

Pollen and Seed Morphology of the Genus *Hesperis* L. (Brassicaceae) in Turkey

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Abstract: Pollen and seed morphology were examined in 35 specimens representing 25 Turkish species of the taxonomically complex genus *Hesperis* L. by light and scanning electron microscopes. Three main types and 2 subtypes were recognized based on the seed coat surface, pollen shape, and exine sculpturing. The seed coat ornamentation of Type I was ocellate, and pollen shape was oblate-spheroidal. While Type II was represented by reticulate seed coat and prolate-spheroidal pollen shape, Type III had tuberculate seed coat. This study revealed that both palynological and seed morphological characters are of significant importance in the taxonomy of the genus.

Key Words: Cruciferae, *Hesperis*, morphology, pollen, seed, Turkey

Türkiye *Hesperis* L. Cinsinin Polen ve Tohum Morfolojisi

Özet: Taksonomik problemleri olan *Hesperis* L. cinsinin Türkiye'de yayılış gösteren 25 türüne ait 35 örneğin polen ve tohum yüzeyi morfolojisi ışık ve taramalı elektron mikroskobu ile çalışılmıştır. Tohum kabuğu yüzeyi, polen şekli ve ekzin skulpturuna göre üç ana tip ve iki alt tip saptanmıştır. Tip I'in tohum yüzeyi süsü ocellat, polen şekli oblat-siferoidal'dır. Tip II, retikülat tohum süsü ve prolat-siferoidal polen şekli ile, Tip III tüberkülat tohum yüzey süsü ile karakterize edilmiştir. Bu çalışma göstermiştir ki, hem palinolojik hemde tohum morfolojik karakterler cinsin taksonomik ayırımında öneme sahiptir.

Anahtar Sözcükler: Cruciferae, *Hesperis*, morfoloji, polen, tohum, Türkiye

Introduction

Hesperis L. is a genus widespread in a broad geographical area in the temperate climate of the northern hemisphere extending from South and Central Europe, Southwest Asia, Caucasia, to the mountainous regions of West China to Mongolia. The total number of taxa in the genus in the world is about 50 (Tzvelev, 1959; Dvorák 1980). It is represented by 14 species in Europe (Ball, 1964a), 11 species in Iran (Dvorák, 1968), 5

species in Iraq (Dvorák, 1980), and 3 species in Italy (Pignatti, 1982). In Turkey, the genus is represented by 27 species (Cullen, 1965; Davis et al., 1988; Duran 2005, 2008, 2006; Duran & Ocak 2005).

The genus was firstly revised by Andrzejowski (1821) and he placed the genus in a single section (*Deilosma* Andrz.). Later, the taxonomy of the genus was treated by several researchers and the genus was divided into various sections on the basis of morphological characters;

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2 sections (*Hesperidium* DC. and *Deilosma* Andr.) by De Candolle (1824), 3 sections (*Hesperidium*, *Deilosma* and *Pachycarpos* Fourn. Emend. Tzvelev) by Fournier (1866) and Tzvelev (1959), and 2 sections (sect. *Purpureae* Boiss. and *Lividae* Boiss.) by Boissier (1867). Dvorák (1973) separated it into 5 subgenera (*Hesperis*, *Mediterranea* Borbas, *Cvelevia* Dvorák, *Contorta* Dvorák and *Diaplectos* Dvorák). Cullen (1965) did not divide the species of the genus growing in Turkey into sections. Despite numerous studies on the infragenetic and infraspecific classification of the genus, problems have not been clarified yet (Fournier, 1866; Tzvelev, 1959; Hayek, 1927; Dvorák, 1968, 1973; Savulescu, 1955; Löve & Löve, 1967; Busch, 1939; Engler & Prantl, 1936; Pignatti, 1982; Boissier, 1867, 1888; Ball, 1964b; De Candolle, 1824; Borbas, 1902, 1903).

Pollen morphology has provided an approach to the systematic relationships among the genera of the Cruciferae (İnceoğlu & Karamustafa, 1977; Doğan & İnceoğlu, 1990; Brochmann, 1992). Dvorák (1965, 1966) previously examined pollen grains of 13 taxa of *Hesperis* (*H. novakii* Dvorák, *H. bicuspidata* (Willd.) Poir., *H. podocarpa* Boiss., *H. verroniana* Dvorák, *H. rechingeri* Dvorák, *H. siliqua-glandulosa* (Rahl) Dvorák, *H. sibirica* L., *H. sylvestris* Crantz., *H. pycnotricha* Borbas et Degen, *H. matronalis* L., *H. balansae* Forn., *H. pendula* DC. subsp. *campicarpa* (Boiss.) Dvorák, *H. pendula* DC. subsp. *pendula*). On the other hand, İnceoğlu and Karamustafa (1977) examined in detail the pollen of *H. pendula* by light microscopy in the context of their study pertaining to the pollen morphology of the Turkish members of the Cruciferae family.

Seed surface morphology also reflects natural selection and adaptation. Therefore, it is of systematic significance at generic and specific levels (Brochmann, 1992; Bernand, 2000; Koul et al., 2000).

Our objective is to examine the pollen and seed morphology of almost all Turkish *Hesperis* taxa recognized and to test their taxonomic value. This study attempts to make the systematics of the genus clearer.

Materials and Methods

Materials used for this study were collected from wild populations. Collectors and localities are shown in the specimens investigated below. The specimens of the plants are deposited in the Selçuk University Herbarium (KNYA).

Pollen slides were prepared using the technique of Wodehouse (1935). LM studies were performed using a Leitz-Wetzlar microscope. Measurements were based on 20 or more pollen grains per specimen. Ten seeds from each plant were measured for length and width under a stereomicroscope lens to the nearest 0.1 mm. For SEM studies, pollen grains and seeds were coated with gold for 4 min in a sputter-coater. Morphological observations were made in a Jeol 100 CXII electron microscope.

The pollen terminology adopted by Faegri and Iversen (1975) and Brochmann (1992), and shape classification follows that of Erdtman (1969) based on P/E ratio in Table 1. The seed terminology adopted by Murley (1951) and Koul et al. (2000) is followed. The Simpson and Roe graphical test (Van der Pluym & Hideux 1997) was used for statistical calculations.

Specimens Investigated

The list of the genus *Hesperis* taxa:

Section: *Cvelevia*

H. breviscapa Boiss.; B7 Erzincan, A.Duran 4825 & Akgul (KNYA).

H. kotschyi Boiss.; C5 Konya, A.Duran 5274 & Hamzaoglu (KNYA).

Section: *Hesperis*

H. armena Boiss.; C2 Muğla, A.Duran 5879 & Varol (KNYA).

H. pisidica Hub.-Mor.; C2 Antalya, A.Duran 4843 (KNYA).

H. bicuspidata (Willd.) Poir.; C3 Isparta, A.Duran 4578 & Sağıroğlu (KNYA); C5 Niğde, A.Duran 4491 & Adıgüzel (KNYA); B7 Erzincan, A.Duran 4830 & Akgül (KNYA).

H. ozcelikii A.Duran; C3 Isparta, A.Duran 4636, H.Özçelik & Sağıroğlu (KNYA).

H. cilicica Siehe ex Bornm; C3 Isparta, A.Duran 4639, Özçelik & Sağıroğlu (KNYA).

H. matronalis L. subsp. *matronalis*; A1 Kırklareli, A.Duran 5156 & Hamzaoglu (KNYA); A9 Ardahan, A.Duran 4987 (KNYA); A9 Artvin, A.Duran 4742 & Akgül (KNYA).

