

Pollen morphology of *Hymenosphace* and *Aethiopis* sections of the genus *Salvia* (Lamiaceae) in Turkey

Hülya ÖZLER^{1,*}, Sevil PEHLİVAN², Ferhat CELEP³, Musa DOĞAN⁴, Ahmet KAHRAMAN⁵,
Ahter YAVRU FİŞNE², Birol BAŞER⁶, Safi BAGHERPOUR⁴

¹Department of Biology, Faculty of Arts and Sciences, Sinop University, Sinop, Turkey

²Department of Biology, Faculty of Sciences, Gazi University, Ankara, Turkey

³Department of Biology, Faculty of Arts and Sciences, Nevşehir University, Nevşehir, Turkey

⁴Department of Biological Sciences, Middle East Technical University, Ankara, Turkey

⁵Department of Biology, Faculty of Arts and Sciences, Uşak University, Uşak, Turkey

⁶Department of Biology, Faculty of Arts and Sciences, Bitlis Eren University, Bitlis, Turkey

Received: 24.09.2012

Accepted: 21.07.2013

Published Online: 30.10.2013

Printed: 25.11.2013

Abstract: Palynological characteristics of 30 *Salvia* taxa in sections *Hymenosphace* and *Aethiopis* from Turkey were investigated by light and scanning electron microscopy. *S. aethiopis* (sect. *Aethiopis*) has the smallest pollen while *S. blepharochlaena* (sect. *Hymenosphace*) has the largest pollen. The basic shape of the pollen grains in most taxa is suboblate, oblate-spheroidal, or prolate-spheroidal to spheroidal; however, subprolate pollen grains are occasionally found in *S. cassia* of sect. *Aethiopis*. Hexocolpate pollen is dominant in all studied taxa, but heptacolpate and octacolpate pollen grains are mixed together in *S. palaestina* (heptacolpate, 20%) and *S. candidissima* subsp. *candidissima* (heptacolpate, 2% and octacolpate, 40%). The exine sculpturing is bireticulate (the common type) or reticulate-perforate. The bireticulate and the reticulate-perforate sculpturing patterns can be divided into subtypes according to the number of primary lumina. Taxonomic implications of the pollen data are also discussed.

Key words: *Salvia*, Labiate, pollen morphology, Turkey, light microscopy, scanning electron microscopy

1. Introduction

The morphologically diverse genus *Salvia* L. (Lamiaceae: tribe Mentheae) consists of approximately 1000 species (Harley et al., 2004). *Salvia* is separated from other genera of the tribe Mentheae by only 2 fertile stamens (Clasen-Bockhoff et al., 2004).

The first infrageneric delimitation for the genus was done by Bentham (1833). In the *Flora Orientalis*, Boissier (1875) adopted Bentham's classification and placed the Turkish *Salvia* species in 7 sections, namely the sections *Salvia* (syn. *Eusphace*), *Hymenosphace*, *Horminum*, *Aethiopis*, *Drymosphace*, *Plethiosphace*, and *Hemisphace*. Later, Hedge (1972) changed sect. *Eusphace* to sect. *Salvia*. The genus is represented by 86 species in the flora of Turkey (Hedge, 1982). Since its publication, some new species and records have been added and 2 synonymous species have been reevaluated as valid species from Turkey. To sum up, the total number of species has reached 98 (Kahraman et al., 2011, 2012).

There are a large number of studies on pollen morphology in Lamiaceae (Erdtman, 1945; Cantino et al.,

1992; Harley et al., 1992; Abu-Asab and Cantino, 1993, 1994; Celenk et al., 2008; Moon et al., 2008a, 2008b, 2008c; Salmaki et al., 2008; Hassan et al., 2009; Aytac et al., 2012), but only a few studies have been conducted on *Salvia* (Henderson et al., 1968; Jafari and Nikian, 2008; Hassan et al., 2009; İlçim et al., 2009; Kahraman et al., 2009a, 2009b, 2010a, 2010b, 2010c, 2011; Kahraman and Doğan, 2010; Celep et al., 2011; Özler et al., 2011). Henderson et al. (1968) gave brief descriptions of the pollen morphology of 59 *Salvia* taxa, 20 of which grow in Turkey. Moon et al. (2008c) studied the pollen morphology and ultrastructure of 32 taxa of *Salvia* (subtribe Salviinae). Özler et al. (2011) studied pollen grains of 30 taxa of *Salvia*, belonging to sections *Salvia*, *Horminum*, *Drymosphace*, *Plethiosphace*, and *Hemisphace*, using light microscopy (LM) and scanning electron microscopy (SEM).

In Turkey, sect. *Hymenosphace* includes 16 taxa, 13 of which are endemic. The largest number of taxa in the section grows in Turkey (Hedge, 1965). This section is characterized by simple or pinnatisect leaves, stamens with short connectives and large upper theca (type A),

* Correspondence: hulyaozler06@gmail.com

and greatly enlarged (membranous) calyx after anthesis (Hedge, 1982; Walker and Systma, 2007).

In Turkey, the section *Aethiopis* includes 35 taxa, 14 of which are endemic. Members of this section are characterized by a falcate upper corolla lip, stamens with long connective, lower theca reduced to a usually dolabriform plate, and articulating stamens (type B) (Hedge, 1982; Walker and Systma, 2007).

The morphological properties of the pollen of *Salvia* species found in Turkey have been poorly studied. Therefore, the main objectives of the present study are to provide a detailed account of the pollen morphology of

30 Turkish taxa of the genus, including members of the sections *Hymenophace* and *Aethiopis*, using LM and SEM, and to assess the utility of the pollen data for classification at infraspecific and sectional levels within the genus.

2. Materials and methods

Pollen grains of 30 taxa belonging to sections *Aethiopis* (22 spp.) and *Hymenophace* (8 spp.) of the genus *Salvia* were studied by LM and SEM. Pollen material was obtained from plant specimens collected from Turkey between 2005 and 2008. The voucher specimens are listed in Table 1. For LM, pollen grains were first treated with 70% alcohol

Table 1. Collection data of *Salvia* specimens examined here from pollen morphological point of view. Taxa endemic to Turkey are indicated by an asterisk.

<i>S. absconditiflora</i> Greuter & Burdet*	Tokat: Artova: above Artova, 1410 m, <i>S.Bagherpour</i> 290
<i>S. aethiopis</i> L.	Ankara to Kırşehir 5 km to Keskin, 1060 m, <i>S.Bagherpour</i> 243
<i>S. argentea</i> L.	Antalya: Elmali, Elmali to Finike, above Avlan Lake, Ördibek Yayıları, 1573 m, <i>F.Celep</i> 1315
<i>S. atropatana</i> Bunge	Van: between Gürpinar and Van, 2110 m, <i>A.Kahraman</i> 1452
<i>S. blepharochlaena</i> Hedge & Hub.-Mor.*	Kayseri: Sarız to Pınarbaşı, 1650 m, <i>A.Kahraman</i> 1355
<i>S. cadmica</i> Boiss.*	Ankara: Haymana 35 km to Polatlı just few km past Haymana, 1004 m, <i>S.Bagherpour</i> 391
<i>S. candidissima</i> Vahl subsp. <i>candidissima</i>	Ankara: Beynam forest, 1487 m, <i>S.Bagherpour</i> 131
<i>S. cassia</i> Sam. ex Rech.f.	Hatay: Kırıkhan, Cevizyokuşu, 200–210 m, <i>F.Celep</i> 1411
<i>S. ceratophylla</i> L.	Sivas: Zara to Divriği, 4–5 km to Divriği, <i>S.Bagherpour</i> 261
<i>S. chionantha</i> Boiss.*	Antalya: Elmali to Korkuteli, about 17–20 km, 1289 m, <i>F.Celep</i> 1258
<i>S. chrysophylla</i> Stapf *	Muğla: Elmali to Fethiye, Seki, Eren Mountain, 1800–1850 m, <i>F.Celep</i> 1330
<i>S. eriophora</i> Boiss. & Kotschy ex Boiss.*	Kayseri/Sivas: between Pınarbaşı and Gürün, 1870 m, <i>A.Kahraman</i> 1363
<i>S. euphratica</i> Montbret & Aucher ex Benth. var. <i>euphratica</i> *	Malatya: 1–1.5 km from Darende to Malatya, 1030 m, <i>A.Kahraman</i> 1098
<i>S. euphratica</i> Benth. var. <i>leiocalycina</i> (Rech.f.) Hedge*	Sivas: Yıldızeli to Tokat, 5 km N of Yıldızeli, 1403 m, <i>S.Bagherpour</i> 284
<i>S. frigida</i> Boiss.	Sivas: between Divriği and Kemaliye, 1017 m, <i>A.Kahraman</i> 1173
<i>S. hypargeia</i> Fisch. & C.A.Mey.*	Erzurum: İlca to Erzurum, 1817 m, <i>A.Kahraman</i> 1293
<i>S. limbata</i> C.A.Mey.	Mardin: Mardin to Diyarbakır, 14 km before Çınar, 759 m, <i>A.Kahraman</i> 1382
<i>S. macrosiphon</i> Boiss.	Malatya: Malatya to Yeşilyurt, after 1.5 km from the exit of Beydağı, 950 m, <i>A.Kahraman</i> 1114
<i>S. microstegia</i> Boiss. & Balansa	Niğde: Melendiz Mountain, above Tepe village, 2300–2400 m, <i>F.Celep</i> 965
<i>S. modesta</i> Boiss.*	Kayseri, Sarız, Yeşilkent (Yalak), Binboğa Mountain, above Dayoluk village, 2172 m, <i>F.Celep</i> 1072
<i>S. montbrettii</i> Benth.	Mardin: between Mardin and Midyat, 933 m, <i>A.Kahraman</i> 1375
<i>S. multicaulis</i> Vahl	Sivas: between Yıldızeli and Çamlıbeli, 1323, <i>S.Bagherpour</i> 180
<i>S. palaestina</i> Benth.	Gaziantep: between Gaziantep and Nizip 23 km, 733 m, <i>A.Kahraman</i> 1134
<i>S. pomifera</i> L.	Aydın: Kuşadası, Davutlar National Park, 25 m, <i>F.Celep</i> 1050
<i>S. sclarea</i> L.	Mersin: Aslanköy, 847 m, <i>F.Celep</i> 1109
<i>S. smyrnaea</i> Boiss.*	İzmir: Kemalpaşa, Nif Mountain, around summit, 1450–1510 m, <i>F.Celep</i> 1053
<i>S. syriaca</i> L.	Ankara: from Nallıhan to Beypazarı, 47th km, 652 m, <i>S.Bagherpour</i> 241
<i>S. tobeyii</i> Hedge*	Karabük, Keltepe Mountain, around the summit, 1900 m, <i>F.Celep</i> 1759
<i>S. xanthocheila</i> Boiss. ex Benth.	Hakkari: Berçelan, 2661 m, <i>A.Kahraman</i> 1559
<i>S. yosagadensis</i> Freyn & Bornm.*	Aksaray: Hasan Dağı. Helvadere, 1635 m, <i>S.Bagherpour</i> 265

