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Pollen morphology of some *Gypsophila* L. (Caryophyllaceae) species and its taxonomic value

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Abstract: Pollen morphology of 12 taxa (6 of them endemic) that belong to the genus *Gypsophila* L. were investigated using light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM). Differences in pollen morphology between these taxa were determined based on palynological studies. Pollen grains are spheroidal and polyporate. The exine structure is tectate, but that of *G. sphaerocephala* var. *sphaerocephala* is intectate. The exine sculpture is granulate-microechinate-microperforate, but that of *G. sphaerocephala* var. *sphaerocephala* displays clavate-microechinate ornamentation. The operculum exists in the form of scattered pieces in *G. curvifolia*, while it exists as a whole in the other taxa. *G. perfoliata* var. *perfoliata* has the largest pollen grain diameter, whereas *G. tubulosa* has the smallest. The exine consists of 2 parts; the upper part is the thick ectexine and the lower part is the thin endexine. The endexine is thin and continuous.

Key words: Caryophyllaceae, *Gypsophila*, pollen, LM, SEM, TEM

Bazı *Gypsophila* L. (Caryophyllaceae) türlerinin polen morfolojileri ve taksonomik önemleri

Özet: *Gypsophila* L. cinsinde yer alan altı tanesi endemik on iki taksonun polen morfolojileri ışık (LM), scanning electron (SEM) ve transmission electron (TEM) mikroskopları kullanılarak araştırılmıştır. Palinolojik çalışmalar sonucunda taksonlar arasındaki farklılıklar belirlenmiştir. Polenler sferoid ve poliporat'dır. *G. sphaerocephala* var. *sphaerocephala*'da ekzin yapısı intektat, diğer taksonlarda ise tektat'dır. Ekzin skulpturü *G. sphaerocephala* var. *sphaerocephala*'da klavat-mikroekinat, diğer taksonlarda ise granulat-mikroekinat-mikroperforat ornementasyona sahiptir. Operkulum yapısı *G. curvifolia*'da parçalı, diğerlerinde tamdır. *G. perfoliata* var. *perfoliata* en büyük, *G. tubulosa* ise en küçük polen büyüklüğüne sahip taksonlardır. Ekzin tabakası iki katlıdır, üstte kalın ektekzin altta ise entekzin bulunmaktadır. Entekzin ince ve devamlıdır.

Anahtar sözcükler: Caryophyllaceae, *Gypsophila*, polen, LM, SEM, TEM

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Introduction

The *Caryophyllaceae* is a large, cosmopolitan family of 86 genera, and about 2200 species of herbs and small shrubs (Bittrich, 1993; Heywood, 1998), including over 470 species, of which 32 of the genera exist as native species in Turkey (Davis, 1967; Davis et al., 1988; Güner et al., 2000; Menemen & Hamzaoğlu, 2000; Vural & Dönmez, 2002; Duran & Menemen, 2003; Aytaç & Duman, 2004; Deniz & Düşen, 2004; Ataşlar & Ocak, 2005; Mutlu, 2006; Özhatay & Kültür, 2006; Vural et al., 2006; Bağcı et al., 2007; Ecevit-Genç et al., 2007; Aksoy et al., 2008; Bağcı, 2008; Tugay & Ertuğrul, 2008; Vural, 2008; Kandemir et al., 2009).

Gypsophila L. (*Caryophyllaceae*) is a predominantly Eurasian genus. It is not just among the largest genera of the subfamily *Silenoideae*, but is also one of the most polymorphic. It occurs in the north-temperate part of the Old World; mainly between the latitudes of 30° and 60°. Most *Gypsophila* species are concentrated in a very small part of the geographic area of distribution, which may accurately be called the main variation centre of the genus and includes Turkey, Caucasia, northern Iraq, and northern Iran. In all, 75 of the 126 *Gypsophila* species are represented in this region and 49 of them are endemic to the area. Each of the 3 subgenera and all 8 sections of the genus are represented in this centre of diversity (Barkoudah, 1962).

Gypsophila consists of 55 species, of which 33 are endemic to Turkey (Huber-Morath, 1967; Davis et al., 1988; Ataşlar, 2000; Ataşlar & Ocak, 2005). The morphological features of some *Gypsophila* species pollen grains have been previously studied (Barkoudah, 1962; Chanda, 1962; Moore et al., 1991; Punt & Hoen, 1995; Yıldız, 2001a). There has been no comprehensive study of this genus until now. In the present study the pollen morphology of *Gypsophila sphaerocephala* Fenzl ex Tchihat var. *sphaerocephala* (Sect. *Capituliformes*), *G. arrostii* Guss. var. *nebulosa* (Boiss. & Heldr.) Barkoudah, *G. perfoliata* L. var. *perfoliata*, *G. perfoliata* L. var. *araratica* Kit Tan, *G. curvifolia* Fenzl, *G. eriocalyx* Boiss. var. *eriocalyx*, *G. eriocalyx* Boiss. var. *henrici* (Czecz.) Barkoudah (Sect. *Rokejeka*), *G. parva* Barkoudah, *G. viscosa* Murray (Sect. *Dichoglottis*), *G. tubulosa* (Jaub. & Spach) Boiss. (Sect. *Macrorrhizaea*), *G. pilosa* Huds., and *G. venusta* Fenzl (Sect. *Hagenia*) were investigated. The purpose of this study was to use LM, SEM, and TEM to determine the extent to which morphological differences affect pollen morphology in some species of *Gypsophila*.

Materials and methods

Pollen material was obtained from the Eskişehir Osmangazi University Faculty of Science and Literature Herbarium (OUFE). For LM pollen grains were prepared according to the methods of Wodehouse (1959) and Erdtman (1960). LM observations of non-acetolysed and acetolysed pollen were made using a Prior microscope. Non-acetolysed and acetolysed pollen were photographed with a Spot in-sight colour digital camera on an Olympus microscope equipped with an apochromatic 100× oil immersion objective and compensating 10× eyepieces. Pollen diameter, pore diameter, distance between 2 pori, and exine and intine thickness measurements were made with 50 pollen grains so that the resulting data would follow Gaussian curves (Özdamar, 2004).

Pollen from each species was mounted on stubs using double-sided adhesive tape. Each sample was coated with a 100-Å-thick layer of gold in a Polaron SC7620 rotating and tilting vacuum coating apparatus for 60 s, and scanned using a JEOL 5600 LV SEM with 20-kV accelerating voltage (Walker, 1974a, 1974b).

For TEM acetolysed pollen grains were stained with 2% OsO_4 and with uranyl acetate, dehydrated, and embedded in epon-araldite, according to the method described by Skvarla (1966). Ultrathin sections of pollen grains were obtained with a glass knife in Reichert Ultracut-R microtome. Post-staining was performed with lead citrate for 5 min (Reynolds, 1963) and the sections were examined with a JEOL 1220. Terminology for pollen morphology proposed by Skvarla (1966), Erdtman (1969), Walker (1974a, 1974b), Charpin et al. (1974), Faegri and Iversen (1975), and Punt and Hoen (1995) was used. In all, 5 pollen grain specimens were measured using SEM and TEM.

Specimens investigated

— *G. sphaerocephala* var. *sphaerocephala*: C4: Karaman: Karaman to Mut, 16 km, around Yeniköy, 1450 m, 10 viii 1997, *Ataşlar* (OUFE 7999).

— *G. arrostii* var. *nebulosa*: B3 Afyon: Dinar, Karakuyu, near railway, 1020 m, 27 vii 1996, *Ataşlar* (OUFE 7908). Isparta: Kozluçay, 1110 m, 2 viii 1997, *Ataşlar* (OUFE 7978). C3 Konya: Şarkikaraağaç to Beyşehir, 44 km, 1190 m, 31 vii 1996, *Ataşlar* (OUFE 7910). C4 Karaman: Karaman-Konya highway, 35 km, 1080 m, 10 viii 1997, *Ataşlar* (OUFE 7991).

