Bangladesh J. Bot. **39**(1): 37-46, 2010 (June)

POLLEN MORPHOLOGY OF SOME *ALLIUM* L. (LILLIACEAE) TAXA IN TURKEY

H. ÖZLER[*] AND S. PEHLIVAN[1]

Forest Tree Seeds and Tree Breeding Research Directorate, P.O. Box.11, Ankara-06560, Turkey

Key words: Allium, Codonoprasum, Rhizirideum, Alliaceae, Pollen morphology, Turkey

Abstract

Pollen grains of 16 taxa of *Allium* L. belonging to sections *Rhizirideum* G. Don ex Koch., *Codonoprasum* Reichb. and *Allium* L. were investigated using light and scanning electron microscope, and pollens of four taxa were also examined with transmission electron microscope. Pollens were monosulcate and ellipsoidal. It was observed that the sulcus extends from distal to proximal in all taxa. The exine was semitectate and the tectum was perforate. Columellae were simplicolumellate. Exine sculpture was striate-perforate, striate-rugulate-perforate and rugulate-perforate. *A. albidum* Fischer ex Bieb. subsp. *caucasicum* (Regel) Stearn, *A. rupicola* Boiss ex Mouterde and *A. asperiflorum* Miscz. were seen to have an operculum.

Introduction

Allium L. (Lilliaceae) is represented by nearly 174 taxa in Turkey, under 14 sections (Davis *et al.* 1984, 1988, Seçmen *et al.* 1998, Güner *et al.* 2000). The taxa give the characteristic onion and garlic smell and also include species that are of medicinal and economic importance.

The members of the genus *Allium* present in Turkey are polymorphic and are extremely difficult to identify (Kollmann 1984). To solve the systematic problems of these polymorphic groups further cytological, anatomical and palynological studies are urgently needed. Cytological and palynological studies on *Allium* have been carried out by Radulescu (1973), Özhatay (1977), Schulze (1980) and Güler and Pehlivan (2006). However, pollen morphology and aperture evolution of the family Liliaceae have been examined by many authors (Walker 1974a, b, 1976, Harley and Zavada 2000, Pehlivan and Özler 2003, Özler and Pehlivan 2007). Some authors investigated the phylogeny of *Allium* using PCR-RFLP (Dubouzet and Shinoda 1998, He *et al*. 2000, Gurushidze *et al*. 2008).

In the present study, pollen morphology of 16 taxa of the genus *Allium* were examined.

Materials and Methods

The pollen grains were obtained from the Faculty of Pharmacy of Ankara University (AEF) and the Faculty of Arts and Science, Gazi University (GAZI) herbarium (Table 1). For morphological analysis, pollen grains were prepared according to the methods of Wodehouse (1935) and Erdtman (1960) and observations were made with Kyowa microlux-11 microscope under 1000x magnification. The measurement was based on 30 - 40 counts from each specimen. LM photographs were taken by a Zeiss microscope. For SEM investigations, pollen grains were put on stubs, sputter-coated with gold plate, and examined under a Jeol JSM-840A (Turkish Petroleum Corporation, TPAO, Turkey). For TEM studies, acetolyzed pollen grains were stained with 2% OsO_4 and uranyl acetate, dehydrated and embedded in epon araldite according to the method described by Skvarla and Turner (1966). Ultrathin sections of pollen grains were

[*]E-mail: hulyaozler@hotmail.com [1]Department of Biology, Faculty of Arts and Science, Gazi University, Ankara-06500, Turkey.