and allowed to evaporate, then embedded in glycerin jelly (Wodehouse, 1935). Polar axis (P), equatorial axis (E), colpus length (Clt), colpus width (Clt), exine thickness (Ex), intine thickness (I), apocolpium diameter (Ap), and mesocolpium diameter (Me) were measured from at least 30 fully developed grains per sample under an Olympus CX31 microscope (1000 \times). For SEM studies, pollen grains obtained from each specimen were transferred onto stubs and coated with gold (JEOL 6060, JSM-6400). From the micrographs, the average means of the number of primary lumina per 25 μm^2 , diameter of primary and secondary lumina, and thickness of primary and secondary muri were measured on the mesocolpium. The terminology follows mainly that of Henderson et al. (1968), Faegri and Iversen (1989), and Punt et al. (2007).

3. Results

The main pollen characteristics of the studied taxa are given in Tables 2 and 3. LM and SEM micrographs of the examined pollen grains are shown in Figures 1–5.

3.1. Size

The pollen grains are dispersed as monads. The size of the polar axis (P) ranges from 25.0 μm in *Salvia aethiopis* to 61.4 μm in *S. blepharochlaena*; the size of the equatorial axis (E) ranges from 30.7 μm in *S. syriaca* to 67.2 μm in *S. candidissima* subsp. *candidissima* (Table 2).

3.2. Shape

The shape of the pollen grains in equatorial view varies from suboblate to spheroidal, whereas their shape in polar view is slightly elliptic to circular (Table 2; Figures 1–5). Often pollen shape classes vary and coexist between suboblate and prolate-spheroidal.

3.3. Apertures

The pollen grains are radially symmetric and isopolar in all the taxa. They are mostly hexocolpate, but also heptacolpate (2%) and octacolpate (40%) in *S. candidissima* subsp. *candidissima*, and heptacolpate (20%) in *Salvia palaestina* (Figures 1 and 2).

Simple colpi are distributed symmetrically. Colpus length varies from 22.1 μm in *Salvia aethiopis* and *S. eriophora* to 60.5 μm in *S. blepharochlaena*. Colpus width varies from 4.1 μm in *S. palaestina* to 12.0 μm in *S. candidissima* subsp. *candidissima* (Table 2). Colpus length is strongly correlated with the length of the polar axis. Colpi are narrow towards the poles and their ends are acute. Colpi membranes are grouped with granulate, as in *S. multicaulis*, and grouped with granulate-scabrate, as in *S. aethiopis* (Figure 5). In the polar view, 2 of the mesocolpia are larger than the other 4. The mesocolpial area varies from 5.5 μm in *S. aethiopis* to 14.4 μm in *S. blepharochlaena*. The apocolpium diameter varies from 3.4 μm in *S. absconditiflora* to 10.1 μm in *S. chrysophylla* (Table 2).

3.4. Exine sculpturing

Exine sculpturing displays 2 distinct types of surface structures: bireticulate (the common type) and reticulate-perforate (Hassan et al., 2009). Based on the detailed configuration of the exine sculpturing, reticulate-perforate and bireticulate patterns can be subdivided into 2 subtypes. Exine thickness is 1.0 to 2.2 μm and intine thickness is 0.2 to 1.2 μm (Table 2).

3.4.1. Bireticulate (BR)

The bireticulate sculpturing (a 2-layered reticulum consisting of a suprareticulum supported by a microreticulate layer) pattern is the most common (18 taxa) among the examined taxa. It can be divided into 2 types according to the number of primary lumina per 25 μm^2 : in type 1a, the number of primary lumina is ≤ 10 per primary lumen in *Salvia argentea*, *S. candidissima* subsp. *candidissima*, *S. cassia*, *S. chionantha*, *S. ceratophylla*, *S. chrysophylla*, *S. eriophora*, *S. limbata*, *S. macrosiphon*, *S. microstegia*, *S. modesta*, *S. palaestina*, *S. sclarea*, *S. tobeyii*, and *S. xanthocheila* from sect. *Aethiopis* and *S. blepharochlaena* and *S. cadmica* from sect. *Hymenosphace* (Figures 4–5); and in type 1b, the number of primary lumina is > 10 per primary lumen in *S. yosgadensis* from sect. *Aethiopis* (Figure 5). Type 1a can be also divided into 2 subtypes, whether having 1–4 large central secondary lumina per primary lumen (e.g., *S. candidissima* subsp. *candidissima*, *S. cassia*, *S. ceratophylla*, *S. chrysophylla*, *S. eriophora*, *S. limbata*, *S. macrosiphon*, *S. palaestina*, and *S. sclarea* from sect. *Aethiopis*; type 1a-1) or not (e.g., *S. argentea*, *S. chionantha*, *S. microstegia*, *S. modesta*, *S. tobeyii*, and *S. xanthocheila* from sect. *Aethiopis* and *S. cadmica* and *S. blepharochlaena* from sect. *Hymenosphace*; type 1a-2).

The secondary muri of *S. chionantha*, *S. microstegia*, *S. modesta*, *S. tobeyii*, and *S. xanthocheila* are discontinuous (Figures 4 and 5). *S. palaestina* has thicker primary muri and secondary lumina than the others and is almost circular (Figure 4).

3.4.2. Reticulate-perforate (R-per)

The reticulate-perforate (a 2-layered tectum consisting of a suprareticulate intratectal layer and pores in an infratectal layer restricted next to muri) sculpturing pattern occurs in 12 taxa. It can be divided into 2 subtypes according to the number of primary lumina. In type 2a, the number of primary lumina is ≤ 10 in *Salvia aethiopis*, *S. atropatana*, *S. frigida*, *S. hypargeia*, *S. montbrettii*, and *S. syriaca* from sect. *Aethiopis* and *S. euphratica* var. *euphratica*, *S. euphratica* var. *leicocalycina*, *S. pomifera*, and *S. smyrnaea* from sect. *Hymenosphace* (Figure 5). In type 2b, the number of primary lumina is > 10 in *S. absconditiflora* and *S. multicaulis* from sect. *Hymenosphace* (Figure 5).

Among the investigated taxa, *S. absconditiflora* and *S. multicaulis*, belonging to sect. *Hymenosphace*, have

Table 2. Pollen morphological data for *Salvia* taxa examined.