— *G. perfoliata* var. *perfoliata*: B3 Afyon: Emirdağ-Çifteler crossroads, 1035 m, 7 vii 1996, *Ataşlar* (OUFE 7907a). Afyon: Afyon to Çay, 12 km, 1035 m, 31 vii 1996, *Ataşlar* (OUFE 7911). B4 Aksaray: Sultanhanı to Konya, 2 km, 990 m, 6 vii 1996, *Ataşlar* (OUFE 7904). Aksaray: Eskil, Koçlar, 1050 m, 6 vii 1996, *Ataşlar* (OUFE 7905a). Kırıkkale: Kırıkkale to Ankara, 12 km, 690 m, 17 viii 1997, *Ataşlar* (OUFE 7993). Konya: Cihanbeyli, Boluk Lake, 1000 m, 7 vii 1996, *Ataşlar* (OUFE 7906). Konya: Konya-Karaman highway, 20 km Kaşınhan, 1035 m, 9 viii 1997, *Ataşlar* (OUFE 7987a).

— *G. perfoliata* var. *araratica*: B3 Afyon: Emirdağ-Çifteler crossroads, 1035 m, 7 vii 1996, *Ataşlar* (OUFE 7907b). B4 Aksaray: Eskil, Koçlar, 1050 m, 6 vii 1996, *Ataşlar* (OUFE 7905b). C4 Konya: Konya-Karaman highway, 20 km Kaşınhan, 1035 m, 9 viii 1997, *Ataşlar* (OUFE 7987b).

— *G. curvifolia*: C4 Karaman: Başyayla to Ermenek, 28 km, 1650 m, 9 viii 1997, *Ataşlar* (OUFE 7989). Karaman: Sarıveliler, Uğurlu, 1600 m, 30 vii 1996, *Ataşlar* (OUFE 7909).

— *G. eriocalyx* var. *eriocalyx*: A4 Çankırı: Kalecik to Çankırı, 3 km, 710 m, 5 vii 1996, *Ataşlar* (OUFE 7901). B3 Eskişehir: Sivrihisar to Afyon, 11 km, 870 m, 4 vii 1996, *Ataşlar* (OUFE 7893). B4 Ankara: 30 km west of Polatlı, 840 m, 4 vii 1996, *Ataşlar* (OUFE 7894).

— *G. eriocalyx* var. *henrici*: A4 Çankırı: Çankırı to Korgun, 740 m, 5 vii 1996, *Ataşlar* (OUFE 7896). Çankırı: Yapraklı, Yukarıöz road, 920 m, 5 vii 1996, *Ataşlar* (OUFE 7898). Çankırı: İkizören road, 980 m, 5 vii 1996, *Ataşlar* (OUFE 7899). Çankırı: Eldivan road, 4 km, 675 m, 19 vii 1997, *Ataşlar* (OUFE 7968). B4 Ankara: Ankara to Şereflikoçhisar, starting point of Tuz Gölü, 960 m, 6 vii 1996, *Ataşlar* (OUFE 7902). B5 Aksaray: north of Aksaray, 50 km, 980 m, 6 vii 1996, *Ataşlar* (OUFE 7903).

— *G. parva*: A4 Çankırı: Korgun, Yukarı Çavuş, 870 m, 7 vi 1997, *Ataşlar* (OUFE 7934). Çankırı: Yapraklı, Yüklü, 970 m, 7 vi 1997, *Ataşlar* (OUFE 7936). Çankırı: İkizören, Subaşı village, Musuyeri, 1325 m, 7 vi 1997, *Ataşlar* (OUFE 7938). Çankırı: İkizören, Yamaçbağ village, Kötüoluk, 1420 m, 7 vi 1997, *Ataşlar* (OUFE 7939).

— *G. viscosa*: B3 Eskişehir: Eskişehir to Sivrihisar, 40 km, 910 m, 26 v 1996, *Ataşlar* (OUFE 7883). Afyon: Benliyaver village, 865 m, 31 v 1997, *Ataşlar* (OUFE 7919). B4 Aksaray: Sultanhanı to Akhan, 4 km, 965 m, 9 vi 1997, *Ataşlar* (OUFE 7954). Ankara: Gölbaşı to Ahiboz, 1110 m, 9 vi 1997, *Ataşlar* (OUFE 7955). Konya: Cihanbeyli Bozdağ, 940 m, 1 vi 1997, *Ataşlar* (OUFE 7925). Kırıkkale: Keskin road, 3 km, 750 m, 8 vi 1997, *Ataşlar* (OUFE 7942). B5 Nevşehir: Nevşehir to Aksaray, 4 km, 1100 m, 9 vi 1997, *Ataşlar* (OUFE 7953).

— *G. tubulosa*: B1 Manisa: Kula, Volcano (Divlit Mountain), 690 m, 14 vi 1996, *Ataşlar* (OUFE 7886). B2 Uşak: 12 km, west of Kayaağıl village, 830 m, 14 vi 1996, *Ataşlar* (OUFE 7885). Manisa: Sarıgöl to Buldan, 2 km, 390 m, 16 vi 1996, *Ataşlar* (OUFE 7887). Denizli: Buldan, Yaylagölü, 1200 m, 16 vi 1996, *Ataşlar* (OUFE 7889). C1 Aydın: Nazilli, Hamidiye village, 160 m, 29 vi 1997, *Ataşlar* (OUFE 7966).

— *G. pilosa*: A4 Çankırı: Korgun road, 2 km, 755 m, 7 vi 1997, *Ataşlar* (OUFE 7933). B3 Eskişehir: Osmangazi University Campus, 810 m, 18 vi 1997, *Ataşlar* (OUFE 7964). Konya: Akşehir, Yeşilköy, 970 m, 1 vi 1997, *Ataşlar* (OUFE 7923). B4 Ankara: Ankara to Polatlı, 40 km, 870 m, 4 vii 1996, *Ataşlar* (OUFE 7895). Aksaray: Akhan to Sultanhanı, 4 km, 965 m, 9 vi 1997, *Ataşlar* (OUFE 7954).

— *G. venusta*: B4 Aksaray: 1 km, north-west of Topakkaya, 980 m, 9 vi 1997, *Ataşlar* (OUFE 7952). Ankara: Şereflikoçhisar, Kaldırım Tuzlası, 950 m, 8 vi 1997, *Ataşlar* (OUFE 7950). Kırıkkale: Çelebi to Kaman, 3 km, 1020 m, 8 vi 1997, *Ataşlar* (OUFE 7943). Konya: Ahırlı, 1115 m, 14 vi 1997, *Ataşlar* (OUFE 7960).

Results

General pollen properties and structure of the exine of *Gypsophila* species

Gypsophila pollen grains ranged in size range from 23.79 to 32.84 μm in non-acetolysed pollen and from