H. matronalis L. subsp. *adzharica* (Tzelev) Cullen; A9 Artvin, A.Duran 4751 & Akgül (KNYA); A6 Giresun, A.Duran 5546 & Kandemir (KNYA).

H. theophrasti Borbás subsp. *sintensisii* Dvorák; B1 Balıkesir, *A.Duran* 5641 & *Sagiroğlu* (KNYA).

H. buschiana Tzvelev; A8 Artvin, *A.Duran* 5237 & *Kandemir* (KNYA).

H. aspera Fourn.; A5 Kastamonu, *A.Duran* 5657 & *Hamzaoğlu* (KNYA).

Section: *Mediterranea*

H. schischkinii Tzvelev; B7 Erzincan, *A.Duran* 5234 (KNYA).

H. varolii A.Duran; C2 Muğla, *A.Duran* 4458 (KNYA).

H. tristis L.; A1 Kırklareli, *A.Duran* 5157 & *Hamzaoğlu* (KNYA, GAZI, ANK).

Section: *Delicate*

H. kitiana P.H.Davis; B8 Bingöl, *A.Duran* 4673 & *Akgül* (KNYA).

H. hedgei P.H.Davis & Kit Tan; C7 Urfa, *A.Duran* 5185 & *Hamzaoğlu* (KNYA).

Section: *Diaplectos*

H. novakii Dvorák; C8 Mardin, *A.Duran* 5043 & *Hamzaoğlu* (KNYA).

H. balansae Fourn.; A4 Kırıkkale, *A.Duran* 5856 & *Hamzaoğlu* (KNYA).

H. bottae Fourn.; B7 Elazığ, *A.Duran* 5182 & *Hamzaoğlu* (KNYA).

H. syriaca (DC.) Dvorák; C6 Gaziantep, *A.Duran* 5028 & *Hamzaoğlu* (KNYA); Gaziantep, *A.Duran* 5625 & *Hamzaoğlu* (KNYA).

Section: *Pachycarpus*

H. anatolica A.Duran; C5 Adana, *A.Duran* 4498 & *Adıgüzel* (KNYA).

H. persica Boiss.; B9 Van, *A.Duran* 5198 & *Hamzaoğlu* (KNYA).

H. podocarpa Boiss.; C6 Gaziantep, *A.Duran* 5031 & *Hamzaoğlu* (KNYA).

H. hamzaoglui A.Duran; C6 Osmaniye, *A.Duran* 5694 & *Hamzaoğlu* (KNYA).

H. pendula DC. subsp. *campicarpa* (Boiss.) Dvorák; B7 Malatya, *B.Yıldız* 11935 (KNYA).

H. pendula DC.; C2 Burdur, *A.Duran* 5266 & *Hamzaoğlu* (KNYA).

H. pendula DC.; C6 Kahramanmaraş, *A.Duran* 4964, *Sagiroğlu* & *Varol* (KNYA).

H. pendula DC.; A4 Ankara, *A.Duran* 5644 & *Hamzaoğlu* (KNYA).

Section: *Contorta*

H. cappadocica Fourn.; A7 Gümüşhane, *A.Duran* 5224 & *Kandemir* (KNYA).

Results

Pollen morphology

The main palynological features of the Turkish *Hesperis* taxa examined are summarized in Tables 1 and 2, and they are shown in Figure 1.

Size, symmetry and shape

The pollen grains of *Hesperis* are usually radially symmetrical and isopolar. The pollen grains of the genus is oblate-spheroidal, prolate-spheroidal, spheroidal and subprolate with the polar axes 15.2-30.2 μm and the equatorial axes 12.5-27.1 μm (Table 1 and Figure 1). The outline is elliptic in the equatorial optical section and circular in the meridional optical section (Figures 2-6).

Apertures

The pollen grains are inoperculate and usually tricolpate or rarely syncolpate or tetracolpate. Some species have shown heteromorphic characteristics. For example; both tricolpate and syncolpate pollen grains were observed in *Hesperis breviscapa* and *H. bottae*. Also, *H. matronalis* subsp. *matronalis* has tricolpate, syncolpate, and tetracolpate apertures (Figure 1D). Aperture membranes are generally psilate or rarely granulate (Figures. 2-6).

Exine

The exine is semitectate and 1.2-2 μm in thickness. The ectexine is slightly thicker than the endexine. Intine thickness ranges between 0.3 and 0.5 μm (Table 1). Reticulate sculpturing is observed in the *Hesperis* taxa: the lumen width is 0.5-2.5 μm . The pollen grains of genus *Hesperis* generally have regular and polygonal or rarely irregular and amorphous lumina (Table 2; Figures 2-3). However, only the section *Pachycarpus* and *Contorta* have generally irregular and amorphous or rarely regular polygonal (only *H. anatolica*) shaped lumina (Table 2; Figure 3). Murus width is 0.1-0.75 μm . The members of the sections *Hesperis* and *Mediterranea* have