Taxa and sections	P (μm)	E (μm)	Shape				Clg (μm)	Clt (μm)	Ex (μm)	Ap (μm)	Me (μm)
			SO	OS	PS	SP					
Sect. Hymenosphaece											
<i>S. absconditiflora</i>	(31.7-) 39.5 ± 3.7 (-47.0)	(38.4-) 44.6 ± 2.7 (-49.0)	++	+	-	-	+ (25.9-) 34.1 ± 3.7 (-41.3)	7.6 ± 0.7 (-8.6)	1.7 ± 0.2 (-1.9)	0.4 ± 0.1 (-0.5)	5.3 ± 1.0 (-6.7)
<i>S. blepharochlaena</i>	(49.9-) 57.0 ± 2.8 (-61.4)	(45.1-) 53.0 ± 5.0 (-65.3)	-	-	++	-	(48.0-) 52.9 ± 3.2 (-60.5)	(5.3-) 6.5 ± 0.8 (-8.2)	(1.0-) 1.2 ± 0.2 (-1.4)	(0.2-) 0.3 ± 0.1 (-0.5)	(4.8-) 6.4 ± 0.9 (-7.7)
<i>S. cadmia</i>	(43.2-) 47.7 ± 2.4 (-51.8)	(43.2-) 50.0 ± 3.5 (-54.7)	-	-	++	-	(37.4-) 42.6 ± 2.4 (-48.0)	(4.6-) 5.7 ± 0.9 (-7.7)	(1.2-) 1.4 ± 0.2 (-1.7)	(0.2-) 0.4 ± 0.1 (-0.5)	(4.8-) 5.4 ± 0.4 (-6.0)
<i>S. euphratica</i> var. <i>euphratica</i>	(38.4-) 46.1 ± 2.8 (-51.8)	(34.6-) 42.8 ± 4.2 (-52.8)	-	-	++	-	(34.6-) 40.1 ± 3.2 (-46.1)	(4.8-) 5.3 ± 0.7 (-6.7)	(1.2-) 1.4 ± 0.2 (-1.7)	(0.2-) 0.3 ± 0.1 (-0.5)	(5.8-) 6.4 ± 0.5 (-7.4)
<i>S. euphratica</i> var. <i>leioachryna</i>	(40.3-) 46.4 ± 3.6 (-51.8)	(42.2-) 50.0 ± 4.6 (-61.4)	-	++	-	-	(33.6-) 40.0 ± 3.8 (-46.1)	(6.7-) 8.7 ± 0.9 (-10.1)	(1.4-) 1.6 ± 0.2 (-1.9)	(0.5-) 0.7 ± 0.2 (-1.0)	(7.2-) 8.4 ± 0.9 (-9.6)
<i>S. multicaulis</i>	(36.5-) 42.2 ± 3.1 (-49.0)	(38.4-) 41.5 ± 3.0 (-48.0)	-	-	++	-	(32.6-) 36.0 ± 2.4 (-41.3)	(4.6-) 5.6 ± 0.6 (-6.7)	(1.4-) 1.6 ± 0.2 (-1.9)	(0.5-) 0.6 ± 0.3 (-1.2)	(4.8-) 5.7 ± 0.7 (-7.0)
<i>S. pomifera</i>	(38.4-) 46.1 ± 3.6 (-53.8)	(51.8-) 55.3 ± 2.6 (-59.5)	++	-	-	-	(34.6-) 40.6 ± 3.1 (-48.0)	(6.7-) 8.6 ± 1.2 (-10.6)	(1.2-) 1.7 ± 0.3 (-2.2)	(0.5-) 0.7 ± 0.2 (-1.0)	(4.8-) 5.9 ± 0.6 (-6.7)
<i>S. smyrnaea</i>	(39.4-) 42.7 ± 2.7 (-49.9)	(42.2-) 49.1 ± 3.1 (-53.8)	++	-	-	-	(34.6-) 38.1 ± 2.8 (-45.6)	(6.7-) 8.3 ± 0.9 (-9.6)	(1.2-) 1.6 ± 0.2 (-1.9)	(0.5-) 0.7 ± 0.2 (-1.0)	(6.2-) 7.1 ± 0.6 (-8.2)
Sect. Aethiopis											
<i>S. aethiopis</i>	(25.0-) 30.7 ± 2.4 (-33.6)	(35.5-) 39.2 ± 2.2 (-43.2)	++	+	-	-	(22.1-) 26.1 ± 2.0 (-28.8)	(6.2-) 7.7 ± 1.0 (-9.6)	(1.2-) 1.5 ± 0.2 (-1.7)	(0.5-) 0.6 ± 0.2 (-1.0)	(4.8-) 5.7 ± 0.5 (-6.7)
<i>S. argentea</i>	(37.4-) 41.5 ± 3.2 (-50.9)	(43.2-) 48.6 ± 3.3 (-56.6)	++	-	+	-	(31.7-) 35.3 ± 3.2 (-47.0)	(7.7-) 9.2 ± 0.8 (-10.6)	(1.2-) 1.6 ± 0.3 (-1.9)	(0.5-) 0.8 ± 0.2 (-1.0)	(3.6-) 4.4 ± 0.6 (-5.3)

Table 2. (Continued).

Taxa and sections	P (μm)	E (μm)	Shape						Clt (μm)	Ex (μm)	Ap (μm)	Me (μm)
			SO	OS	PS	SP	S	Ctg (μm)				
<i>S. atropatana</i>	(38.4-) 42.5 ± 2.6 (-48.0)	(46.1-) 49.2 ± 2.6 (-58.6)	++	+	-	-	-	(30.7-) 36.8 ± 2.7 (-40.3)	(7.4-) 9.3 ± 1.1 (-11.5)	(0.5-) 1.6 ± 0.2 (-1.9)	(4.8-) 0.7 ± 0.2 (-1.0)	(7.9-) 6.8 ± 0.9 (-8.2)
<i>S. candidissima</i> subsp. <i>candidissima</i>	(36.5-) 46.7 ± 6.1 (-62.4)	(46.1-) 59.7 ± 4.6 (-67.2)	++	+	-	-	-	(32.6-) 40.7 ± 5.4 (-54.7)	(8.6-) 10.2 ± 1.0 (-12.0)	(0.5-) 1.9 ± 0.2 (-2.2)	(6.5-) 0.8 ± 0.2 (-1.0)	(5.8-) 7.6 ± 0.7 (-8.6)
<i>S. cassia</i>	(38.4-) 44.3 ± 3.2 (-50.9)	(45.1-) 51.4 ± 3.3 (-57.6)	++	-	+	+	-	(32.6-) 38.5 ± 3.4 (-45.1)	(7.7-) 9.2 ± 0.8 (-10.6)	(1.4-) 1.7 ± 0.2 (-1.9)	(0.5-) 0.7 ± 0.2 (-1.0)	(4.8-) 6.3 ± 0.9 (-7.7)
<i>S. ceratophylla</i>	(31.7-) 38.4 ± 2.9 (-43.2)	(44.2-) 47.5 ± 2.5 (-52.8)	++	+	-	-	-	(25.0-) 32.5 ± 3.0 (-36.5)	(7.7-) 9.2 ± 0.8 (-10.6)	(1.4-) 1.6 ± 0.2 (-1.9)	(0.5-) 0.7 ± 0.2 (-1.0)	(5.5-) 6.9 ± 0.8 (-8.4)
<i>S. chionantha</i>	(36.5-) 40.3 ± 2.6 (-48.0)	(45.1-) 49.4 ± 3.5 (-63.4)	++	-	-	-	-	(28.8-) 33.3 ± 3.6 (-41.3)	(7.7-) 9.6 ± 0.9 (-11.0)	(1.4-) 1.7 ± 0.2 (-1.9)	(0.5-) 0.7 ± 0.2 (-1.0)	(8.2-) 7.6 ± 0.7 (-9.6)
<i>S. chrysophylla</i>	(40.3-) 43.0 ± 2.0 (-48.0)	(48.0-) 51.5 ± 2.4 (-57.6)	++	-	+	-	-	(32.6-) 35.7 ± 1.8 (-40.3)	(8.4-) 9.6 ± 0.7 (-10.6)	(1.4-) 1.8 ± 0.3 (-2.2)	(0.5-) 0.7 ± 0.2 (-1.0)	(8.6-) 7.6 ± 0.7 (-10.1)
<i>S. eriophora</i>	(26.9-) 32.6 ± 2.8 (-37.44)	(32.6-) 38.5 ± 2.6 (-42.2)	++	+	-	-	-	(22.1-) 27.1 ± 2.0 (-31.7)	(4.8-) 5.9 ± 0.6 (-6.7)	(1.4-) 1.4 ± 0.2 (-1.7)	(0.5-) 0.6 ± 0.1 (-0.7)	(4.6-) 8.9 ± 0.7 (-10.1)
<i>S. frigida</i>	(30.7-) 37.3 ± 3.1 (-44.2)	(37.4-) 42.5 ± 2.6 (-46.1)	++	+	-	-	-	(24.0-) 31.3 ± 3.7 (-37.4)	(7.2-) 8.2 ± 0.7 (-9.6)	(1.2-) 1.4 ± 0.2 (-1.7)	(0.5-) 0.6 ± 0.1 (-0.7)	(4.6-) 5.4 ± 0.5 (-6.0)
<i>S. hypargea</i>	(38.4-) 42.4 ± 3.3 (-48.0)	(42.2-) 48.8 ± 2.7 (-52.8)	++	+	+	-	-	(32.6-) 37.2 ± 3.0 (-42.2)	(6.7-) 7.6 ± 0.8 (-9.6)	(1.4-) 1.7 ± 0.2 (-1.9)	(0.5-) 0.5 ± 0.1 (-0.7)	(5.5-) 6.7 ± 0.7 (-7.7)
<i>S. limbata</i>	(35.5-) 43.6 ± 4.9 (-54.7)	(43.2-) 52.7 ± 4.9 (-65.3)	++	++	-	-	-	(29.8-) 37.1 ± 4.2 (-47.0)	(7.7-) 9.2 ± 0.9 (-10.6)	(1.2-) 1.5 ± 0.2 (-1.7)	(0.5-) 0.6 ± 0.1 (-0.7)	(5.8-) 6.2 ± 0.4 (-6.7)
<i>S. macrostaphon</i>	(38.4-) 42.7 ± 3.4 (-51.8)	(47.0-) 51.2 ± 2.7 (-58.6)	++	-	+	-	-	(30.7-) 37.3 ± 5.4 (-48.0)	(7.7-) 8.9 ± 0.8 (-10.6)	(1.4-) 1.7 ± 0.2 (-1.9)	(0.5-) 0.8 ± 0.2 (-1.0)	(8.6-) 8.1 ± 0.6 (-9.4)