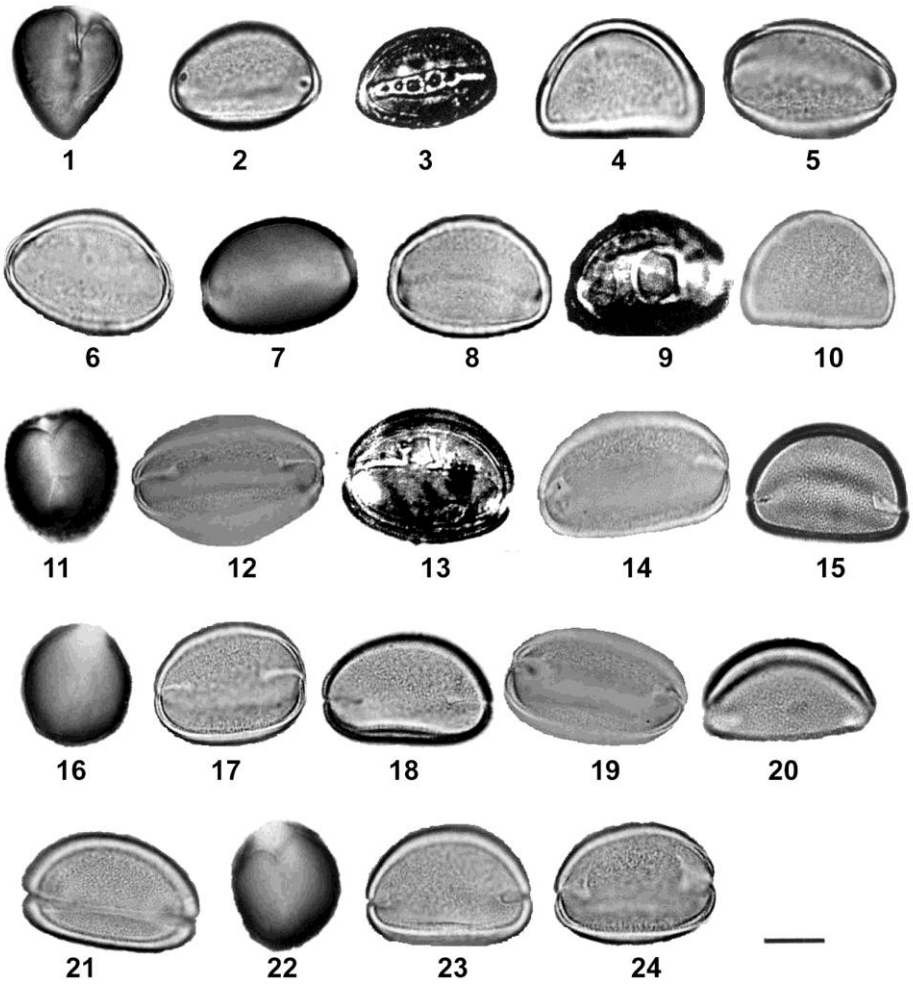
obtained with a glass knife in a Reichert Supernova microtome (Gazi University, Faculty of Medicine, Ankara, Turkey). Post-staining was performed with lead citrate for 5 min (Reynold 1963) and sections were examined under a Zeiss EM9 (Ankara University Research Center, Ankara, Turkey). Pollen morphological terminology of Walker (1974a), Faegri *et al.* (1989) and Punt *et al*. (1994) was followed.

Table 1. List of voucher specimens belonging to the genus *Allium*.

Taxa	Localities and date of collections	Collectors and herbaria numbers
Section *Rhizirideum* G. Don ex W. Koch		
A. albidum Fischer ex Bieb. subsp. *caucasicum* Regel (Stearn)	A9 Kars, Göle, above Karlıyazı village, plateau, rocky places ca 2 200 m, 22.07.90	M Koyuncu 15230, AEF
A. hymenorrhizum Ledeb.	A9 Ardahan, Göle-Karlıyazı village, Ahmet meadow, arid areas, ca 850-2 000 m, 28.08.97	N Demirkuş 6000, GAZI
Section *Codonoprasum* Reichb.		
A. kunthianum Vved.	B2 Kütahya, around radar ca 1 750 m, 18.08.92	KHC Başer 17140, AEF
A. sipyleum Boiss.	B2 Kütahya, Gediz, Murat mountain, Çakırören village, between Sığırkuyruğu and Aseralan, ca 1550m, 21.07.93	Ö Seçmen 18453, AEF
A. wiedemannianum Regel	A4 Ankara, surrounding Çubuk I dam side protected 21.07.76	S Başaran 5373, AEF
A. rupicola Boiss. ex Moulerde	C4 İçel, Anamur, above Anamur hills, forest openings, ca 200 m, 28.05.93	M Koyuncu 18065, AEF
Section *Allium* L.		
A. trachycoleum Wendelbo	C10 Hakkari, Yüksekova, Veregöz road, ca 2 150 m, 01.07.83	M Koyuncu 12432, AEF
A. asperiflorum Miscz.	B6 Sivas, between Divriği and Cürek, 03.06.83	H Başer, H Öğütveren, H Malyer 3320, AEF
A. calyptratum Boiss.	C5 İçel, Mersin, Arslanköy, gardens, ca 1 400 m, 28.07.83	M Koyuncu 17699, AEF
A. curtum Boiss. & Gaill.	C4 İçel, Silifke, Silifke castle, ca 200 m, 27.06.92	M Koyuncu 17380, AEF
A. artvinense Miscz.	A8 Bayburt, Çoruh valley, between Çakırbağ (Abusta) and Darıca (Tanzut), ca 1 550 m, 26.07.91	M Koyuncu 17867, AEF
A. affine Ledeb.	A8 Erzurum, İspir, Çamlıkaya, Yavuzlar neighbourhood, Quercus shrub, ca 1 640 m, 28.07.91	M Koyuncu 17886, AEF
A. aucheri Boiss.	A9 Kars, Sarıkamış, Yağbasan plateau, meadows, 2 100-2 400 m, 21.07.90	M Koyuncu 15232, AEF
A. jubatum Macbride	A4 Çankırı, between Çerkeş, İsmetpaşa, rocky places, ca 1000 m, 12.07.92	M Koyuncu 17489, AEF
A. dictyoprasum C.A. Meyer ex Kunth	B9 Ağrı, between Eleşkirt and Horasan, 40 km before Horasan, ca 2 000 m, 05.07.83	M Koyuncu, M Coşkun 12495, AEF
A. karyeteini Post	C5 Adana, Feke-Saimbeyli Road, 13 km, ca 650-750 m, 26.07.93	M Koyuncu 17717, AEF

