait compared with a large one. The tribe Hibiscieae, including *Hibiscus,* has been observed to have larger pollen grains as well as larger chromosome numbers compared to other tribes and genera in the family Malvaceae (Youngman, 1927; Ford, 1938; Tahavi, 2000; El Naggar, 2004). The current results confirm these findings. Accordingly, the largest pollen grains (along with the highest number of chromosomes) were detected in some genera such as *Alcea*, *Althaea, Hibiscus* L.*,* and *Lavatera* L. from Malvoideae, as reported in previous studies (Youngman, 1927; Ford, 1938; Tahavi, 2000; El Naggar, 2004). The smallest pollen grains were found to belong to the Tilioideae and Grewioideae subfamilies.

Erdtman (1952) divided the family Tiliaceae into three based on pollen grain type; *Tilia*-type and *Grewia*-type were in *Tilia* and *Grewia*, respectively (Fig. 2). The different pollen types of these two genera add further support to the current classification of Malvaceae which recognizes the subfamilies Tilioideae and Grewioideae. Based on data from the current study, however, no character state in pollen grains was synapomorphic for the tribes identified in Malvoideae (Bayer and Kutbitzki, 2003).

Controversy has always existed among researchers regarding the delimitation as well as the separation or integration of the genera *Althaea* and *Alcea* (Tournefort, 1700, Willdenow 1800, Linnaeus 1789, Candolle 1824, Edlin 1935, Bentham and Hooker 1862, Alefeld 1862, Boissier 1867, Baker 1890, Iljin 1949). The present study focused especially on these two genera, and the findings revealed that *Alcea* and *Althaea* are two separate genera in terms of pollen characters such as staminal columns; fruit features also confirm this finding. The baculate structure is present only on the pollen grains of *Alcea*, distinguishing this genus from all others. Phylogenetic studies also support the distinctness of *Alcea* as suggested by morphology (Escobar Garcia 2009, 2012). Throughout the taxonomic history of the family Malvaceae, *Alcea* (the largest genera of this family in Iran) has always been one of the most challenging genera taxonomically among the flora of SW Asia (Zohary 1963 a, b, Riedl 1976, Townsend, 1980). To date, two infrageneric classifications in *Alcea* have been suggested by Boissier (1867) and Zohary (1963 a, b), who respectively classified *Alcea* in two and nine informal groups based on one or a combination of several morphological traits (such as leaf shape, indumentum, and mericarp features). The current results showed that pollen characters are relatively uniform within *Alcea* species and have no discriminative value at a specific level or in natural species groups. Previous palynological studies on *Alcea* have yielded similar results (Cabi et al. 2009). On the other hand, our results support the separation of *Alcea* from *Althaea* which is consistent with the results of Cabi et al. (2009). However, there are significant differences to separate the various species of this family as confirmed by Cabi et al. (2009), Bibi et al. (2010), and Khalik et al. (2021).

Phylogenetic analysis of the Malvadendrina clade (Malvaceae sl) based on plastid DNA sequences indicates that Malvatheca (including Bombacoideae and Malvoideae) are different taxa from Tilioideae and Grewioideae. Saad (1972) and Perveen (1993) also referred to Malvoideae as an advanced group because of the presence of both echinate and pantoporate pollen grains. Moreover, the echinate sculpturing of pollen in Malvoideae improved adhesion, thus causing it to adhere strongly to the hair of honeybees (Shoemaker 1908).

The molecular and morphological data strongly support the monophyly of the subfamily Malvoideae (Eumalvoideae of Baum et al. 2004) and divide it into three tribes: Gossypieae, Hibisceae, and Malveae (Judd and Manchester 1997, Alverson et al. 1998, Bayer et al. 1999, Bayer & Kubitzki 2003, Baum et al. 2004).

As the most diverse genus of Malvaceae in Iran (34 species), *Alcea* exhibits a considerable taxonomic complexity and is one of the most taxonomically challenging genera of Malvaceae in the flora of SW Asia because of its uniformity and pronounced morphological plasticity (Iljin 1949, Zohary 1963b, Riedl 1976, Townsend 1980, Pakravan 2001).

Therefore, based on the present results and comparison with basal taxa, the following evolutionary trends are suggested regarding the pollen features in Malvaceae. The tricolporate structure is primitive compared with the pantoporate structure,the presence of spines is greater than their absence, the presence of a few equatorially distributed pores is deemed more primitive than the typically abundant and dispersed ones, and The existence of a baculate structure in the majority of *Alcea* species is to be viewed as a derived condition in contrast to the lack of one.

The result of the study emphasizes that some palynological characteristics represent high systematic value and can be useful for the systematic differentiation of Malvaceae. However, the use of palynological evidence in conjunction with other characteristics, can be effective in addressing the systematic issues within this family.

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