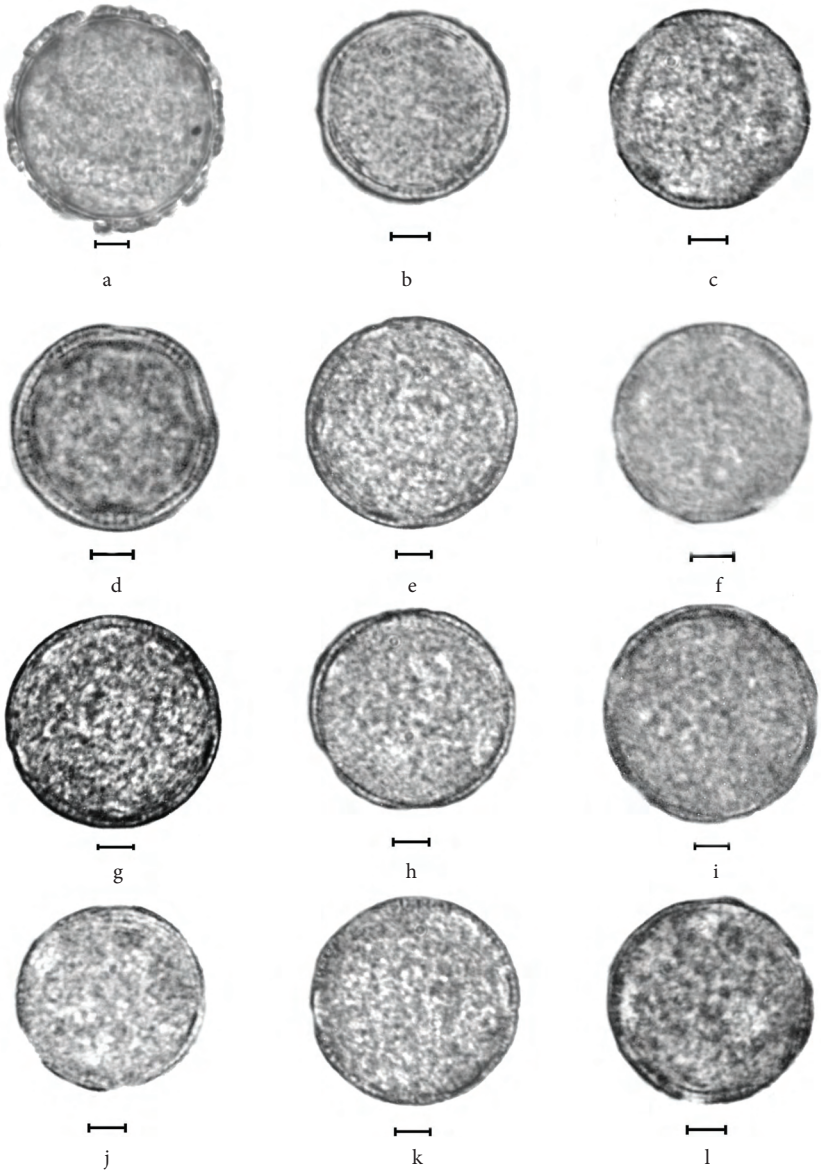

Figure 1. Non-acetolysed pollen, LM (bar: 5 μm). a. *Gypsophila sphaerocephala* var. *sphaerocephala*, b. *G. arrostii* var. *nebulosa,* c. *G. perfoliata* var. *perfoliata,* d. *G. perfoliata* var. *araratica,* e. *G. curvifolia,* f. *G. eriocalyx* var. *eriocalyx,* g. *G. eriocalyx* var. *henrici,* h. *G. parva,* i. *G. viscosa,* j. *G. tubulosa,* k. *G. pilosa,* l. *G. venusta*.

19.48 to 25.94 μm in acetolysed pollen. The structure of the exine is tectate. Mean exine thickness between the regions of the pores varies from 1.03 to 1.85 μm. It tapers gradually towards the pore endings. While ornamentation is clavate-microechinate in *G. sphaerocephala* var. *sphaerocephala*, it is granulate-microechinate-microperforate in the other species. While spinules have a homogeneous distribution over the surface of the pollen grain exine, they have a circular distribution around the aperture (Figures 1-6).

The exine consists of 2 parts: the upper part is the thick ectexine and the lower part is the thin endexine. The tectum, with spinules, is thick with thin lines cutting across it at intervals. Infratectal columellae hang down from the tectum. Being thick and short,

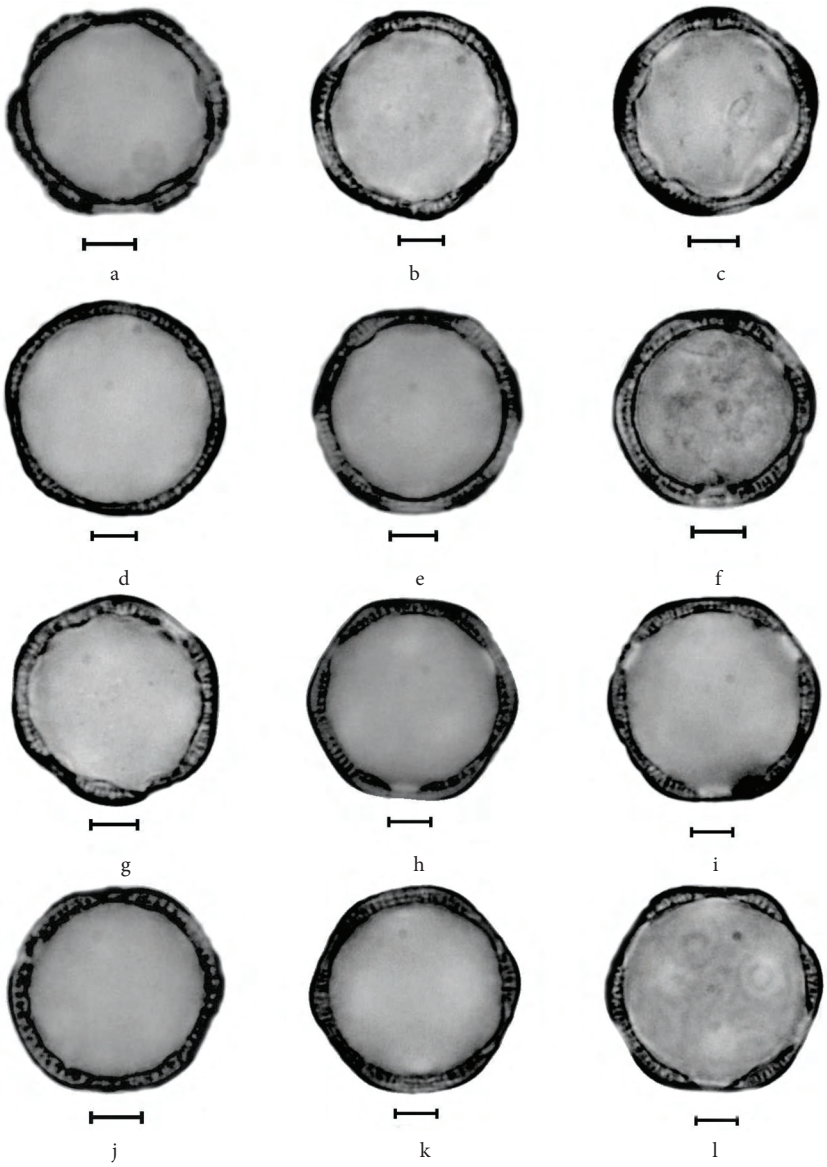

Figure 2. Acetolysed pollen, LM (bar: 5 µm). a. *Gypsophila sphaerocephala* var. *sphaerocephala,* b. *G. arrostii* var. *nebulosa,* c. *G. perfoliata* var. *perfoliata,* d. *G. perfoliata* var. *araratica,* e. *G. curvifolia,* f. *G. eriocalyx* var. *eriocalyx,* g. *G. eriocalyx* var. *henrici,* h. *G. parva,* i. *G. viscosa,* j. *G. tubulosa,* k. *G. pilosa,* l. *G. venusta.*

infratectal columellae do not branch out. The foot layer is continuous and is always thinner than the tectum. The endexine is thin and continuous. The operculum covers the entire pore and is surrounded by an annulus. The ectexine of the pore membrane is fairly thin (Figures 5, 6).

There are spinules in the form of convex cones that vary from 5-25 in number over the operculum, according to the species. The endexine is thick, with a large granule extending under the operculum and the thin ectexine of the pore membrane.

LM investigations show that the pollen grains are spheroidal, polyporate, tectate, and granulate (Figures 1, 2), while those of *G. sphaerocephala* var. *sphaerocephala* are spheroidal, polyporate, intectate, and clavate (Figures 1a, 2a).The comparative results of LM are given in Table 1; those of SEM and TEM are in Table 2.