Table 2. (Continued).

Taxa and sections	P (μm)	E (μm)	Shape					Clg (μm)	Clt (μm)	Ex (μm)	Ex (μm)	Ap (μm)	Me (μm)
			SO	OS	PS	SP	S						
<i>S. microstegia</i>	(32.6-) 41.3 ± 6.1 (-50.9)	(39.4-) 47.7 ± 5.5 (-60.5)	++	+	-	-	-	(26.9-) ± 5.3 (-43.2)	(7.2-) 8.6 ± 0.9 (-9.8)	(1.2-) 1.4 ± 0.2 (-1.7)	(0.2-) 0.5 ± 0.2 (-0.7)	(4.8-) 5.4 ± 0.4 (-6.5)	(7.2-) 8.9 ± 0.9 (-10.6)
<i>S. modesta</i>	(28.8-) 33.3 ± 2.5 (-37.4)	(35.5-) 39.4 ± 2.4 (-43.2)	++	-	-	-	-	(23.0-) 26.7 ± 1.7 (-29.8)	(6.5-) 8.1 ± 1.0 (-9.6)	(1.2-) 1.4 ± 0.2 (-1.7)	(0.2-) 0.6 ± 0.2 (-0.7)	(4.8-) 5.5 ± 0.6 (-6.7)	(8.6-) 9.7 ± 0.7 (-11.5)
<i>S. montbretii</i>	(34.6-) 39.7 ± 3.0 (-45.1)	(43.2-) 47.7 ± 2.8 (-53.8)	++	+	+	-	-	(28.8-) 34.0 ± 3.1 (-40.3)	(7.7-) 8.9 ± 1.0 (-11.0)	(1.2-) 1.5 ± 0.2 (-1.7)	(0.2-) 0.5 ± 0.2 (-0.7)	(6.2-) 8.1 ± 0.9 (-9.4)	(8.6-) 9.6 ± 0.8 (-12.5)
<i>S. palaeastina</i>	(31.7-) 36.2 ± 3.2 (-42.2)	(33.6-) 39.7 ± 3.5 (-46.1)	-	++	++	-	-	(25.9-) 31.2 ± 3.2 (-36.5)	(4.1-) 5.8 ± 1.2 (-7.7)	(1.2-) 1.5 ± 0.2 (-1.7)	(0.2-) 0.6 ± 0.2 (-0.7)	(5.5-) 6.1 ± 0.3 (-6.7)	(6.5-) 8.2 ± 0.9 (-10.6)
<i>S. sclarea</i>	(38.4-) 42.3 ± 2.6 (-47.0)	(47.0-) 53.0 ± 3.4 (-59.5)	++	+	-	-	-	(33.6-) 37.2 ± 2.5 (-41.3)	(7.2-) 8.8 ± 0.8 (-10.6)	(1.2-) 1.4 ± 0.2 (-1.7)	(0.2-) 0.5 ± 0.2 (-0.7)	(6.0-) 7.4 ± 0.8 (-8.6)	(7.7-) 9.1 ± 0.8 (-10.6)
<i>S. syriaca</i>	(29.8-) 35.5 ± 3.1 (-40.3)	(30.7-) 39.1 ± 3.2 (-44.2)	-	+	++	-	-	(24.0-) 29.6 ± 3.2 (-35.5)	(6.0-) 7.3 ± 0.8 (-8.6)	(1.4-) 1.6 ± 0.2 (-1.9)	(0.5-) 0.6 ± 0.2 (-1.0)	(4.8-) 6.0 ± 0.7 (-7.7)	(6.5-) 8.6 ± 1.3 (-10.6)
<i>S. toveyii</i>	(29.8-) 33.3 ± 2.1 (-38.4)	(35.5-) 39.7 ± 2.9 (-45.1)	++	-	-	-	-	(23.0-) 27.2 ± 2.5 (-32.6)	(6.5-) 7.9 ± 0.9 (-9.6)	(1.4-) 1.6 ± 0.2 (-1.9)	(0.7-) 0.9 ± 1.0 (-1.0)	(4.1-) 5.0 ± 0.5 (-5.8)	(6.7-) 7.9 ± 0.7 (-9.1)
<i>S. xanthochilea</i>	(38.4-) 43.1 ± 3.4 (-51.8)	(39.4-) 46.9 ± 3.0 (-53.8)	+	++	+	-	-	(32.6-) 37.1 ± 3.3 (-46.1)	(6.7-) 8.8 ± 1.4 (-11.5)	(1.4-) 1.6 ± 0.2 (-1.9)	(0.2-) 0.5 ± 0.2 (-0.7)	(4.8-) 6.0 ± 0.5 (-6.7)	(7.7-) 9.4 ± 0.9 (-10.6)
<i>S. yosgadensis</i>	(28.8-) 31.5 ± 1.8 (-36.5)	(34.6-) 38.8 ± 2.4 (-44.2)	++	-	+	-	-	(23.0-) ± 1.8 (-29.8)	(7.7-) 8.5 ± 0.6 (-9.6)	(1.2-) 1.5 ± 0.2 (-1.7)	(0.5-) 0.6 ± 0.1 (-0.7)	(3.8-) 4.6 ± 0.4 (-5.8)	(7.7-) 8.9 ± 0.9 (-10.6)

Abbreviations: Numbers refer to (minimum-) mean ± standard deviation (-maximum); P = polar axis, E = equatorial axis, Clg = colpus length, Clt = colpus width, Ap = apocolpium diameter, In = intine thickness, Ex = exine thickness, Me = mesocolpium diameter, Os = oblate-spheroidal, PS = suboblate, SP = subprolate, S = spheroidal, -, absent, +, rarely present, ++, dominant.

Table 3. Summary of morphometric data from SEM micrographs of *Salvia* taxa examined (* indicates endemic species).