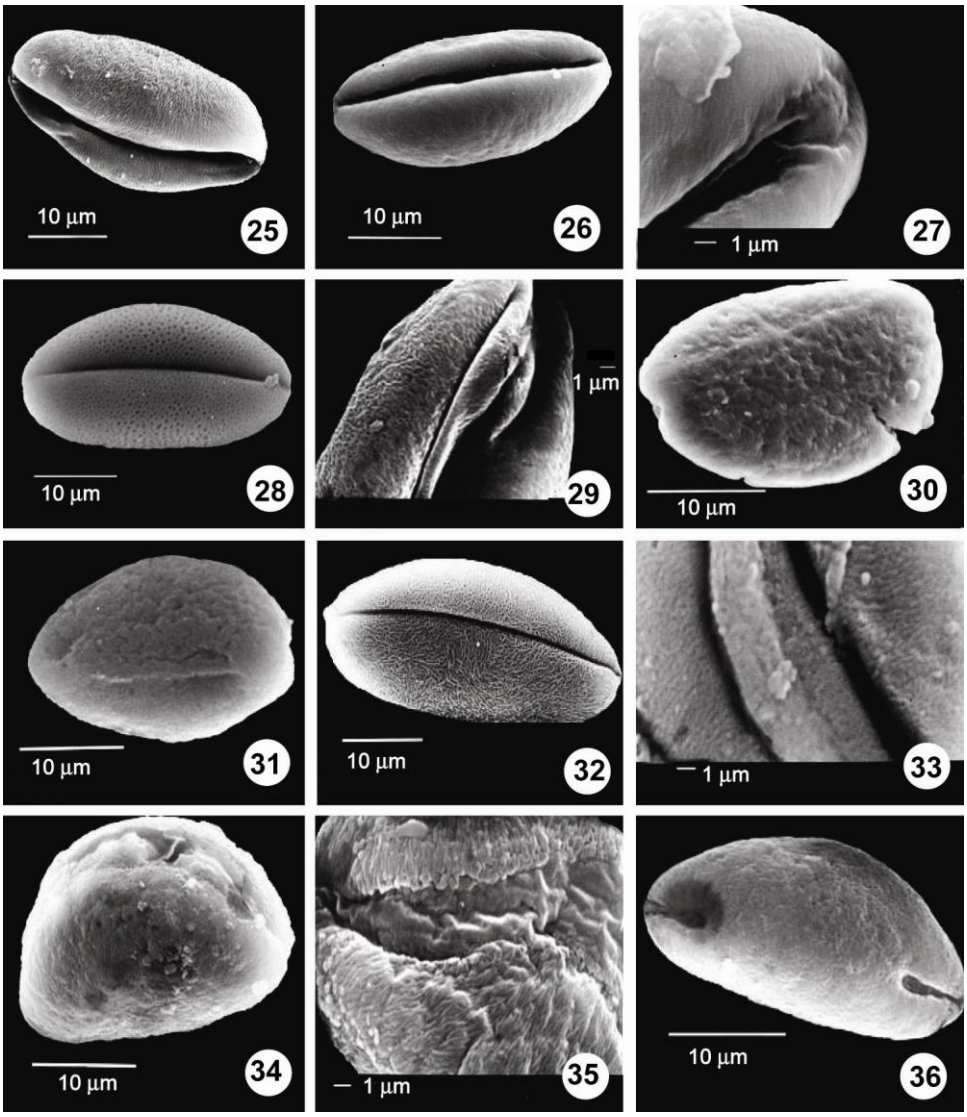
Results and Discussion

Pollen morphology of 16 taxa of *Allium* was investigated under LM (Figs. 1-24), SEM (Figs. 25-53) and TEM (Figs. 54-57). The common characteristics of pollen grains were monads, monosulcate, ellipsoidal, and heteropolar. However, pollen of *A. wiedemannianum* is paraisopolar (Figs. 8, 31).