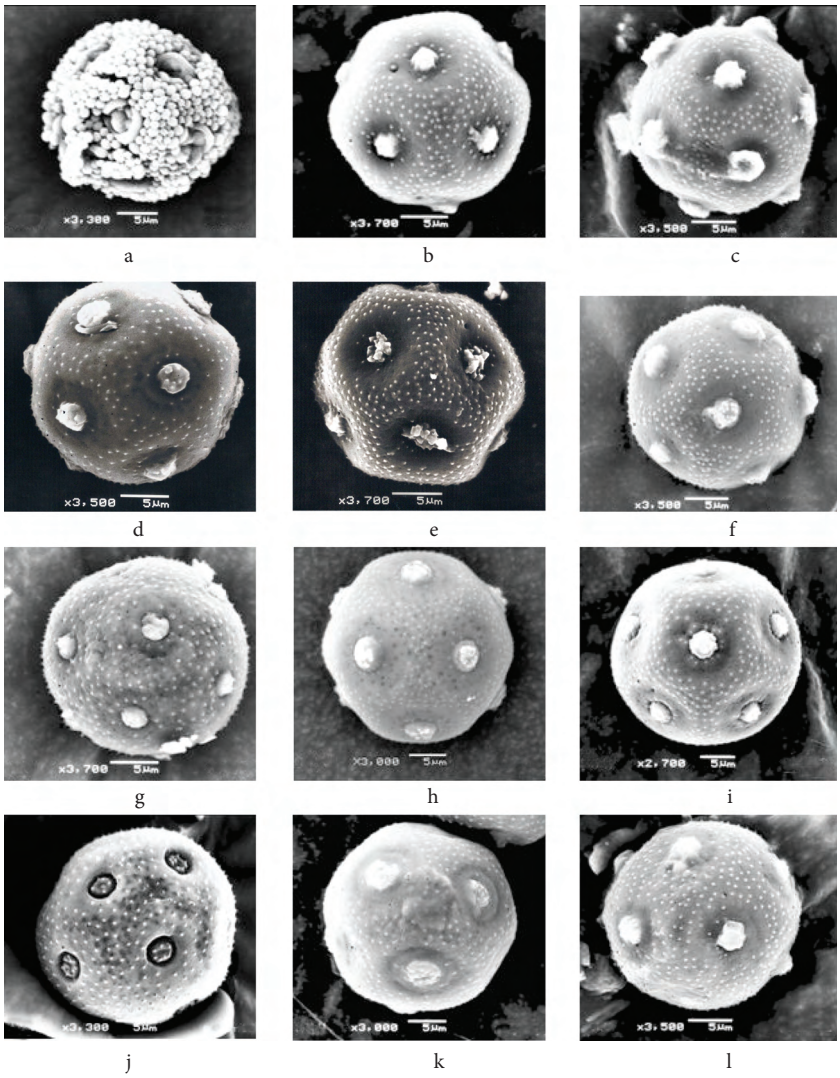

Figure 3. Ornamentation of the pollen, SEM (bar: 5 μm). a. *Gypsophila sphaerocephala* var. *sphaerocephala,* b. *G. arrostii* var. *nebulosa,* c. *G. perfoliata* var. *perfoliata,* d. *G. perfoliata* var. *araratica,* e. *G. curvifolia,* f. *G. eriocalyx* var. *eriocalyx,* g. *G. eriocalyx* var. *henrici,* h. *G. parva,* i. *G. viscosa,* j. *G. tubulosa,* k. *G. pilosa,* l. *G. venusta*.

In *G. sphaerocephala* var. *sphaerocephala***,** the exine is caveate, and the endexine is thin and continuous. The intectal layer is thick and clavate-microechinate in the interspine regions. The pollen surface is covered with clavae and spinules. Clavae are 1.15 μm long × 1.41 μm wide and spinules are 1.1 μm long × 0.94 μm wide. There are 21.92 spinules

100 μm^2 and the distance between 2 spinules is 2.5-3 μm. The intectum is 1.5 μm, the foot layer is 0.25 μm, and the endexine is 0.125 μm. The foot layer is continuous and the foot layer/endexine ratio is 5:1. The ectexine/endexine ratio is 11:1. The operculum is entire. The pore and operculum are covered with clavae and spinules. Mean operculum length is 3.05 μm and the endexine is continuous on the operculum (Figures 1a, 2a, 3a, 4a, 5a, and 6a).

In *G. arrostii* var. *nebulosa* the exine is caveate and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with supratectal spinules. Supratectal spinules are 0.26 μm

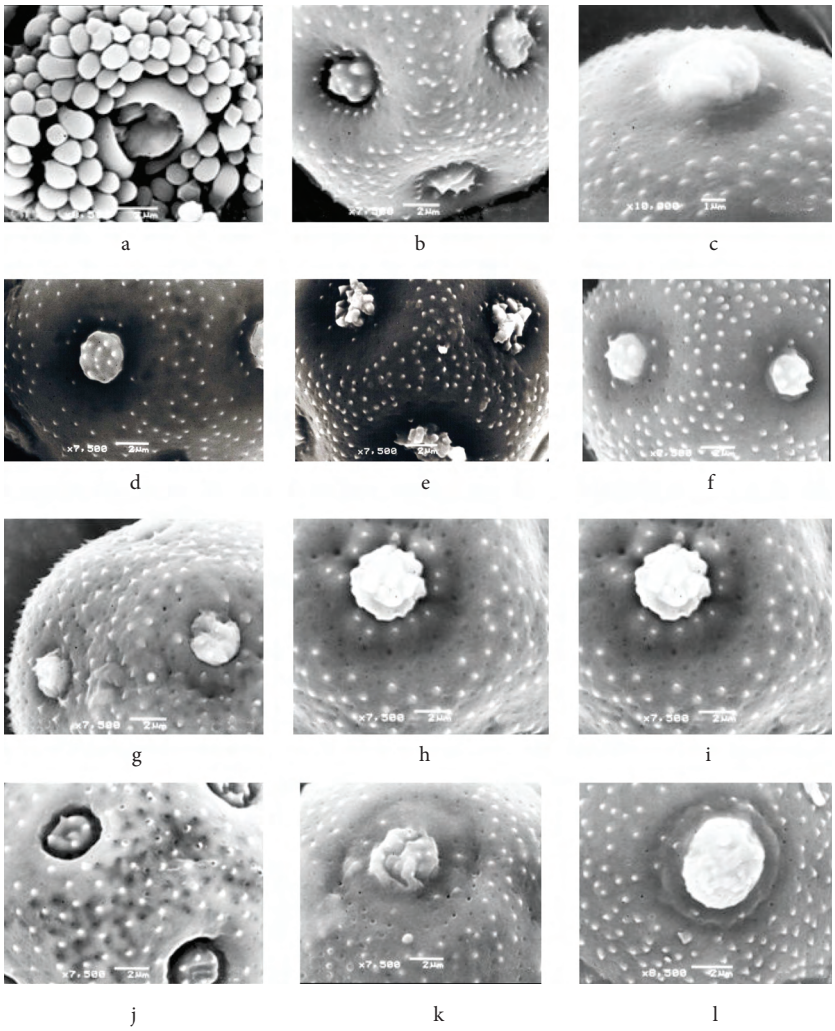

Figure 4. Detail of ornamentation, SEM (bar: 2 µm). a. *Gypsophila sphaerocephala* var. *sphaerocephala,* b. *G. arrostii* var. *nebulosa,* c. *G. perfoliata* var. *perfoliata,* d. *G. perfoliata* var. *araratica,* e. *G. curvifolia,* f. *G. eriocalyx* var. *eriocalyx,* g. *G. eriocalyx* var. *henrici,* h. *G. parva,* i. *G. viscosa,* j. *G. tubulosa,* k. *G. pilosa,* l. *G. venusta.*

long × 0.28 µm wide. There are 85.76 spinules 100 µm^2 and the distance between 2 spinules is 0.5-2 µm. The tectum is 1 µm, the foot layer is 0.375 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 3:1. The ectexine/endexine ratio is 10:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 2.8 µm (Figures 1b, 2b, 3b, 4b, 5b, and 6b).