Taxa	Number of primary lumina per 25 μm^2	Diameter of primary lumina (μm)	Diameter of secondary lumina (μm)	Number of secondary lumina per lumen	Thickness of primary muri (μm)	Thickness of secondary muri (μm)	Shape of primary lumina	Sculpturing types	SEM figures
Sect. <i>Hymenophace</i>									
<i>S. absconditiflora</i> *	16	1.0	0.2	7	0.4	0.2	Angular	R-per (IIb)	5N
<i>S. blepharochlaena</i> *	8	1.7	0.8	5	0.5	0.3	Angular	BR (Ia-2)	4M
<i>S. cadmica</i> *	5	2.6	1.2	4	0.4	0.2	Angular	BR (Ia-2)	4N
<i>S. euphratica</i> var. <i>euphratica</i> *	8	2.1	0.8	8	0.3	0.2	Angular	R-per (IIa)	5F
<i>S. euphratica</i> var. <i>leiochrysa</i> *	4	2.5	0.7	9	0.5	0.3	Angular	R-per (IIa)	5G
<i>S. multicaulis</i>	18	1.2	0.2	12	0.2	0.1	Extended-angular	R-per (IIIb)	5O
<i>S. pomifera</i>	8	1.5	0.3	10	0.4	0.2	Extended-angular	R-per (IIa)	5K
<i>S. smyrnaea</i> *	6	1.6	0.6	4	0.4	0.2	Angular	R-per (IIa)	5L
Sect. <i>Aethiopis</i>									
<i>S. aethiopis</i>	10	1.9	0.7	8	0.3	0.2	Angular	R-per (IIa)	5C, 5D
<i>S. argentea</i>	2	3.5	1.2	15>	0.5	0.2	Angular	BR (Ia-2)	4L
<i>S. arropatana</i>	10	2.3	0.4	15	0.5	0.2	Angular	R-per (IIa)	5E
<i>S. candidissima</i> subsp. <i>candidissima</i>	10	2.1	0.7	9	0.4	0.2	Angular	BR (Ia-1)	4A
<i>S. cassia</i>	3	3.0	1.1	17>	0.4	0.3	Angular	BR (Ia-1)	4B
<i>S. ceratophylla</i>	10	1.5	0.6	6	0.4	0.2	Angular	BR (Ia-1)	4C
<i>S. chionantha</i> *	3	3.6	1.0	13>	0.4	0.1	Extended-angular	BR (Ia-2)	4O
<i>S. chrysophylla</i> *	7	2.9	0.9	10	0.4	0.2	Angular	BR (Ia-1)	4D, 4E
<i>S. eriophora</i> *	9	2.0	0.8	7	0.3	0.2	Angular	BR (Ia-1)	4F
<i>S. frigida</i>	9	1.8	0.5	9	0.4	0.2	Angular	R-per (IIa)	5H
<i>S. hypargea</i> *	6	2.4	0.5	15	0.4	0.2	Extended-angular	R-per (IIa)	5I
<i>S. limbata</i>	3	2.9	0.9	17>	0.4	0.2	Angular	BR (Ia-1)	4G, 4H
<i>S. macrosiphon</i>	6	2.0	0.6	19	0.4	0.2	Angular	BR (Ia-1)	4I
<i>S. microstegia</i>	3	3.5	1.0	16	0.4	0.1	Extended-angular	BR (Ia-2)	4P
<i>S. modesta</i> *	4	2.5	1.0	5	0.4	0.2	Angular	BR (Ia-2)	4Q
<i>S. montbretii</i>	7	2.8	0.6	10	0.3	0.2	Angular	R-per (IIa)	5J
<i>S. palaestina</i>	6	2.6	0.7	17	0.5	0.2	Angular	BR (Ia-1)	4J
<i>S. sclarea</i>	3	3.9	0.8	24	0.3	0.2	Angular	BR (Ia-1)	4K
<i>S. syriaca</i>	10	1.6	0.5	5	0.3	0.2	Angular	R-per (IIa)	5M
<i>S. tomentella</i> *	6	2.6	0.8	7	0.4	0.1	Angular	BR (Ia-2)	4R
<i>S. xanthothecila</i>	4	2.9	1.0	14	0.4	0.1	Extended-angular	BR (Ia-2)	5A
<i>S. yosgadensis</i> *	13	1.4	0.6	8	0.4	0.2	Angular	BR (Ib)	5B

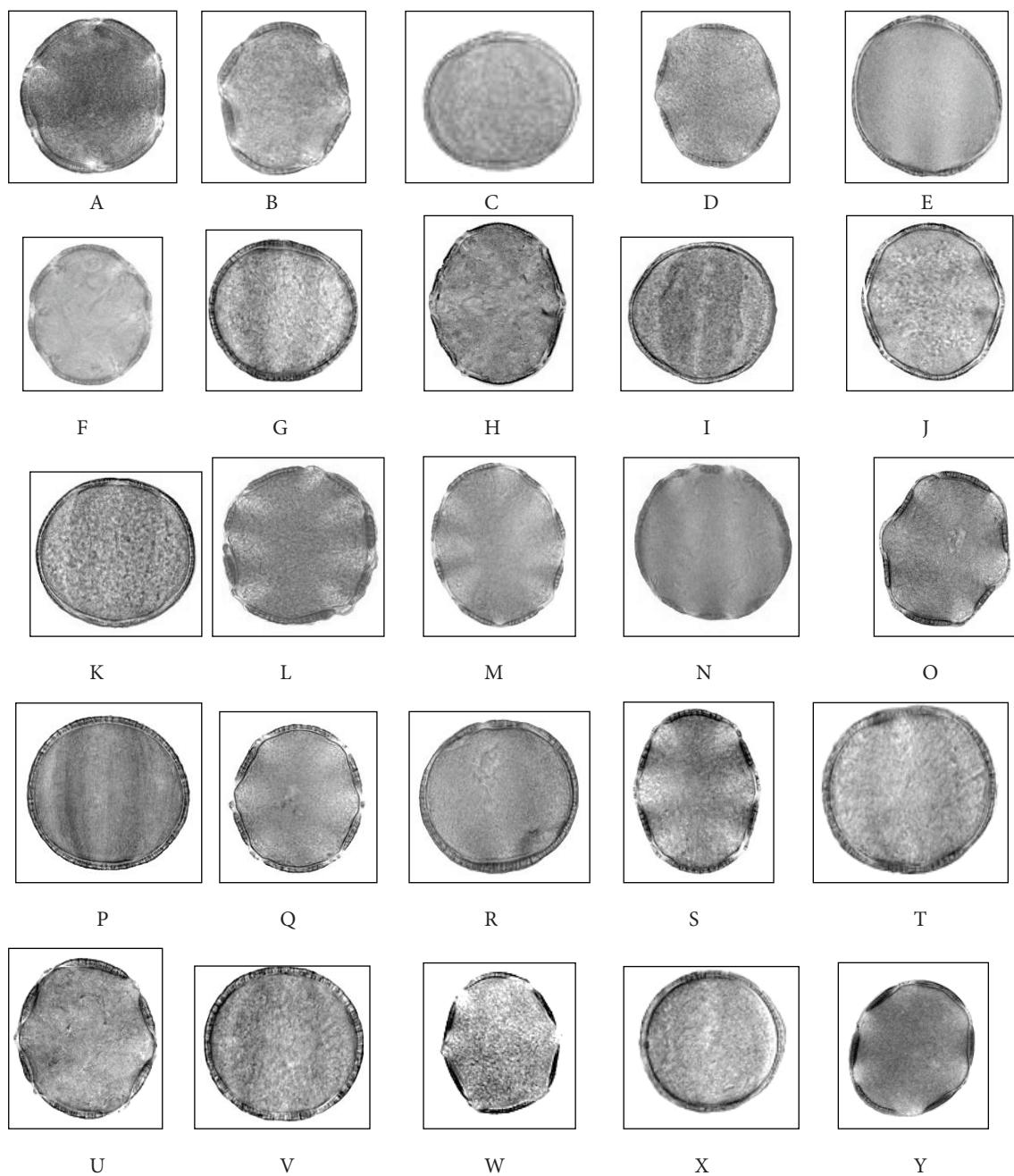


Figure 1. LM micrographs of pollen grains in the *Salvia* taxa examined. A- *Salvia absconditiflora*, B & C- *S. aethiopis*, D & E- *S. argentea*, F & G- *S. atropatana*, H & I- *S. blepharochlaena*, J & K- *S. cadmica*, L, M, & N- *S. candidissima* subsp. *candidissima*, O & P- *S. cassia*, Q & R- *S. ceratophylla*, S & T- *S. chionantha*, U & V- *S. chrysophylla*, W & X- *S. eriophora*, Y- *S. euphratica* var. *euphratica*. Polar view = A, B, D, F, H, J, L, M, O, Q, S, U, W, Y; equatorial view = C, E, G, I, K, N, P, R, T, V, X. Scale bar = 20 μm .