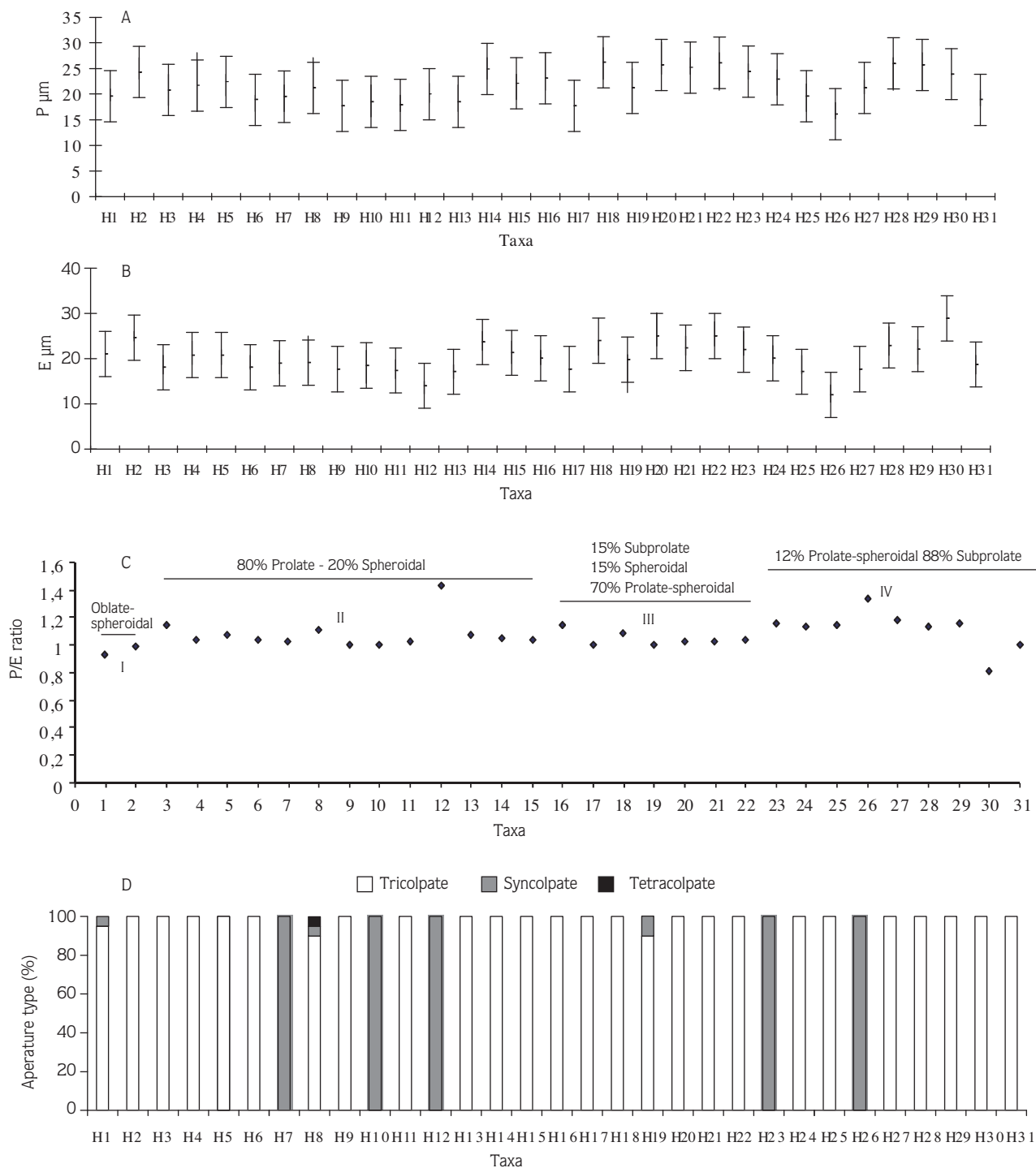


Figure 1. A: for P., B: for E., C: for P/E ratio, D: for Aperture type; Polar axes (P), Equatorial axes (E), and Aperture types for the taxa studied.

generally 4-5 sided and smooth muri (Table 2; Figure 2). Also, the members of the sections *Diaplectos* and *Delicate* have generally 4-5 sided and undulate muri (Table 2;

Figure 3). None of the species of the sections *Pachycarpus* and *Contorta* have 4-5 sided and smooth muri (Table 2; Figure 3).

Table 1. Pollen morphology of *Hesperis* (values in μm).

Taxa	Polar axes (P)						Equatorial axes (E)						P/E ratio and shape	Thickness	Ornamentation						Intine thickness	Aperture type	Pollen type
	min		mean		max		min		mean		max				Lumen width		Murus width						
	min	max	mean	min	max	mean	min	max	mean	min	max	min			max	min	max	min	max				
Section: Cvelevia																							
<i>H. breviscapa</i> (H1)	18.7	21	19.6	-	-	21	0.93	Oblate-spheroidal	1.5	Reticulate	0.75	2	1	0.4	1.2	0.75	0.5	95%Tricolpate 5%Syncolpate	Type I				
<i>H. kotschyi</i> (H2)	22.9	27.1	24.3	23.9	26	24.6	0.99	Oblate-spheroidal	1.7	Reticulate	1.5	2.25	2	0.15	1	0.5	0.3	Tricolpate	Type I				
Section: Hesperis																							
<i>H. armena</i> (H3)	17.8	23.9	20.8	16.6	20.8	18.1	1.15	Prolate-spheroidal	1.4	Reticulate	1	2	1.5	0.1	0.5	0.3	0.4	Tricolpate	Type II				
<i>H. pisidica</i> (H4)	16.6	28.1	21.7	18.7	23.9	20.8	1.04	Prolate-spheroidal	1.4	Reticulate	1.5	2.25	1.75	0.09	0.75	0.25	0.3	Tricolpate	Type II				
<i>H. bicuspidata</i> (H5)	19.7	23.9	22.4	18.7	22	20.8	1.08	Prolate-spheroidal	1.4	Reticulate	1	2	1.5	0.15	0.95	0.4	0.4	Tricolpate	Type II				
<i>H. özeleklii</i> (H6)	16.6	19.8	18.9	17.7	20.8	18.1	1.04	Prolate-spheroidal	1.5	Reticulate	1	3	2.25	0.085	0.5	0.25	0.5	Tricolpate	Type II				
<i>H. cilicia</i> (H7)	16.6	21.8	19.5	16.6	21.8	19	1.03	Prolate-spheroidal	1.2	Reticulate	0.75	2	1.15	0.1	0.5	0.35	0.5	Syncolpate	Type II				
<i>H. matronalis</i> subsp. <i>matronalis</i> (H8)	16.6	27.1	21.2	14.6	25	19.1	1.11	Prolate-spheroidal	1.4	Reticulate	0.75	2	1.25	0.2	0.65	0.5	0.5	90%Tricolpate 5%Syncolpate	Type II				
<i>H. theophrasti</i> subsp. <i>sintenisii</i> (H9)	-	-	17.7	-	-	17.7	1	Spheroidal	1.2	Reticulate	0.75	2	1.25	0.1	0.4	0.25	0.3	5%Tetracolpate Tricolpate	Type II				
<i>H. matronalis</i> subsp. <i>adzharica</i> (H10)	15.6	21.8	18.5	14.6	21.8	18.5	1	Spheroidal	1.2	Reticulate	0.25	1	0.5	0.1	0.6	0.35	0.3	Syncolpate	Type II				
<i>H. buschiana</i> (H11)	16.6	19.8	17.9	15.6	19.8	17.4	1.03	Prolate-spheroidal	1.2	Reticulate	0.75	2	1.75	0.5	1	0.75	0.3	Tricolpate	Type II				
<i>H. aspera</i> (H12)	18.4	22.1	20	12.2	15	14	1.43	Subprolate	1.4	Reticulate	1	2	1.75	0.05	0.25	0.12	0.3	Syncolpate	Type II				
Section: Mediterranea																							
<i>H. schischkini</i> (H13)	16.6	21.8	18.5	15.6	18.7	17.1	1.08	Prolate-spheroidal	1.3	Reticulate	1	2	1.5	0.25	0.75	0.5	0.3	Tricolpate	Type II				
<i>H. varolii</i> (H14)	22.9	27.1	24.9	21.8	26	23.7	1.05	Prolate-spheroidal	1.4	Reticulate	1	2	1.75	0.25	1	0.85	0.5	Tricolpate	Type II				
<i>H. tritis</i> (H15)	18.9	23.9	22.1	18.9	23.9	21.3	1.04	Prolate-spheroidal	1.3	Reticulate	1	1.5	1.25	0.25	0.75	0.5	0.5	Tricolpate	Type II				
Section: Delicate																							
<i>H. kitiiana</i> (H16)	20.8	28.1	23.1	18.7	21.8	20.1	1.15	Subprolate	1.6	Reticulate	0.5	1.25	1	0.5	1	0.75	0.5	Tricolpate	Type II				
<i>H. hedgeri</i> (H17)	-	-	17.7	-	-	17.7	1	Spheroidal	1.2	Reticulate	1	1.75	1.25	0.42	1	0.55	0.4	Tricolpate	Type II				
Section: Diaplectos																							
<i>H. novakii</i> (H18)	22.9	29.1	26.2	20.8	21.8	24	1.09	Prolate-spheroidal	1.8	Reticulate	1.75	2.5	2.25	0.25	0.75	0.6	0.3	Tricolpate	Type II				
<i>H. bottae</i> (H19)	16.6	25	21.2	12.5	20.9	19.8	1.01	Prolate-spheroidal	1.7	Reticulate	1.75	2.5	2	0.12	0.55	0.4	0.3	90%Tricolpate 10%Syncolpate	Type II				
<i>H. balanse</i> (H20)	23.9	30.2	25.7	22.8	30.2	25	1.03	Prolate-spheroidal	1.8	Reticulate	2	2.5	2.1	0.2	0.65	0.5	0.3	Tricolpate	Type II				
<i>H. syriaca</i> (A.Duran 5028) (H21)	23.9	27.1	25.2	20.8	25	22.4	1.03	Prolate-spheroidal	1.7	Reticulate	1.5	2	1.75	0.3	0.75	0.5	0.4	Tricolpate	Type II				
<i>H. syriaca</i> (A.Duran 5625) (H22)	20.8	28.1	26.1	22.8	28.1	25	1.04	Prolate-spheroidal	1.8	Reticulate	1.5	2	1.75	0.5	0.95	0.75	0.4	Tricolpate	Type II				
Section: Pachycarpus																							
<i>H. anatolica</i> (H23)	22.9	26	24.4	20.8	26	22	1.16	Subprolate	2	Reticulate	1.25	2	1.5	0.5	1	0.75	0.3	Syncolpate	Type II				
<i>H. persica</i> (H24)	19.8	24.7	22.9	18.9	22.9	20.1	1.14	Subprolate	1.7	Reticulate	0.75	1.5	0.95	0.4	1	0.75	0.5	Tricolpate	Type II				
<i>H. podocarpa</i> (H25)	16.6	22	19.6	16.6	20.8	17.1	1.15	Subprolate	1.5	Reticulate	0.75	2	1.15	0.2	0.55	0.35	0.3	Tricolpate	Type II				
<i>H. hamzaoglu</i> (H26)	15.2	18.4	16.1	10.4	14.2	12	1.34	Subprolate	1.7	Reticulate	0.75	2.5	1.25	0.1	0.5	0.25	0.5	Syncolpate	Type II				
<i>H. pendula</i> (A.Duran 5266) (H27)	20	22.8	21.2	-	-	17.7	1.19	Subprolate	1.6	Reticulate	0.75	2	1.25	0.2	0.6	0.35	0.3	Tricolpate	Type II				
<i>H. pendula</i> subsp. <i>complicarpa</i> (H28)	20.8	27.1	26	20.8	27.1	22.9	1.14	Subprolate	1.6	Reticulate	0.75	1.5	1.85	0.5	1.1	0.85	0.3	Tricolpate	Type II				
<i>H. pendula</i> (A.Duran 4964) (H29)	20.8	28.1	25.7	18.7	24.2	22.1	1.16	Subprolate	1.9	Reticulate	0.75	2	1.25	0.5	0.75	0.65	0.3	Tricolpate	Type II				
<i>H. pendula</i> (A.Duran 5644) (H30)	-	-	23.9	-	-	28.9	0.82	Subprolate	1.9	Reticulate	0.75	1.5	1.1	0.35	0.75	0.5	0.3	Tricolpate	Type II				
Section: Contorta																							
<i>H. cappadocica</i> (H31)	17.7	20.8	18.9	16.6	20.8	18.7	1.01	Prolate-spheroidal	1.3	Reticulate	0.75	1.5	0.95	0.25	0.75	0.5	0.3	Tricolpate	Type III				