In *G. perfoliata* var. *perfoliata* the exine is caveate, and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with supratectal spinules. Supratectal spinules are 0.28 µm long × 0.32 µm wide. In total, there are 104.09 spinules 100 µm^2 and the distance between 2 spinules is 0.5-2 µm. The tectum is 1.5 µm, the foot layer is 0.25 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 6:1. The ectexine/endexine ratio is 13:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 4 µm (Figures 1c, 2c, 3c, 4c, 5c, and 6c).

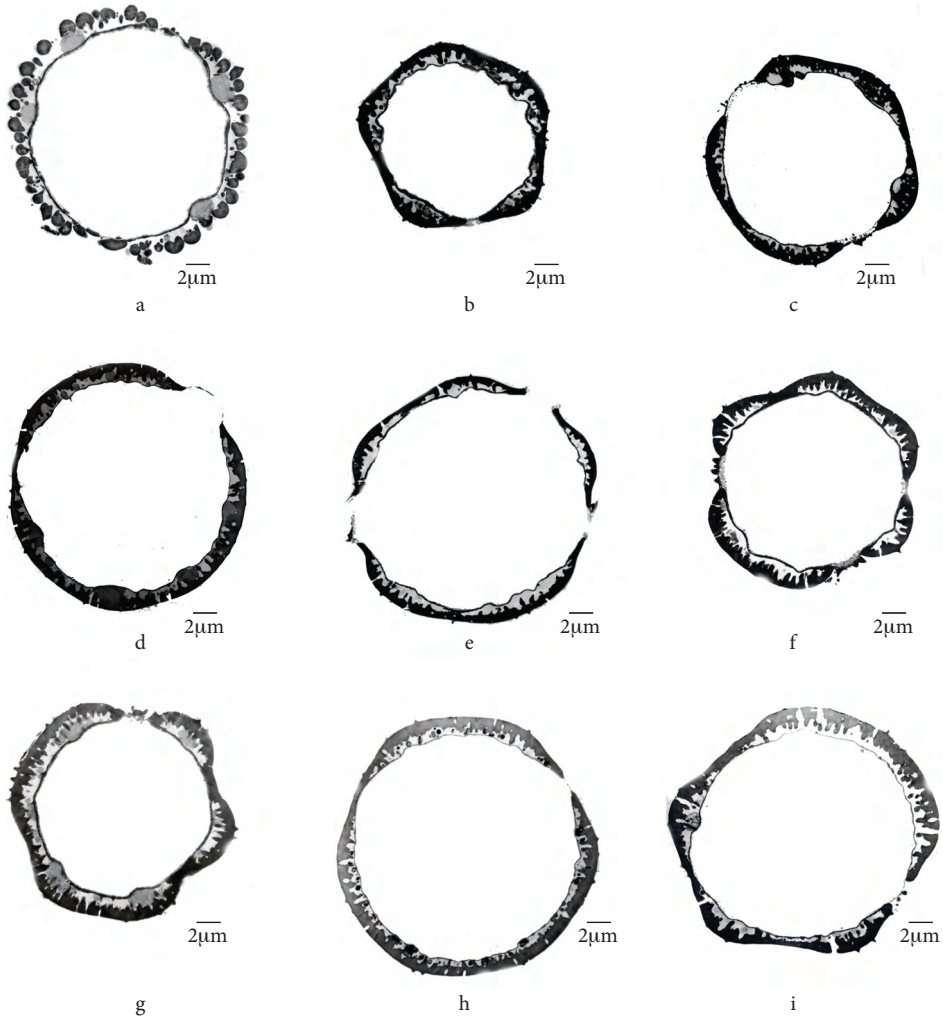

Figure 5. Transverse section of the exine structure, TEM (bar: 2 µm). a. *Gypsophila sphaerocephala* var. *sphaerocephala,* b. *G. arrostii* var. *nebulosa,* c. *G. perfoliata* var. *perfoliata,* d. *G. perfoliata* var. *araratica,* e. *G. curvifolia,* f. *G. eriocalyx* var. *eriocalyx,* g. *G. eriocalyx* var. *henrici,* h. *G. parva,* i. *G. viscosa,* j. *G. tubulosa,* k. *G. pilosa,* l. *G. venusta*.

In *G. perfoliata* var. *araratica* the exine is caveate, and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with supratectal spinules. Supratectal spinules are 0.22 µm long × 0.26 µm wide. There are 74.46 spinules 100 µm^2 and the distance between 2 spinules is 0.5-2 µm. The tectum is 1.25 µm, the foot layer is 0.5 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 1:1. The ectexine/endexine ratio is 13:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 2.87 µm (Figures 1d, 2d, 3d, 4d, 5d, and 6d).

In *G. curvifolia* the exine is caveate and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with supratectal spinules. Supratectal spinules are 0.18 µm long × 0.24 µm wide. There are 87.65 spinules

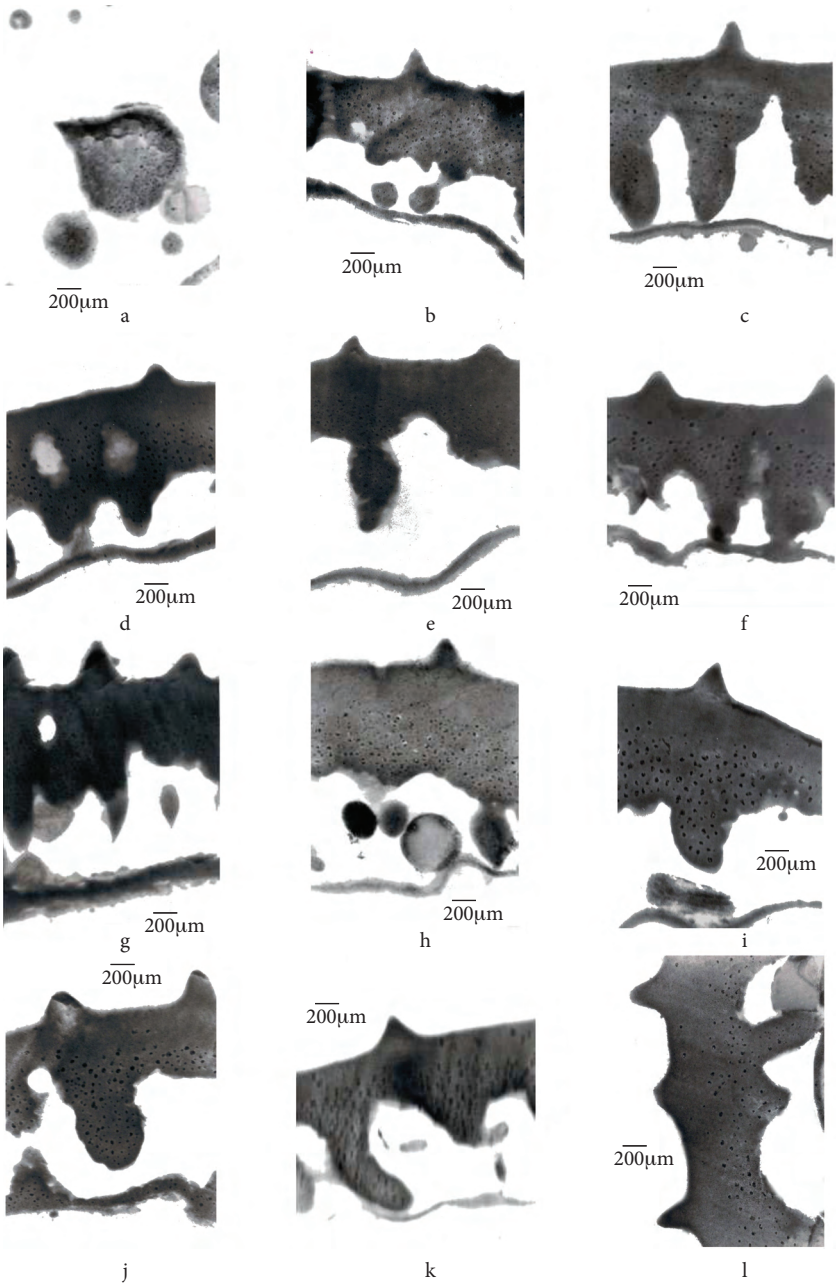

Figure 6. Detail of a transverse section of the exine structure, TEM (bar: 200 nm). a. *Gypsophila sphaerocephala* var. *sphaerocephala,* b. *G. arrostii* var. *nebulosa,* c. *G. perfoliata* var. *perfoliata,* d. *G. perfoliata* var. *araratica,* e. *G. curvifolia,* f. *G. eriocalyx* var. *eriocalyx,* g. *G. eriocalyx* var. *henrici,* h. *G. parva,* i. *G. viscosa,* j. *G. tubulosa,* k. *G. pilosa,* l. *G. venusta*.