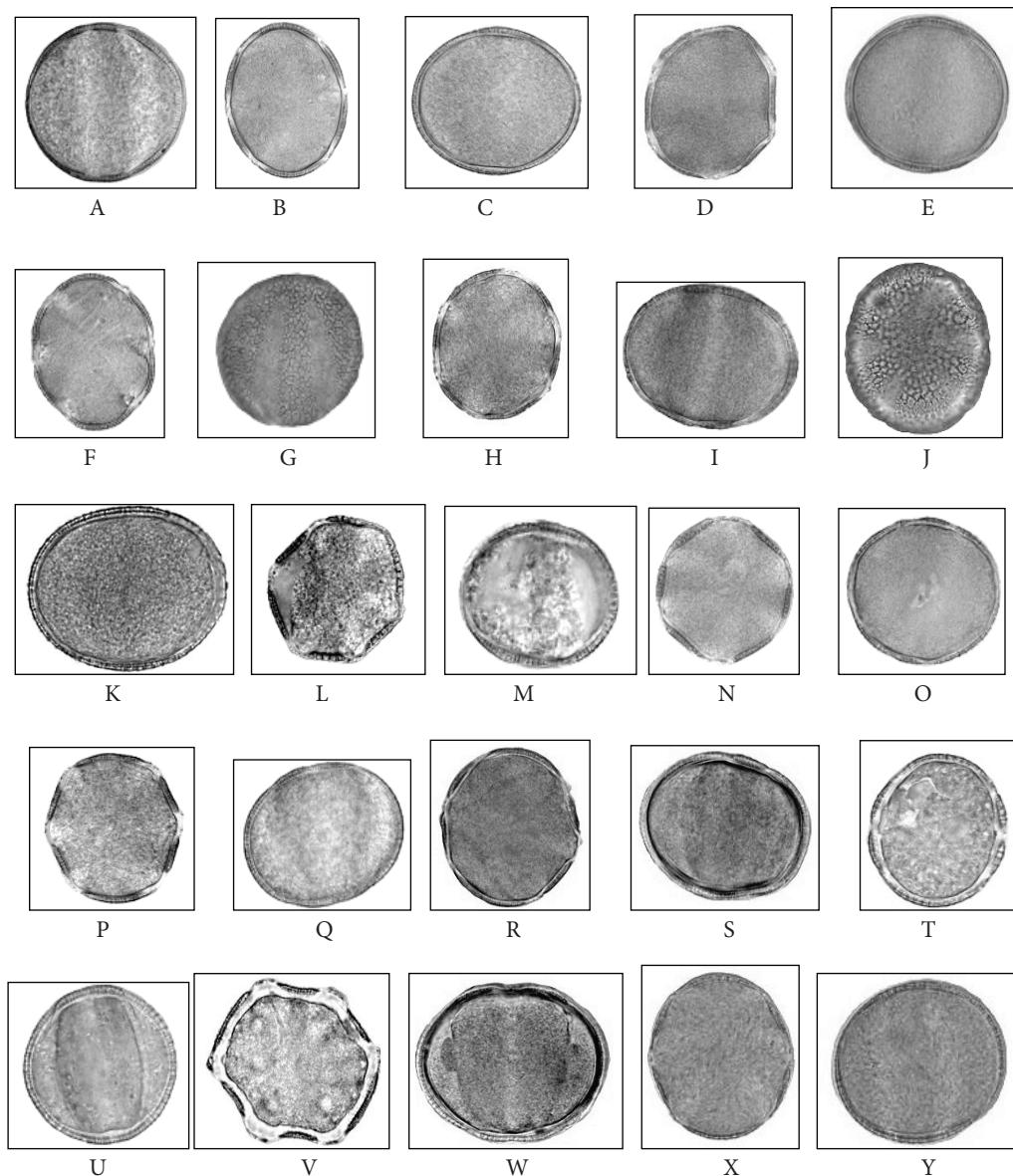


Figure 2. LM micrographs of pollen grains in the *Salvia* taxa examined. A- *Salvia euphratica* var. *euphratica*, B & C- *S. euphratica* var. *leiocalyicina*, D & E- *S. frigida*, F & G- *S. hypargeia*, H & I- *S. limbata*, J & K- *S. macrosiphon*, L & M- *S. microstegia*, N & O- *S. modesta*, P & Q- *S. montbretii*, R & S- *S. multicaulis*, T & U- *S. palaestina*, V & W- *S. pomifera*, X & Y- *S. sclarea*. Polar view = B, D, F, H, J, L, N, P, R, T, V, X; equatorial view = A, C, E, G, I, K, M, O, Q, S, U, W, Y. Scale bar = 20 μ m.

the highest primary lumen number in $25 \mu\text{m}^2$ (Table 3). The largest primary lumina were found in *S. argentea*, *S. chionantha*, *S. microstegia*, and *S. sclarea*, and the largest secondary lumina in *S. argentea*. The thickest primary muri were present in *S. argentea*, *S. atropatana*, *S. blepharochlaena*, and *S. euphratica* var. *leiocalyicina*, and the thickest secondary muri in *S. blepharochlaena*,

S. cassia, and *S. euphratica* var. *leiocalyicina* (Table 3). *S. atropatana* has irregular muri (Figure 5). Size and number of the secondary lumina decrease towards the poles and apertures. The shape of primary lumina was mostly angular, except *S. chionantha*, *S. microstegia*, *S. xanthocheila*, *S. hypargeia*, *S. pomifera*, and *S. multicaulis* (Table 3; Figures 4 and 5).

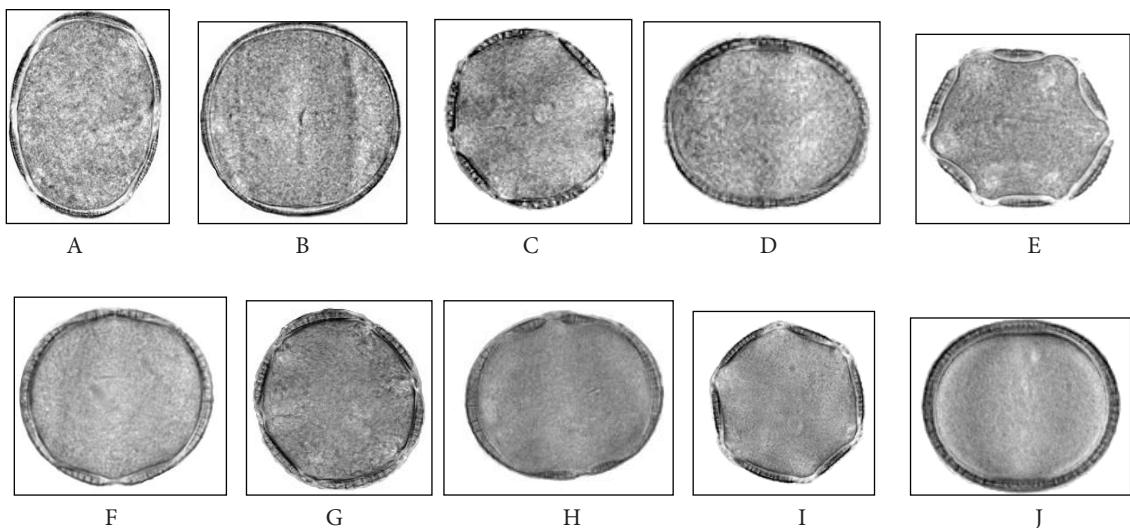


Figure 3. LM micrographs of pollen grains in the *Salvia* taxa examined. A & B- *Salvia smyrnaea*, C & D- *S. syriaca*, E & F- *S. tomentella*, G & H- *S. xanthochela*, I & J- *S. yosogadensis*. Polar view = A, C, E, G, I; equatorial view = B, D, F, H, J. Scale bar = 20 μm .

4. Discussion

The present study shows that the pollen grains of all taxa examined are hexocolpate and rarely heptacolpate (20%) in *Salvia palaestina*, and heptacolpate (2%) and octacolpate (40%) in *S. candidissima* subsp. *candidissima*. These results agree with those of Özler et al. (2011) (Figures 1 and 2). Similarly, Moon et al. (2008c) observed that *S. eremostachya* Jeps., *S. leucantha* Cav., and *S. palaestina* have less than 1% tetracolpate pollen grains; *S. eremostachya* and *S. splendens* Sellow ex Wied-Neuw. have a few pentacolpate pollen grains; and *S. barrelieri*, *S. palaestina*, and *S. uliginosa* have 1 octacolpate pollen grain. Perveen and Qaiser (2003) also found 6-zonocolpate pollen in *S. bucharia* Popov, *S. plebeia* R.Br., *S. lanata* Salisb., *S. macrosiphon*, *S. moorcroftiana* Wall. ex Benth., *S. aegyptiaca* L., and *S. nubicola* Wall. ex Sweet placed into the *S. aegyptiaca* type.

The pollen grains of the *Salvia* taxa examined are small to large ($P = 25.0\text{--}61.4 \mu\text{m}$, $E = 30.7\text{--}67.2 \mu\text{m}$). The smallest pollen occurs in *Salvia aethiopis*, belonging to sect. *Aethiopis*, whereas the largest pollen occurs in *S. blepharochlaena*, belonging to sect. *Hymenophace* (Table 2; Figure 1). Hamzaoglu et al. (2005), using the Wodehouse method, and Moon et al. (2008c) and Hassan et al. (2009), using the acetolyzed method, found some differences in the size and shape of the *Salvia* species examined. These differences can be mainly caused by different preparation techniques. The content of the pollen grain does not dissolve in the Wodehouse method (Reitsma, 1969). However, Hao and Zhang (1988) found that after

acetolysis, the size of the colporate pollen grains increased or their shape was changed.