Table 2. Microsculpturing features of reticulate pollen ornamentation (values in μm).

Taxa	Lumen				Murus						
	Width			Shape	Width			Shape			
	Min.	Max.	Mean		Min.	Max.	Mean	4-5 sided	Sharply angled	Smooth	Undulate
Section: Cvelevia (I)											
<i>H. breviscapa</i>	0.75	2	1	Irregular amorphous	0.4	1.2	0.75	-	-	+	-
<i>H. kotschyi</i>	1.5	2.25	2	Regular polygonal	0.15	1	0.5	+	+	+	-
Section: Hesperis (II)											
<i>H. armena</i>	1	2	1.5	Regular polygonal	0.1	0.5	0.3	+	-	+	-
<i>H. pisidica</i>	1.5	2.25	1.75	Regular polygonal	0.09	0.75	0.25	+	-	+	-
<i>H. bicuspidate</i>	1	2	1.5	Regular polygonal	0.15	0.95	0.4	+	-	+	-
<i>H. ozcelikii</i>	1	3	2.25	Regular polygonal	0.085	0.5	0.25	+	+	+	-
<i>H. cilicica</i>	0.75	2	1.15	Regular polygonal	0.1	0.5	0.35	+	+	+	-
<i>H. matronalis</i> subsp. <i>matronalis</i>	0.75	2	1.25	Irregular amorphous	0.2	0.65	0.5	-	-	+	-
<i>H. matronalis</i> subsp. <i>adzharica</i>	0.25	1	0.5	Irregular amorphous	0.1	0.6	0.35	-	-	+	-
<i>H. theophrasti</i> subsp. <i>sintensisii</i>	0.75	2	1.25	Irregular amorphous	0.1	0.4	0.25	-	-	+	-
<i>H. buschiana</i>	0.75	2	1.75	Regular polygonal	0.5	1	0.75	-	-	+	-
<i>H. aspera</i>	1	2	1.75	Regular polygonal	0.05	0.25	0.12	-	-	-	+
Section: Mediterranea											
<i>H. schischkinii</i>	1	2	1.5	Regular polygonal	0.25	0.75	0.5	-	-	+	-
<i>H. varolii</i>	1	2	1.75	Regular polygonal	0.25	1	0.85	+	-	+	-
<i>H. tritis</i>	1	1.5	1.25	Regular polygonal	0.25	0.75	0.5	+	+	+	-
Section: Delicate											
<i>H. kitiana</i>	0.5	1.25	1	Regular polygonal	0.5	1	0.75	+	-	+	-
<i>H. hedgei</i>	1	1.75	1.25	Regular polygonal	0.42	1	0.55	+	-	+	-
Section: Diaplectos											
<i>H. novakii</i>	1.75	2.5	2.25	Regular polygonal	0.25	0.75	0.6	+	-	-	+
<i>H. bottae</i>	1.75	2.5	2	Regular polygonal	0.12	0.55	0.4	+	-	-	+
<i>H. balanse</i>	2	2.5	2.1	Regular polygonal	0.2	0.65	0.5	+	-	-	+
<i>H. syriaca</i> (A.Duran 5028)	1.5	2	1.75	Regular polygonal	0.3	0.75	0.5	+	-	-	+
<i>H. syriaca</i> (A.Duran 5625)	1.5	2	1.75	Regular polygonal	0.5	0.95	0.75	+	-	-	+
Section: Pachycarpus											
<i>H. anatolica</i>	1.25	2	1.5	Regular polygonal	0.5	1	0.75	+	-	+	-
<i>H. persica</i>	0.75	1.5	0.95	Irregular amorphous	0.4	1	0.75	-	-	+	-
<i>H. podocarpa</i>	0.75	2	1.15	Irregular amorphous	0.2	0.55	0.35	-	-	+	-
<i>H. hamzaoglui</i>	0.75	2.5	1.25	Irregular amorphous	0.1	0.5	0.25	-	-	+	-
<i>H. pendula</i> (A.Duran 5266)	0.75	2	1.25	Irregular amorphous	0.2	0.6	0.35	-	-	+	-
<i>H. pendula</i> subsp. <i>compicarpa</i>	0.75	1.5	1.85	Irregular amorphous	0.5	1.1	0.85	-	-	+	-
<i>H. pendula</i> (A.Duran 4964)	0.75	2	1.25	Irregular amorphous	0.5	0.75	0.65	-	-	+	-
<i>H. pendula</i> (A.Duran 5644)	0.75	1.5	1.1	Irregular amorphous	0.35	0.75	0.5	-	-	+	-
Section: Contorta											
<i>H. cappadocica</i>	0.75	1.5	0.95	Irregular amorphous	0.25	0.75	0.3	-	-	+	-