100 µm^2 and the distance between 2 spinules is 0.5-1 µm. The tectum is 1.5 µm, the foot layer is 0.375 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 5:1. The ectexine/endexine ratio is 15:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 3.6 µm (Figures 1e, 2e, 3e, 4e, 5e, and 6e).

Table 1. Morphological parameters of *Gypsophila* species pollen.

Taxa	A (µm)	B (µm)	A/B	pa (µm)	pb (µm)	p (µm)	Ex (µm)	I (µm)	i (µm)
G. sphaerocephala var. *sphaerocephala* (N)*	30.76 ± 3.77	29.96 ± 3.53	1.02	non-meas.	non-meas.	5.74 ± 0.82	1.74 ± 0.30	0.92 ± 0.23	non-meas.
G. sphaerocephala var. *sphaerocephala* (Ac)	23.36 ± 1.45	22.96 ± 1.57	1.01	non-meas.	non-meas.	4.20 ± 0.67	1.85 ± 0.70	non-meas.	non-meas.
G. arrostii var. *nebulosa* (N)*	25.49 ± 1.18	25.17 ± 1.16	1.01	5.43 ± 0.66	4.59 ± 0.75	non-meas.	1.50 ± 0.35	1.43 ± 0.39	0.61 ± 0.21
G. arrostii var. *nebulosa* (Ac)	23.26 ± 0.96	22.76 ± 1.04	1.02	non-meas.	non-meas.	4.18 ± 0.80	1.82 ± 0.28	non-meas.	non-meas.
G. perfoliata var. *perfoliata* (N)*	32.84 ± 1.36	32.62 ± 1.44	1.00	7.55 ± 0.80	6.64 ± 0.80	non-meas.	1.51 ± 0.42	1.04 ± 0.13	0.60 ± 0.20
G. perfoliata var. *perfoliata* (Ac)	22.96 ± 1.24	22.62 ± 1.25	1.01	non-meas.	non-meas.	3.80 ± 0.72	1.49 ± 0.37	non-meas.	non-meas.
G. perfoliata var. *araratica* (N)*	28.96 ± 1.12	28.96 ± 1.12	1.00	7.55 ± 0.80	4.83 ± 0.74	non-meas.	1.25 ± 0.25	1.00 ± 0.00	0.50 ± 0.00
G. perfoliata var. *araratica* (Ac)	23.44 ± 1.24	22.84 ± 1.34	1.02	non-meas.	non-meas.	3.95 ± 0.65	1.63 ± 0.31	non-meas.	non-meas.
G. curvifolia (N)*	29.38 ± 2.44	29.36 ± 2.41	1.00	5.58 ± 0.64	5.18 ± 0.69	non-meas.	1.20 ± 0.28	1.00 ± 0.00	0.50 ± 0.00
G. curvifolia (Ac)	23.90 ± 1.28	23.36 ± 1.42	1.02	non-meas.	non-meas.	4.06 ± 0.58	1.24 ± 0.30	non-meas.	non-meas.
G. eriocalyx var. *eriocalyx* (N)*	24.32 ± 0.86	24.14 ± 0.80	1.00	5.16 ± 0.42	4.58 ± 0.57	non-meas.	1.54 ± 0.29	0.92 ± 0.17	0.54 ± 0.14
G. eriocalyx var. *eriocalyx* (Ac)	20.00 ± 0.83	19.48 ± 0.81	1.02	non-meas.	non-meas.	3.64 ± 0.59	1.55 ± 0.32	non-meas.	non-meas.
G. eriocalyx var. *henrici* (N)*	27.46 ± 2.40	27.10 ± 2.44	1.01	5.72 ± 0.68	4.98 ± 0.87	non-meas.	1.74 ± 0.30	1.07 ± 0.33	0.58 ± 0.18
G. eriocalyx var. *henrici* (Ac)	22.22 ± 1.09	22.22 ± 1.09	1.02	non-meas.	non-meas.	4.06 ± 0.58	1.59 ± 0.35	non-meas.	non-meas.
G. parva (N)*	29.55 ± 1.02	29.38 ± 1.07	1.00	5.92 ± 0.70	4.92 ± 0.61	non-meas.	1.42 ± 0.34	1.18 ± 0.29	0.57 ± 0.18
G. parva (Ac)	24.24 ± 0.98	23.64 ± 0.92	1.02	non-meas.	non-meas.	4.04 ± 0.60	1.22 ± 0.30	non-meas.	non-meas.
G. viscosa (N)*	32.27 ± 1.07	31.96 ± 1.14	1.00	6.59 ± 0.62	5.37 ± 0.49	non-meas.	1.03 ± 0.12	1.26 ± 0.27	0.51 ± 0.07
G. viscosa (Ac)	25.94 ± 1.62	25.28 ± 1.66	1.02	non-meas.	non-meas.	4.24 ± 0.71	1.21 ± 0.28	non-meas.	non-meas.
G. tubulosa (N)*	24.17 ± 1.30	23.79 ± 1.42	1.01	4.98 ± 0.42	4.37 ± 0.59	non-meas.	1.34 ± 0.38	1.54 ± 0.37	0.64 ± 0.22
G. tubulosa (Ac)	20.92 ± 1.04	20.44 ± 0.86	1.02	non-meas.	non-meas.	3.82 ± 0.59	1.16 ± 0.25	non-meas.	non-meas.
G. pilosa (N)*	28.32 ± 1.47	27.83 ± 1.42	1.01	6.49 ± 0.61	5.40 ± 0.77	non-meas.	1.37 ± 0.28	1.06 ± 0.16	0.54 ± 0.13
G. pilosa (Ac)	24.72 ± 1.40	24.20 ± 1.48	1.02	non-meas.	non-meas.	4.66 ± 0.82	1.11 ± 0.25	non-meas.	non-meas.
G. venusta (N)*	27.00 ± 1.08	26.61 ± 1.18	1.01	5.86 ± 0.62	4.88 ± 0.66	non-meas.	1.49 ± 0.34	1.25 ± 0.32	0.60 ± 0.20
G. venusta (Ac)	24.36 ± 1.10	23.94 ± 1.11	1.01	non-meas.	non-meas.	4.60 ± 0.67	1.25 ± 0.29	non-meas.	non-meas.

N: Non-acetolysed pollen grains (LM); **Ac:** acetolysed pollen grains (LM); **A:** long axis; **B:** short axis; **p:** pore; **pa:** pore length; **pb:** pore width; **Ex:** exine at the thickest area; **I:** intine at the thickest area; **i:** intine; **non-meas.:** non-measurable. *These data are from Ataşlar's PhD thesis.

Table 2. Morphological parameters of *Gypsophila* species pollen.