The pollen grains of all taxa examined in this study vary from suboblate to spheroidal in equatorial view. Colpi are long and their ends are acute. Colpus membranes are grouped with granulate-scabrate in *S. aethiopis* and grouped with granulate in *S. multicaulis* (Figure 5). An operculum with granule was seen in all the taxa (Figures 1–3). Similarly, some authors (Perveen and Qaiser, 2003; Moon et al., 2008c; Hassan et al., 2009) found colpi with granulate membranes and pointed, acute, and obtuse ends. The exine is semitectate (Walker, 1974; Hamzaoglu et al., 2005; Jafari and Nikian, 2008) and muri are simply columellate (Figures 4 and 5).

Hassan et al. (2009) examined the pollen morphology of 7 *Salvia* species distributed in Egypt, including *Salvia aegyptiaca* L., *S. deserti* Decne, *S. lanigera* Poir, *S. palaestina*, *S. sclarea*, *S. spinosa*, and *S. verbenaca* L., and distinguished 4 pollen types: reticulate-perforate in *S. aegyptiaca* and *S. lanigera*; reticulate-granulate in *S. spinosa*; bireticulate in *S. palaestina*, *S. sclarea*, and *S. verbenaca*; and microreticulate in *S. deserti*. According to the present study, SEM microphotographs show that *S. palaestina* and *S. sclarea* also have bireticulate exine sculpturing.

Henderson et al. (1968) sorted 9 pollen grain types of the genus *Salvia* and its allies into somewhat arbitrary groups using only LM. Our results mainly confirm the conclusion of Henderson et al. (1968). However, our study showed that *Salvia montbretii* has perforations in

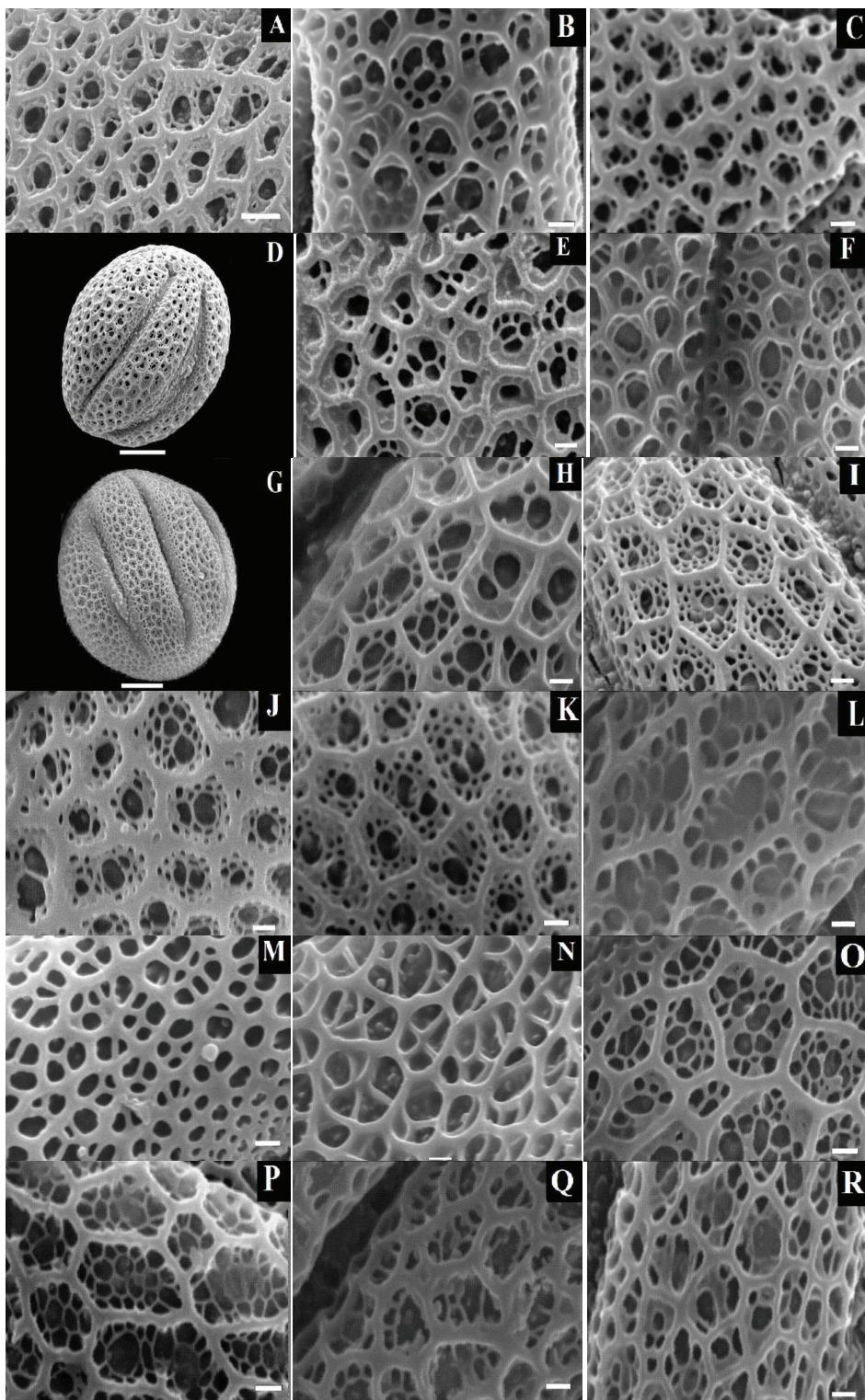


Figure 4. SEM micrographs of pollen grains in the *Salvia* taxa examined. A- *Salvia candidissima* subsp. *candidissima*, B- *S. cassia*, C- *S. ceratophylla*, D & E- *S. chrysophylla*, F- *S. eriophora*, G & H- *S. limbata*, I- *S. macrosiphon*, J- *S. palaestina*, K- *S. sclarea*, L- *S. argentea*, M- *S. blepharochlaena*, N- *S. cadmica*, O- *S. chionantha*, P- *S. microstegia*, Q- *S. modesta*, R- *S. tobeyii*. Scale bars: B, C, E, F, H-R = 1 μm ; D, G = 10 μm ; A = 2 μm .