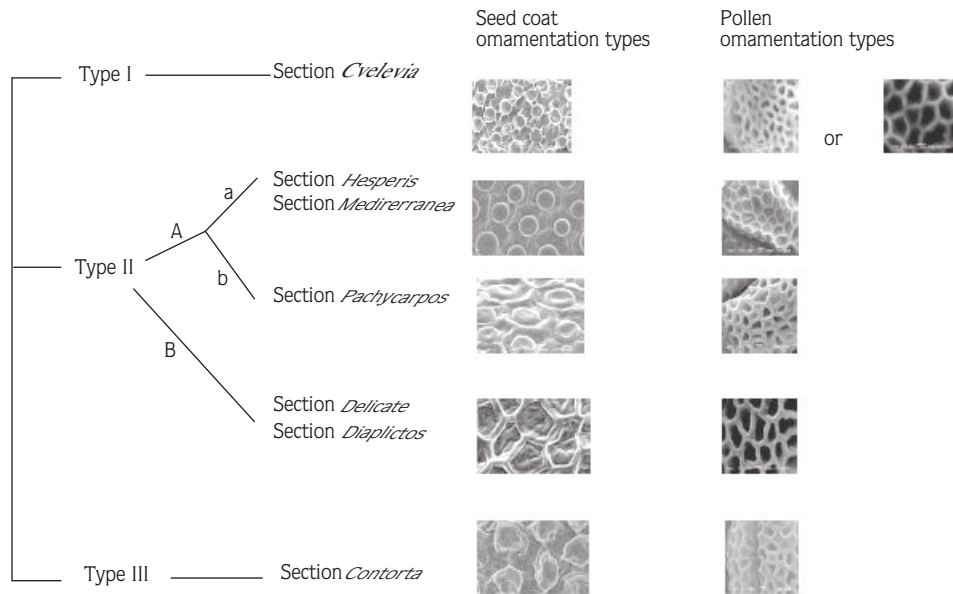


Figure 2. Seed and pollen ornamentation types observed in the sections of Turkish *Hesperis*.

Seed morphology

Homogeneity in seed size and shape was found among *Hesperis* taxa (Table 3). The largest seeds occur in *H. syriaca* (average 5.5 mm in length, 1.5 mm in width) and *H. varolii* (average 4.7 mm in length and 1.7 mm in width). The smallest seeds are found in *H. matronalis* subsp. *adzhарica* (average 1.9 mm in length and 1.25 mm in width) (Table 3). The shapes of the seeds are very similar to each other in general; elliptic to oblong with a visible hilum and a more or less perceptible furrow. Only in *H. breviscapa*, the outline of the seed is circular and in *H. varolii* is ovate. The colour of the seeds gives a complementary taxonomic indication (Brochmann, 1992; Bernand, 2000). It is yellowish or light brown only in *H. kotschyi* and is greenish to brownish in *H. pisidica*. The other taxa are brown-light brown or dark brown. By scanning electron microscopy, several types of ornamentation have been observed on surface structures. The salient features of the testa topographies of the various taxa examined are presented in Tables 3 and 4. The taxa are within the 3 basic types, i.e. ocellate (section *Cvelevia*), reticulate (sections *Hesperis*, *Mediterranea*, *Delicate* and *Pachycarpus*), and tuberculate (section *Contorta*) (Table 3). Those demonstrating reticulate

ornamentation are classified as taxa with papillae (Sections *Hesperis*, *Mediterranea* and *Pachycarpus*) and without papillae (only sections *Diaplictos* and *Delicate*) (Table 3; Figure 4). Taxa with papillae are classified as those with pitted papillae (*H. buschiana*, *H. aspera*, *H. schischkinii*, *H. anatolica*, *H. persica*, *H. padocarpa*, and *H. pendula*) and unpitted papillae (*H. armena*, *H. pisidica*, *H. ozcelikii*, *H. cilicica*, *H. matronalis* subsp. *matronalis*, *H. matronalis* subsp. *adzhарica*, *H. theophrasti* subsp. *sintensisii*, *H. varolii* and *H. tristis*) (Figure 4).

On the basis of seed and pollen ornamentation and pollen shape, 3 main types are recognized in the members of the genus *Hesperis* (Figure 5):

Type I: The seed coat ornamentation of this type is ocellate (Table 3; Figure 4). Pollen shape is oblate-spheroidal (Table 1; Figure 1C). The shape of the lumen in the pollen is either irregular and amorphous or regular and polygonal. Muri are smooth. This type has been observed in the section *Cvelevia* (Table 2; Figures 2, 5).

Type II: The seed coat ornamentation is reticulate (sections *Hesperis*, *Mediterranea*, *Delicate*, *Diaplictos*, and *Pachycarpus*). A further classification has been made on the basis of papillae, as those having papillae (Type IIA) (section *Hesperis*, *Mediterranea* and