Taxa	Pollen Type	Pollen Shepe	Ornamentation	Tectum	Columella	Annulus	Supratectal Spinules (µm)	Spinules (100 µm^2)	Distance of two spinules	Footlayer/ Endexine	Ectexine/ Endexine	Operculum length (µm)	Exine N-Ac (µm)
G. sphaerocephala var. *sphaerocephala*	polyporate	spheroidal	clavate-microechinate	intectate	single-layered	1.29	1.1-0.94	21.92	2.5-3.0	5/1	11/1	3.05	1.74-1.85
G. arrostii var. *nebulosa*	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	0.80	0.26-0.28	85.76	0.5-2.0	3/1	10/1	2.80	1.50-1.82
G. perfoliata var. *perfoliata*	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	2.60	0.28-0.32	104.09	0.5-2.0	6/1	13/1	4.00	1.51-1.49
G. perfoliata var. *araratica*	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	0.50	0.22-0.26	74.46	0.5-2.0	1/1	13/1	2.87	1.25-1.63
G. curvifolia	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	1.60	0.18-0.24	87.65	0.5-1.0	5/1	15/1	3.60	1.20-1.24
G. eriocalyx var. *eriocalyx*	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	1.62	0.22-0.34	99.27	0.5-2.0	2/1	13/1	2.62	1.54-1.55
G. eriocalyx var. *henrici*	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	1.33	0.32-0.36	87.90	0.5-2.5	2/1	8/1	2.66	1.74-1.59
G. parva	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	1.46	0.26-0.30	51.98	0.5-2.0	1/1	15/1	2.08	1.42-1.22
G. viscosa	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	1.86	0.28-0.34	46.78	0.5-2.5	8/1	18/1	4.00	1.03-1.21
G. tubulosa	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	0.53	0.28-0.32	42.00	0.5-2.5	1/1	7/1	2.80	1.34-1.16
G. pilosa	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	2.13	0.24-0.34	34.44	0.5-2.0	3/1	16/1	4.00	1.37-1.11
G. venusta	polyporate	spheroidal	granulate-microechinate	pertectate	single-layered	1.41	0.30-0.35	91.08	0.5-2.0	3/1	16/1	3.73	1.49-1.25

In *G. eriocalyx* var. *eriocalyx* the exine is caveate, and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with supratectal spinules. Supratectal spinules are 0.22 µm long × 0.34 µm wide. There are 99.27 spinules 100 µm^2 and the distance between 2 spinules is 0.5-2 µm. The tectum is 1.5 µm, the foot layer is 0.125 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 2:1. The ectexine/endexine ratio is 13:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 2.62 µm (Figures 1f, 2f, 3f, 4f, 5f, and 6f).

In *G. eriocalyx* var. *henrici* the exine is caveate, and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with supratectal spinules. Supratectal spinules are 0.32 µm long × 0.36 µm wide. There are 87.90 spinules 100 µm^2 and the distance between 2 spinules is 0.5-2.5 µm. The tectum is 1.75 µm, the foot layer is 0.375 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 2:1. The ectexine/endexine ratio is 8:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 2.66 µm (Figures 1g, 2g, 3g, 4g, 5g, and 6g).

In *G. parva* the exine is caveate, and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with supratectal spinules. Supratectal spinules are 0.26 µm long × 0.30 µm wide. There are 51.98 spinules 100 µm^2 and the distance between 2 spinules is 0.5-2 µm. The tectum is 1.5 µm, the foot layer is 0.5 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 1:1. The ectexine/endexine ratio is 15:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 2.08 µm (Figures 1h, 2h, 3h, 4h, 5h, and 6h).

In *G. viscosa* the exine is caveate, and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with supratectal spinules. Supratectal spinules are 0.28 µm long × 0.34 µm wide. There are 46.78 spinules 100 µm^2 and the distance between 2 spinules is 0.5-2.5 µm. The tectum is 1.5 µm, the foot layer is 0.375 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 8:1. The ectexine/endexine ratio is 18:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 4 µm (Figures 1i, 2i, 3i, 4i, 5i, and 6i).

In *G. tubulosa* the exine is caveate, and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with supratectal spinules. Supratectal spinules are 0.28 µm long × 0.32 µm wide. There are 42.00 spinules 100 µm^2 and the distance between 2 spinules is 0.5-2.5 µm. The tectum is 1.5 µm, the foot layer is 0.25 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 1:1. The ectexine/endexine ratio is 7:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 2.8 µm (Figures 1j, 2j, 3j, 4j, 5j, and 6j).

In *G. pilosa* the exine is caveate, and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with supratectal spinules. Supratectal spinules are 0.24 µm long × 0.34 µm wide. There are 34.44 spinules 100 µm^2 and the distance between 2 spinules is 0.5-2 µm. The tectum is 1 µm, the foot layer is 0.5 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 3:1. The ectexine/endexine ratio is 16:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 4 µm (Figures 1k, 2k, 3k, 4k, 5k, and 6k).

In *G. venusta* the exine is caveate, and the endexine is thin and continuous. The tectum is thick and pertectate, and granulate-microechinate-microperforate in the interspine regions. Columellae are single-layered. The pollen surface is covered with

supratectal spinules. Supratectal spinules are 0.30 µm long × 0.35 µm wide. There are 91.08 spinules 100 μm^2 and the distance between 2 spinules is 0.5-2 µm. The tectum is 1.25 µm, the foot layer is 0.5 µm, and the endexine is 0.125 µm. The foot layer is continuous and the foot layer/endexine ratio is 3:1. The ectexine/endexine ratio is 16:1. The operculum is entire and covered with spinules. The pore is smooth. Mean operculum length is 3.73 µm (Figures 1l, 2l, 3l, 4l, 5l, and 6l).

Discussion

Our results show that the pollen of all 12 *Gypsophila* taxa are polyporate and spheroidal. The exine sculptures of *G. sphaerocephala* var. *sphaerocephala* were observed to be intectate with clavate-microperforate ornamentation, while those of the remaining *Gypsophila* taxa were tectate with granulate-microechinate-microperforate ornamentaion. *G. sphaerocephala* var. *sphaerocephala* was assumed to be more evolutive than the other species, based on a consideration of all the aforementioned features. It has been reported that the aperture features and exine structures are among the essential criteria for determination of phylogenetic relationships of *Gypsophila* species (Kuprianova, 1967; Cronquist, 1968; Walker, 1974a, 1974b; Takhtajan, 1980).

Caryophyllaceae pollen grains are sub-oblate-subprolate (if 3-colpate), and spherical or ± rounded polyhedral (if porate or pantocolpate). They range in diameter from 24 to 65 µm in pantocolpate and pantoporate pollen grains, and from 12.5 × 8 µm to 28 × 23 µm in tricolpate and triporate grains. The exine is tectate, and the tectum is mostly punctitegillate or occasionally anulopunctate, rarely reticulate (some *Silene* spp. Melzheimer, 1975; *Cerastium indicum* Iwarsson, 1977), and finely spinulose (Bittrich, 1993).

Caryophyllaceae pollen grains are tricolpate (rarely tricolporate in *Polycarpaea* spp. Al-Eisawi, 1989) mainly in Paronychioideae, but it was also reported that 3-colpate pollen from 4 species of Caryophylloideae existed in *Minuartia* subg. *Rhodalsine* (McNeill & Bassett, 1974) and *Pycnophyllum* (Alsinoideae) (Vishnu-Mittre & Gupta, 1964). Nevertheless, this is most certainly due to an error because pollen from specimens of 3 species mentioned by the authors was pantoporate (Bittrich, 1993). All other investigators have invariably observed pantoporate pollen in the Caryophylloideae. Pollen grains of *Spergula arvensis* (Polycarpeae) were 3-12 colpate (Erdtman et al., 1961) and the apertures of *Spergularia salina* pollen grains vary from hexapanto-colpate to pantoporate, or are spiral (Al-Eisawi, 1989). Candau (1978) observed 4-6 colpate and 5-10-porate pollen in 4 different species of *Herniaria*. *Corrigiola litoralis* and *C. capensis* (Paronychioideae) are 3(4)-porate. Pantoporate pollen (with few pores, 6-14) is rare in Paronychioideae. It is, however, coµmon in Alsinoideae and Caryophylloideae, with 12-40 pores in Alsinoideae and 15-38 pores in Caryophylloideae (Bittrich, 1993).

The tectum of Caryophyllaceae pollen grains is rather thick and separated by more or less numerous columellae from the foot layer; sometimes the columellae hang (Iwarsson, 1977). A few minute perforations (internal foramina) in the tectum and columellae of Alsinoideae have been observed (Erdtman, 1968; Skvarla & Nowicke, 1976); vestigial foramina were possibly observed in *Dianthus* (Caryophylloideae). The endexine is thick (*Corrigiola*), thin (*Silene*, *Scleranthus*, *Cerastium*), or even absent (*Cometes*) (Bittrich, 1993).