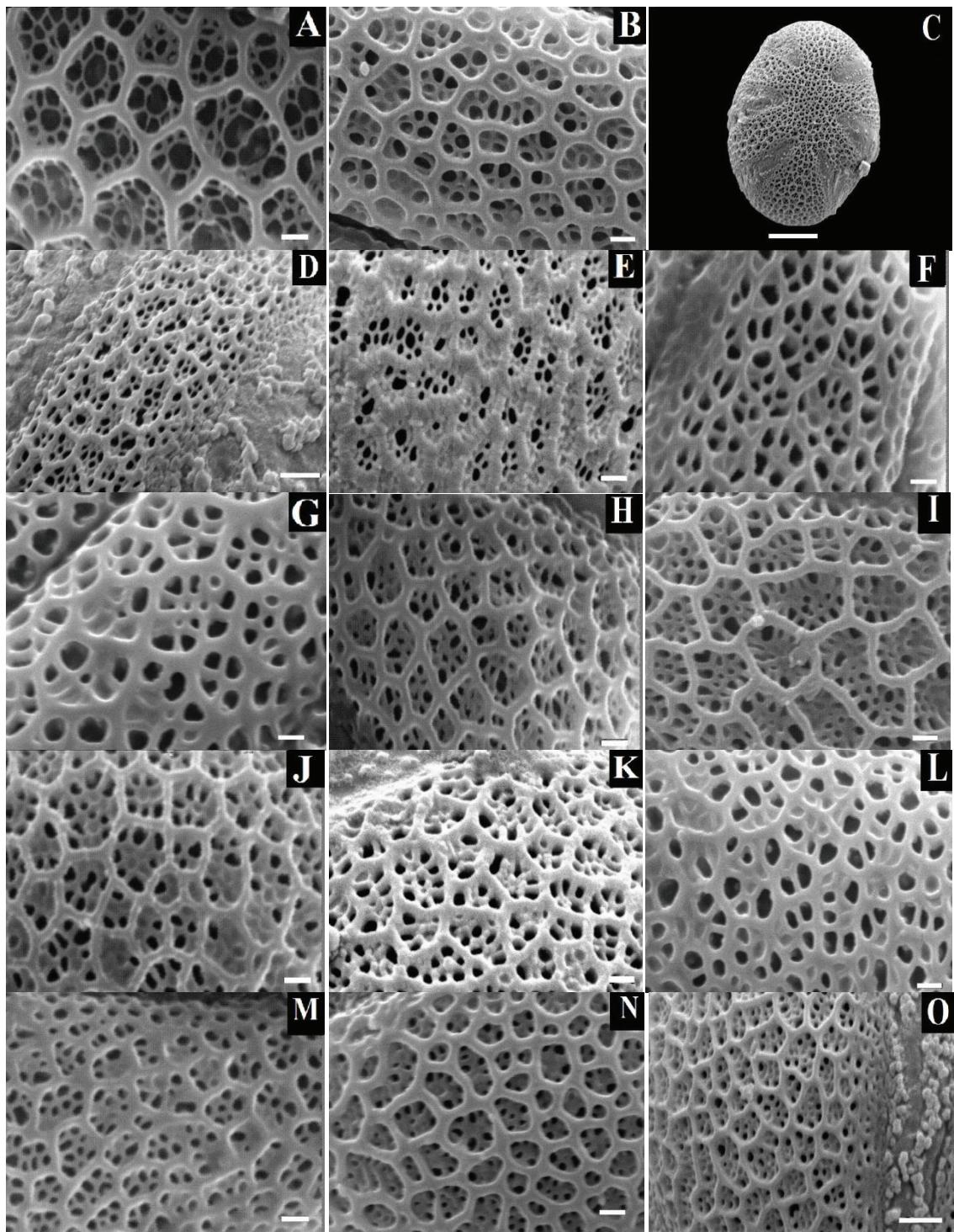


Figure 5. SEM micrographs of pollen grains in the *Salvia* taxa examined. A- *Salvia xanthocheila*, B- *S. yosgadensis*, C & D- *S. aethiopis*, E- *S. atropatana*, F- *S. euphratica* var. *euphratica*, G- *S. euphratica* var. *leiocalycina*, H- *S. frigida*, I- *S. hypargeia*, J- *S. montbretii*, K- *S. pomifera*, L- *S. smyrnaea*, M- *S. syriaca*, N- *S. absconditiflora*, O- *S. multicaulis*. Scale bars: A, B, E-N = 1 µm; C = 10 µm; D, O = 2 µm.

each lumen. In the present study, the free-standing bacula within the lumina, in addition to *S. limbata* and *S. sclarea*, was seen in 14 taxa including *S. candidissima* subsp. *candidissima*, *S. cassia*, *S. chrysophylla*, *S. eriophora*, *S. macrosiphon*, *S. palaestina*, *S. argentea*, *S. blepharochlaena*, *S. cadmica*, *S. chionantha*, *S. microstegia*, *S. modesta*, *S. tobyii*, *S. xanthocheila*, and *S. smyrnaea* (Figures 4 and 5). Heteromorphic exine sculpturing was recorded in *Agastache scrophulariifolia* (Willd.) Kuntze and *Salvia spathacea* Greene by Moon et al. (2008b, 2008c) and in *Nepeta sibthorpii* Benth. subsp. *tumeniana* Dirmenci by Celenk et al. (2008). However, we have not seen this kind of exine sculpturing in the taxa studied.

Moon et al. (2008c) focused on pollen morphology, ultrastructure, and cladistic analyses of subtribe Salviinae and described 3 sexine ornamentation types: perforate, bireticulate, and obviously bireticulate. The bireticulate ornamentation was observed in pollen of the *Salvia* species. According to their findings, *Salvia aethiopis*, *S. palaestina*, and *S. sclarea* consist of 1 or several large lumina in the primary lumen, and their secondary lumina per primary lumen are more than 10. In our study, while the number of secondary lumina per primary lumen is less than 10 in *S. aethiopis*, *S. palaestina* and *S. sclarea* have more than 10 secondary lumina (Table 3; Figures 4 and 5).

The palynological and combined molecular data analysis suggest that sexine sculpturing of pollen in Salviinae may have systematic importance, but some pollen characters may be ecologically constrained (Walker and Sytsma, 2007). The variation in pollen morphological characters appears to have particular value for phylogenetic structuring. They render information not only for classification purposes at sectional rank, but also in delimitation of different species of *Salvia*. However, these characters do not correlate with stamen types, which was suggested by Walker and Systma (2007), even if the character variation appears useful. The value of the pollen characters for taxonomic implications is discussed below.

4.1. Taxonomic consideration of pollen characteristics

The suboblate to spheroidal pollen grains of these taxa have reticulate-perforate and bireticulate sculpturing patterns and angular or extended angular lumina. Based on gross morphology, sect. *Hymenophace* is similar to sect. *Salvia*. The former differs from the latter by its greatly enlarged calyx after anthesis. Pollen morphology of the section *Salvia* was previously studied by Özler et al. (2011). According to the results, pollen morphology does not provide strong evidence in delimitation of the 2 sections. However, in some cases pollen data can be useful for separating closely similar taxa. For example, the morphologically similar species *Salvia cadmica* and *S. smyrnaea* possess different exine sculpturing types: bireticulate and reticulate-perforate, respectively. *S.*

euphratica var. *euphratica* differs from *S. euphratica* var. *leioCALYCINA* by only its hairy inflorescence. The former taxon has mainly prolate-spheroidal pollen grains and the number of primary lumina per 25 μm^2 is 8, while the latter taxon has mainly oblate-spheroidal pollen grains and number of primary lumina per 25 μm^2 is 4.

Salvia absconditiflora and *S. multicaulis* are similar species and their separation based on morphological characters is somewhat difficult, especially in early flowering time. *S. absconditiflora* has angular primary lumina and mostly suboblate pollen grains, while *S. multicaulis* has extended-angular primary lumina and mostly prolate-spheroidal and spheroidal pollen grains.

The suboblate to prolate-spheroidal pollen grains of the examined taxa (except *Salvia cassia*, which is occasionally spheroidal) have reticulate-perforate and bireticulate sculpturing patterns and angular or extended-angular lumina.

In our investigation, there are very closely related species and their separation based on morphological characters is rather difficult. For example, *Salvia argentea*, *S. microstegia*, and *S. xanthochelia*; *S. hypargeia* and *S. montbretii*; *S. cassia* and *S. candidissima* subsp. *candidissima*; *S. atropatana* and *S. chionantha*; and *S. frigida*, *S. tobyii*, and *S. yosgadensis* are each very similar sets of species morphologically. Pollen morphology also does not provide strong evidence in delimitation of *S. argentea*, *S. microstegia*, and *S. xanthochelia* or *S. hypargeia* and *S. montbretii* from each other. Pollen data provide some additional evidence for separating the other closely related species. *S. cassia* has mainly suboblate to subprolate pollen grains and the number of primary lumina per 25 μm^2 is 3; however, *S. candidissima* subsp. *candidissima* has mainly suboblate to oblate-spheroidal pollen grains and the number of primary lumina per 25 μm^2 is 10. In *S. atropatana*, primary lumina are angular and the exine sculpturing is reticulate-perforate. On the other hand, in *S. chionantha*, primary lumina are extended-angular and the exine sculpturing is bireticulate. *S. frigida* has reticulate-perforate sculpturing with type 2a. *S. tobyii* has bireticulate sculpturing with type 1a-2 and *S. yosgadensis* also has bireticulate sculpturing with type 1b.

Among the morphologically distant other taxa (10) in this section, *Salvia aethiopis* and *S. syriaca* are characterized by a reticulate-perforate exine sculpturing pattern, whereas *S. ceratophylla*, *S. chrysophylla*, *S. eriophora*, *S. limbata*, *S. macrosiphon*, *S. modesta*, *S. palaestina*, and *S. sclarea* have a bireticulate exine sculpturing pattern. The number of primary and secondary lumina, diameter of primary and secondary lumina, and pollen size provide support for further separating some of these taxa from each other.

As a conclusion, the results of this study show that pollen morphology sometimes constitutes additional

evidence to delimit the taxa belonging to sections *Hymenophace* and *Aethiopis*. Some taxa of sect. *Aethiopis*, such as *Salvia candidissima* subsp. *candidissima*, *S. cassia*, *S. ceratophylla*, *S. chrysophylla*, *S. eriophora*, *S. limbata*, *S. macrosiphon*, *S. palaestina*, and *S. sclarea* are characterized by 1–4 large central secondary lumina per primary lumen. Some closely related species reveal differences in their pollen structures, and these can serve as differentiating tools.

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Acknowledgments

We wish to thank the curators of the herbaria ANK, AEF, BM, E, G, GAZI, HUB, ISTE, ISTF, K, and W for allowing us to study their *Salvia* collections; the Scientific and Technological Research Council of Turkey (TÜBİTAK, TBAG-104 T 450) for financial assistance; and the anonymous reviewers for their valuable comments and suggestions to improve this paper.

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