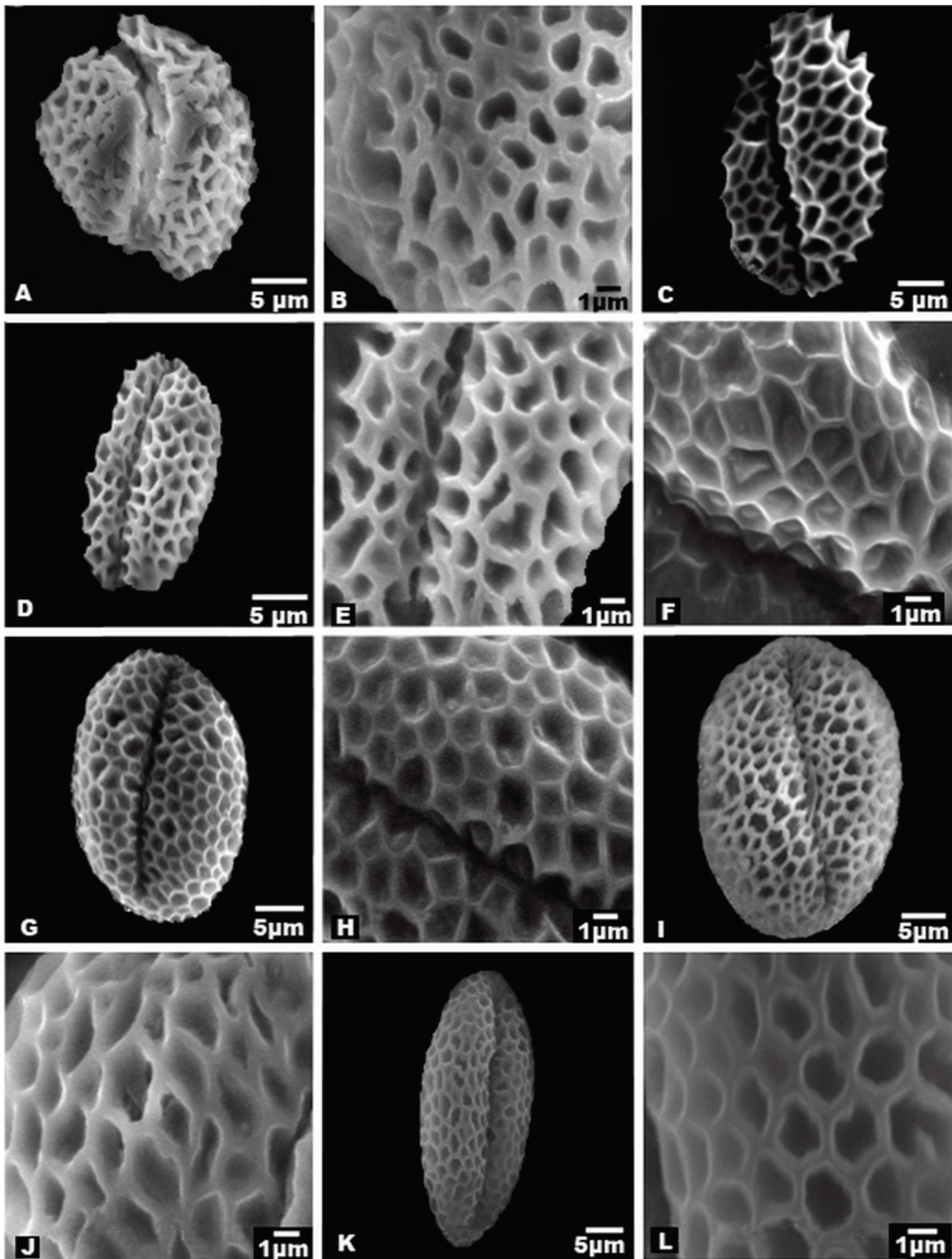


Figure 3. SEM photos of *Hesperis* pollen of The Type I and Type II. A-C Type I: A-B; *H. breviscapa*, C; *H. kotschyi*; Type II Aa: D-E; *H. bicuspidata*, F; *H. ozcelikii*, G-H; *H. cilicica*, I-J; *H. varolii*, K-L; *H. tritis*.

Table 3. Seed morphology of *Hesperis* L. Seed length and width (mm) are based on mean values.

Taxa	Length (L)	Width (W)	Length/Width	Outline	Colour	Ornamentation
Section: Cvelevia						
<i>H. breviscapa</i>	4	2	2	Circular	Dark brown	Ocellate
<i>H. kotschyi</i>	3.4	2.1	1.6	Elliptic	Yellowish or light brown	Ocellate
Section: Hesperis						
<i>H. armena</i>	3.1	1.25	2.5	Oblong	Dark brown	Reticulate
<i>H. pisidica</i>	3.5	1.75	2	Oblong	Greenish to brownish	Reticulate
<i>H. bicuspidata</i>	2.9	1.5	2	Oblong	Brown	Reticulate
<i>H. ozcelikii</i>	3	1.2	2.5	Oblong	Dark brown	Reticulate
<i>H. cilicica</i>	2.7	1.25	2.2	Oblong	Brown	Reticulate
<i>H. matronalis</i> subsp. <i>matronalis</i>	2.7	1.2	2.2	Elliptic	Brown to dark brown	Reticulate
<i>H. matronalis</i> subsp. <i>adzharica</i>	1.9	1.15	1.6	Elliptic	Dark brown	Reticulate
<i>H. theophrasti</i> subsp. <i>sintensisii</i>	2.5	1.25	2	Elliptic	Dark brown	Reticulate
<i>H. buschiana</i>	2.15	1	2.2	Oblong	Brown	Reticulate
<i>H. aspera</i>	2.3	1.2	1.9	Oblong	Dark brown	Reticulate
Section: Mediterranea						
<i>H. schischkinii</i>	2.9	1.4	2.1	Oblong	Dark brown	Reticulate
<i>H. varolii</i>	4.7	1.7	2.8	Ovate	Brown	Reticulate
<i>H. tritis</i>	3.2	1.3	2.5	Oblong	Dark brown	Reticulate
Section: Delicate						
<i>H. kitiana</i>	3.4	1.4	2.4	Elliptic	Dark brown	Reticulate
<i>H. hedgei</i>	3.5	1.3	2.7	Oblong	Brown	Reticulate
Section: Diaplectos						
<i>H. novakii</i>	3.5	1.5	2.3	Oblong	Brown	Reticulate
<i>H. bottae</i>	4.1	1.65	2.5	Oblong	Dark or light brown	Reticulate
<i>H. balanse</i>	3.7	1.4	2.6	Oblong	Brown	Reticulate
<i>H. syriaca</i>	5.5	1.5	3.7	Oblong	Brown	Reticulate
Section: Pachycarpus						
<i>H. anatolica</i>	3.6	1.3	2.8	Oblong	Brown	Reticulate
<i>H. persica</i>	2.8	1.3	2.2	Oblong	Brown	Reticulate
<i>H. podocarpa</i>	3.6	1.3	2.8	Oblong	Light brown	Reticulate
<i>H. hamzaoglui</i>	3.5	1.1	3.5	Oblong	Light brown	Reticulate
<i>H. pendula</i>	3.2	1.35	2.4	Oblong	Brown	Reticulate
Section: Concorta						
<i>H. cappadocica</i>	3.1	2.55	1.2	Elliptic	Brown or dark brown	Tuberculate

Pachycarpus) or not having papillae (Type IIB) (section *Delicate* and *Diaplectos*). Those with papillae are again classified as the ones with unpitted (Type IIAa) (section *Hesperis*, *Mediterranea*) or pitted papillae (Type IIAb) (section *Pachycarpus*) (Table 3; Figures 4 and 5). While the murus of the pollen is smooth in these types, it is

undulating in those without papilla. Besides, the lumen shape is generally irregular and amorphous in the pollen of those types with pitted papillae. Pollen shapes such as prolate-spheroidal or subprolate are a characteristic of this type as well (Table 2; Figures 2-3 and 5-6).