McNeill and Crompton (1978) observed pollen dimorphism in male plants of *Silene latifolia*, with respect to ectexine structure (punctitegillate or reticulate), grain diameter, wall thickness, and pore number, with a characteristic geographic pattern in North America and Europe (Prentice et al., 1984).

Barkoudah (1962) determined the pollen morphology of *G. cerastioides*, *G. elegans*, *G. fastigiata, G. fastigiata* var. *arenaria*, *G. muralis*, *G. pilulifera*, *G. pilosa*, *G. sphaerocephala,* and *G. viscosa* in one of his studies and reported that the number of pollen grain pores varied between 9 and 16, with a mean of 12. Moreover, Barkoudah (1962) determined that mean pollen grain size was 22 µm (range: 16-35.5 µm). Mean annulus diameter was 5.5 µm (2.6-9 µm) and mean exine thickness was 2.27 µm.

According to Chanda (1962), *G. fastigiata* pollen is 29 µm in size, spheroidal-polyhedral with 12 pores,

and 5 µm in diameter, with a distance between pores of 6-7 µm. Their opercula have granules 2.5 µm in size and their tectate exines are 3 µm thick, with rather small spinules. The sexine is no thicker than 2.5-3 µm, tapering towards the pore. As regards to *G. muralis* pollen grains, they are 24 µm in size, with a spheroidal-polyhedral appearance and 17-19 pores; their diameters vary between 2 and 2.5 µm and the distance between them is 4-5 µm. Their operculum has 1-µm granules. The exine has a thickness of 3 µm and has spinules, while the sexine is 2.5 µm.

Punt and Hoen (1995) determined some pollen features of *G. fastigiata*, *G. repens*, and *G. paniculata* using SEM. According to that study, pollen grains are 25-40 µm with a spheroidal appearance and 12 pores, and annulus diameter is greater than 1 µm. Pollen has been determined to be psilate with LM, but was observed as microechinate with SEM.

Pollen morphology of some *Saponaria* L. species has been studied by Arkan and İnceoğlu (1992). Among the 16 species of *Saponaria* they examined, the number of pores was between 9 and 14, except in *Saponaria pumilio* Boiss, in which it was 7-8. Absence of spinules and fewer pores in *S. pumilio* were considered primitive pollen characteristics by the authors.

The pollen morphology of some species of *Caryophyllaceae* was studied by Yıldız (2001a, 2001b), who defined 2 species belonging to *Gypsophila* as *G. elegans* and *G. venusta*. According to Yıldız, the pollen of these species was tectum microperforate, the grains had 9-14 pores, and grain size ranged from 28.11 µm to 31.34 µm.

In the present study mean size of *Gypsophila* taxa pollen varied from 23.79 µm to 32.84 µm in non-acetolysed pollen and from 19.48 µm to 25.94 µm in acetolysed pollen. These results seem to be in agreement with those reported by Barkoudah (1962), Chanda (1962), Punt and Hoen (1995), and Yıldız (2001a). While the present study observed pore diameters varying between 3.64 and 5.74 µm, diameters have been reported to vary between 2 and 5 µm for *G. fastigiata* and *G. muralis* (Chanda, 1962). This difference was attributed to the genotypic variation of species. Mean annulus diameter was 1.42 µm, with the smallest being 0.50 µm in *G. perfoliata* var. *araratica* and the largest being 2.60 µm in *G. perfoliata* var. *perfoliata*. This result seems to agree with that of Punt and Hoen (1995), regardless of the fact that the species studied were different. On the other hand, it does not agree with the results obtained in the study by Barkoudah (1962) for *G. pilosa*, *G. viscosa*, and *G. sphaerocephala* (5.5 µm). Exine thickness varied between 1.11 and 1.85 µm, which seems to contradict the results of Barkoudah (1962) and Chanda (1962). Nevertheless, there appears to be agreement with the results reported by Chanda (1962) and Punt and Hoen (1995), in terms of pollen having spinules, even though different species were studied. This result suggests that spinule formation in *Gypsophila* species could be a genotypic characteristic.

Exine thickness of the species analysed varied between 1.03 and 1.85 µm. Morphological features of exine layers have been reported to be the features that best explain the nature of the phylogenetic relationship between taxa (Kuprianova, 1967; Cronquist, 1968; Walker, 1974a, 1974b; Takhtajan, 1980).

The exine structure of all the species analysed was caveate. The fact that such cavea were present between the foot layer and columella in pollen grains seems to suggest that the species analysed have a more evolutive feature. In other words, the presence of cavea has been accepted as a progressive evolutionary characteristic, according to pollen terminology (Pehlivan, 1995).

There were spinules on the surface of all taxa and spinule length varied between 0.18 and 1.1 µm, and spinule width varied between 0.24 and 0.94 µm. The smallest spinule values were observed for *G. curvifolia* and the largest were found for *G. sphaerocephala* var. *sphaerocephala*. Spinules were 21.92 100 μm^2 in *G. sphaerocephala* var. *sphaerocephala*, and 104.09 100 μm^2 in *G. perfoliata* var. *perfoliata.* The distance between the spinules was not equal, varying between 0.5 and 3 µm in all the species. The clava observed in *G. sphaerocephala* var. *sphaerocephala* was 1.15 µm long × of 1.41 µm wide. The clava could not be observed in the remainder of the species analysed.

While LM revealed that the operculum only had a granulate structure, detailed SEM and TEM showed

that the operculum was wrapped in both granules and spinules. The operculum was present in scattered pieces in *G. curcifolia*, but it was present as a whole in the other species. The operculum had the smallest diameter in *G. parva* (2.08 µm) and had the largest diameter in *G. perfoliata* var. *perfoliata*, *G. viscosa*, and *G. pilosa* (4.0 µm). The difference in measurements was attributed to the fact that all the species analysed had a genetic difference, which seems to comply with the claim that the pollen sculpture types have valid morphological features in taxonomy (Cronquist, 1968).

Columellae were single-layered and the foot layer was continuous in all the species analysed. This feature of the foot layer is considered to be primitive in plant phylogenetics. An imperforate exine, fewer pores, and absence of spinules on the tectum of pollen are generally accepted as primitive characteristics of pollen grains (Van Campo, 1966; Walker, 1974a, 1974b; Takhtajan, 1980). The endexine was thin and continuous in *Gypsophila* taxa.

To the best of our knowledge this is the first study to determine operculum diameter, the distance between 2 spinules, spinule length and width, number of spinules μm^2, and the detailed structure of the exine, as well the ectexine/endexine and foot layer/endexine ratios for *Gypsophila* species.

As mentioned before, ornamentation was clavate-microechinate in *G. sphaerocephala* var. *sphaerocephala*, and granulate-microechinate-microperforate in the other species. The operculum was present in scattered pieces in *G. curvifolia*, but it had a monolithic form in the other species. These 2 distinctive features could be considered as crucial palynological criteria for distinguishing these taxa and in revealing familial relationships among the species. Palynological findings also emphasise evaluative levels. *G. sphaerocephala* var. *sphaerocephala* belongs to the section *Capituliformes* and differs from the other taxa. Moreover, morphological features of these taxa differed from those of other taxa. Future studies could determine the categorisation of this section within the species of *Gypsophila* after a thorough investigation of the remaining 6 taxa belonging to the section *Capituliformes*.

The differences in pollen morphology of 12 *Gypsophila* species could be an indication of their genetic differences. Cronquist (1968) reported that pollen sculpture types have valid morphological features in taxonomy. Thus, the taxonomic value of these taxa in *Gypsophila*, as well as their pollen morphology, could be a distinguishing criterion. In conclusion, morphological structures of pollen seem to be useful for differentiating taxa; thus, it is suggested that they could be of benefit in taxonomical studies.

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