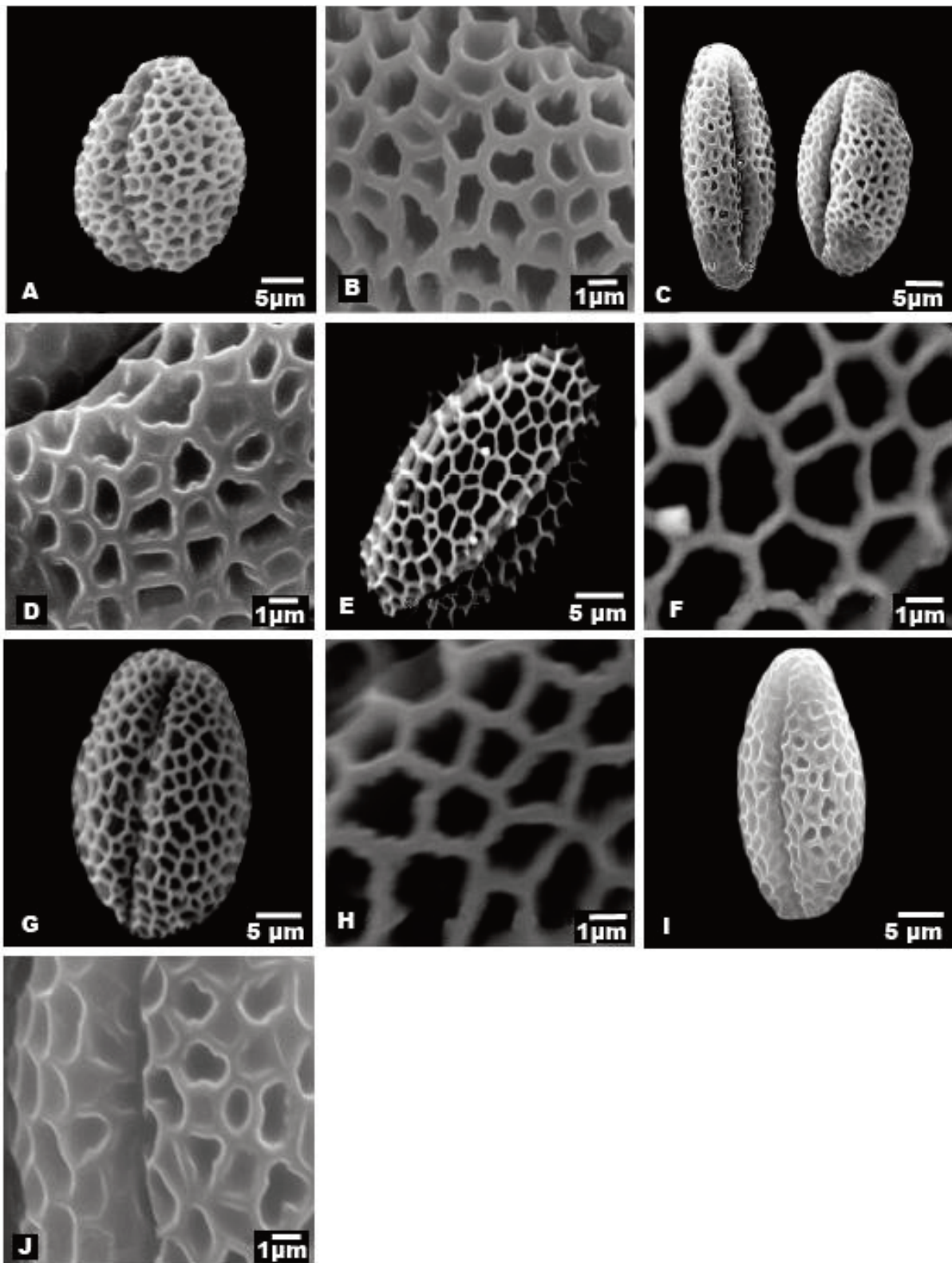


Figure 4. SEM photos of *Hesperis* pollen of The Type II and Type III. Type II Ab; A-B; *H. persica*, C-D; *H. podocarpa*; E-H Type II B; E-F; *H. balanse*, G-H; *H. syriaca*, I-J Type III; *H. cappadocica*.

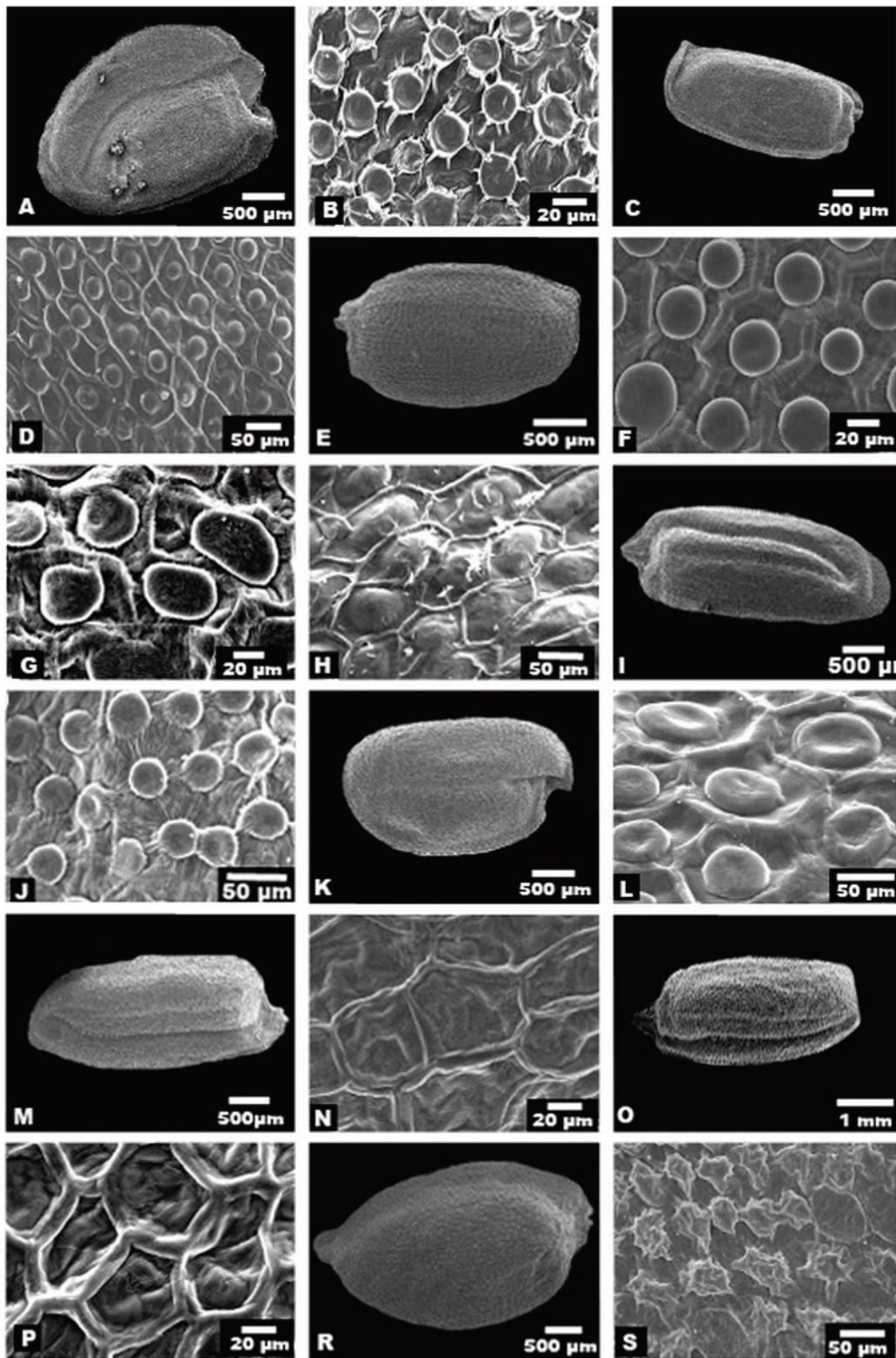


Figure 5. SEM photos of *Hesperis* seed of Type I, Type II and Type III; A-B Type I = *H. kotschyi*; C-H Type II Aa = C-D. *H. ozcelikii*; E-F. *H. aspera*, G. *H. tristis*, *H. varolii*; I-L Type II Ab = I-J. *H. anatolica*, K-L. *H. pendula*, M-P Type IIb; M-N = *H. hedgei*, O-P = *H. bottae*; R-S Type III = *H. cappadocica*.

Type III: The seed coat ornamentation is tuberculate. Among the taxa examined, only the section *Contorta* has this ornamentation. Pollen shape is prolate-spheroidal (Table 2; Figures 4-6).

Discussion

The pollen and seed morphology of the Turkish *Hesperis* taxa are taxonomically significant characters. The main pollen and seed morphological differences have been

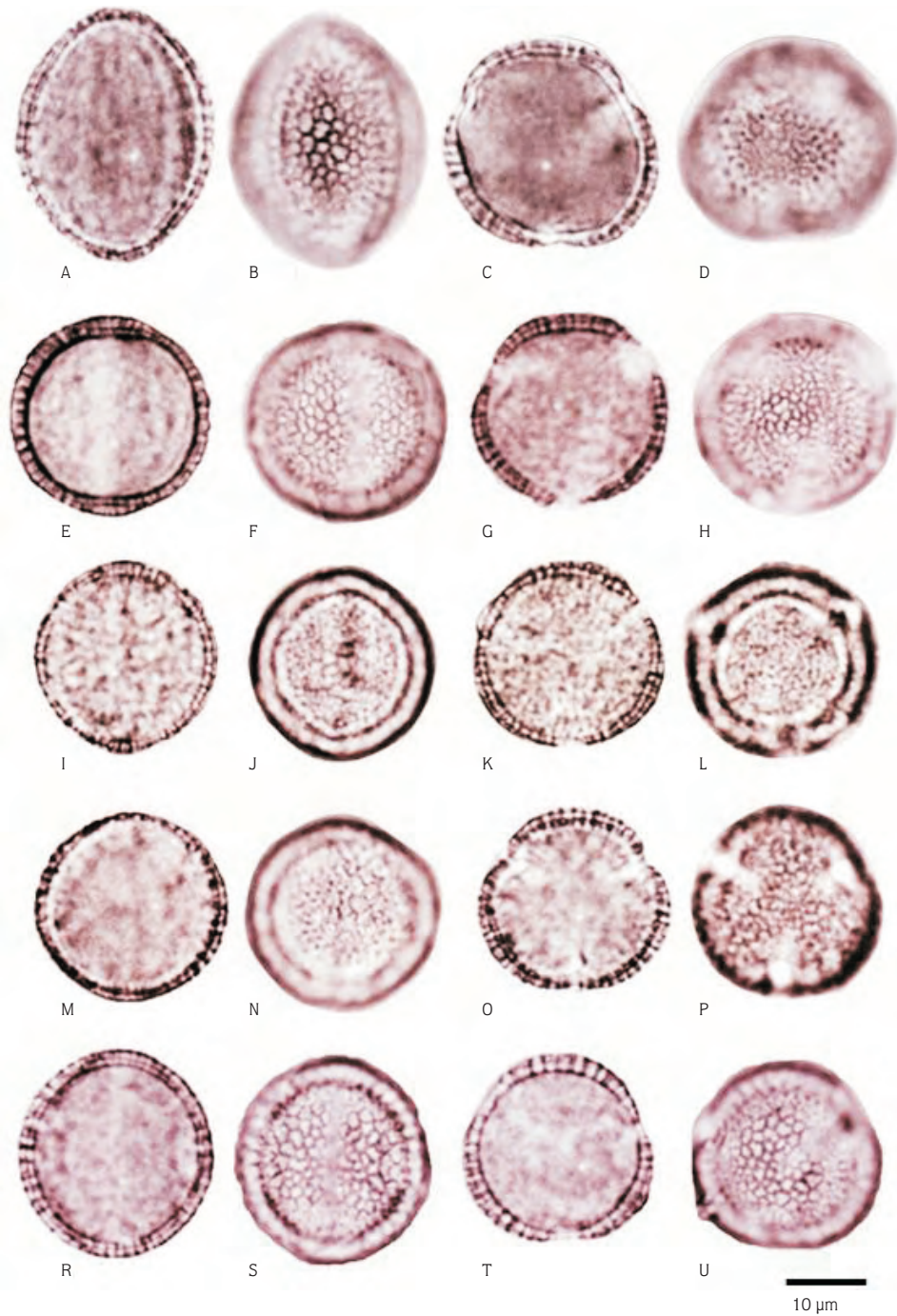


Figure 6. LM photos of *Hesperis* pollen of the Type I, Type II and III: A-D; *H. breviscapa* (Type I), E-H; *H. buschiana* (Type IIa), I-L; *H. podocarpa* (Type IIb), M-P; *H. hedgei* (Type IIb), R-U; *H. cappadocica* (Type III) (LM X 1000).

found at the section level, especially in pollen and seed types. Pollen and seed ornamentations are the most significant characters, which can be used to separate sections, in general. Three main types are recognized (Figure 5). The seed and pollen ornamentations and pollen shape are used to define the types because such features proved useful for ascertaining relationships among taxa (Brochmann, 1992). The seed ornamentation in Type I is ocellate and pollen shape oblate-spheroidal. Furthermore, 2 types of reticulate pollen ornamentations have been determined in which the lumen shape is either irregular and amorphous (*H. breviscapa*) or regular and polygonal (*H. kotschyi*). Type I has been determined in the section *Cvelevia*, which is considered as the most primitive among the sections of *Hesperis* (Tables 1-4; Figures 2, 4-6). In Type II, both pollen and seed ornamentations are reticulate. Pollen shape is prolate-spheroidal (Figure 6). Pitted papillae in the section *Pachycarpus* and unpitted ones in the sections *Hesperis* and *Mediterranea* were observed (Tables 3-4; Figure 5). In the reticulate pollen ornamentation of sections *Hesperis* and *Mediterranea*, the murus shape is smooth and the lumen is regular and amorphous. Also, in the sections *Pachycarpus* and *Contorta*, the murus shape is smooth and the lumen irregular and amorphous. Brochmann (1992) has also classified the genus *Draba* (Brassicaceae) pollen as 4 types on the basis of muri and lumina shapes. A reticulate ornamentation without papillae has been determined in the sections *Diaplectos* and *Delicate*. Koul et al. (2000) also considered reticulate ornamentation characters according to the existence or non-existence of papillae while classifying the subtribes Brassicinae, Raphaninae, and Moricandiinae. In the seed coat ornamentation without papillae, the murus shape of the pollen is undulate. The section *Contorta*, which exhibits a tuberculate seed coat ornamentation, is included within Type III.

In this study, we observed that while the primitive section *Cvelevia* has ocellate ornamentation, other sections have either reticulate or tuberculate ornamentation (Figure 5; Table 4).

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Cullen (1965) has not separated the genus into sections in his revision study on the Turkish *Hesperis*. The genus was separated into 7 sections. Due to the above mentioned variety in pollen and seed characters, it was determined that the separation of the genus into sections has been an accurate systematic classification (Figure 5).

In the analysis of the mean P and E values, the largest grains are found in *H. balansae* and Kızılcahamam population of *H. pendula* and the smallest P values are found in *H. novakii* and *H. pendula* subsp. *compicarpa* while the smallest E values are found in *H. aspera* (Table 1 and Figure 1).

In addition, the differences are also found in pollen shape. The pollen shapes of the sections are as follows: section *Cvelevia* 100% oblate-spheroidal; sections *Hesperis* and *Mediterranea* 80% prolate-spheroidal, 20% spheroidal; sections *Diaplectos* and *Delicate* 70% prolate-spheroidal, 15% subprolate and 15% spheroidal; *Pachycarpus* and *Contorta* 88% subprolate and 12% prolate-spheroidal (Figure 1). Brochmann (1992) has mentioned that aperture types do not have a significant role in the classification of the genus *Draba* L.

The seed shape in the members of the Turkish *Hesperis* taxa is found to be very closely related to the habitat ecology. It is shown that the species with elliptic seeds grow in montane steppes; those having circular seeds in ruderal areas, and those having oblong seeds grow on rocky and stony places. The analysis of the mean L (length) and W (width) values shows that the largest seeds occur in *H. syriaca* and *H. varolii* while the smallest L and W values are recorded for *H. matronalis* subsp. *adzharica* (Table 3).

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