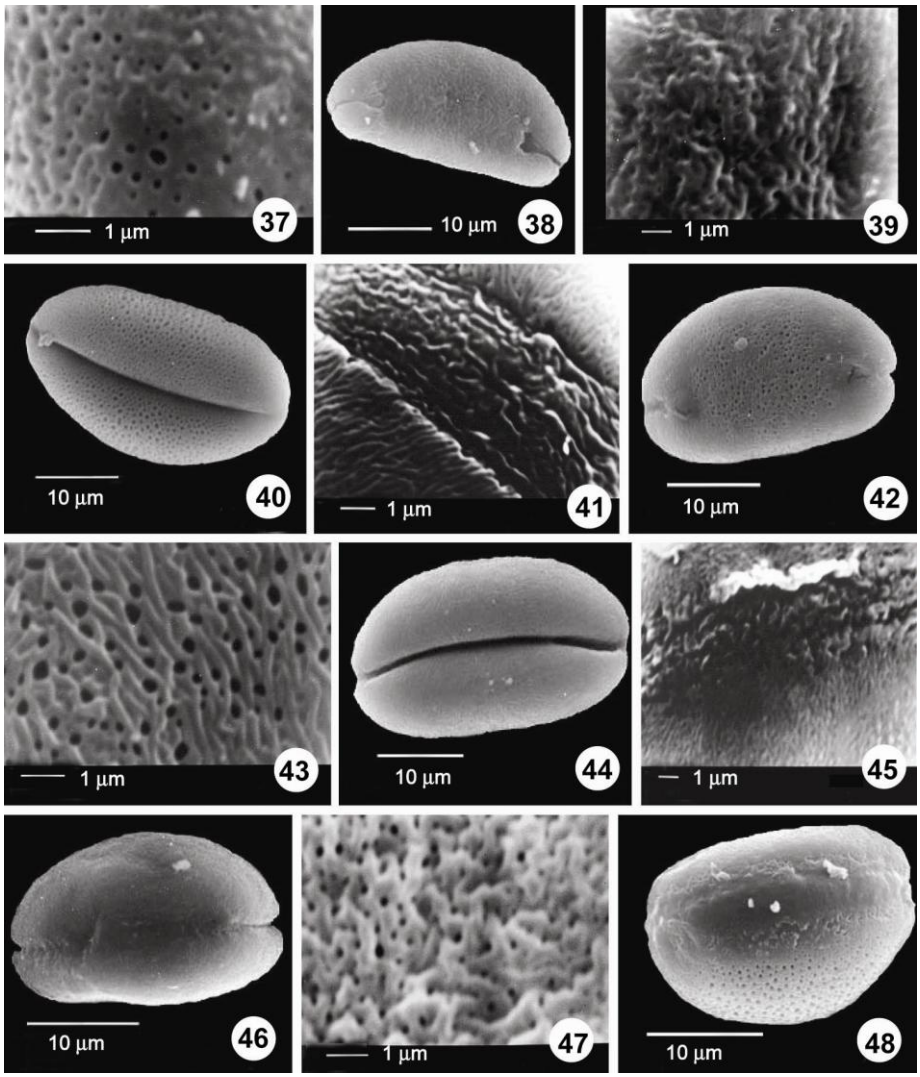
Figs1-24: LM photomicrographs. 1-3. *A. albidum* subsp. *caucasicum* (1. Equatorial distal view (N= non acetolysed). 2. Proximal view with ornamentation (A = Acetolysed). 3. Distal view with an operculum (N)). 4-5. *A. hymenorrhizum* (4. Oblique view (A). 5. Proximal view and sulcus ends (A). 6. *A. kunthianum*, distal view, optical section (A). 7. *A. sipyleum*, distal view (N). 8. *A. wiedemannianum*, distal view with ornamentation (A). 9-10. *A. rupicola* (9. Distal view with an operculum (N), 10. Oblique view (A). 11-12. *A. trachycoleum* (11. Equatorial distal view (N). 12. Proximal view and sulcus ends (A). 13-14. *A. asperiflorum* (13. distal view with an operculum (N). 14. Proximal view and sulcus ends (A). 15. *A. calyptratum*, proximal view with rugulate-perforate ornamentation and sulcus ends (A). 16-17. *A. curtum* (16. equatorial distal view (N), 17. Proximal view and sulcus ends (A). 18. *A. artvinense* proximal view and sulcus ends (A). 19. *A. affine*, proximal view and sulcus ends (A). 20. *A. aucheri*, oblique view with rugulate-perforate ornamentation (A). 21. *A. jubatum*, distal view with ornamentation, in optical section (A). 22-23. *A. dictyoprasum* (22. Equatorial distal view (N). 23. Proximal view and sulcus ends (A). 24. *A. karyeteini*, proximal view and sulcus ends (A). Bar: 10 µm.

The predominance of a monosulcate aperture (extended sulcate) in monocotyledons including *Allium*, is emphasized by Harley and Zavada (2000). Liliaceae and the overwhelming majority of the lilialean complex have monosulcate pollen grains. The evolution of distal sulcate pollen may have occurred during the Mezosoic geological period.



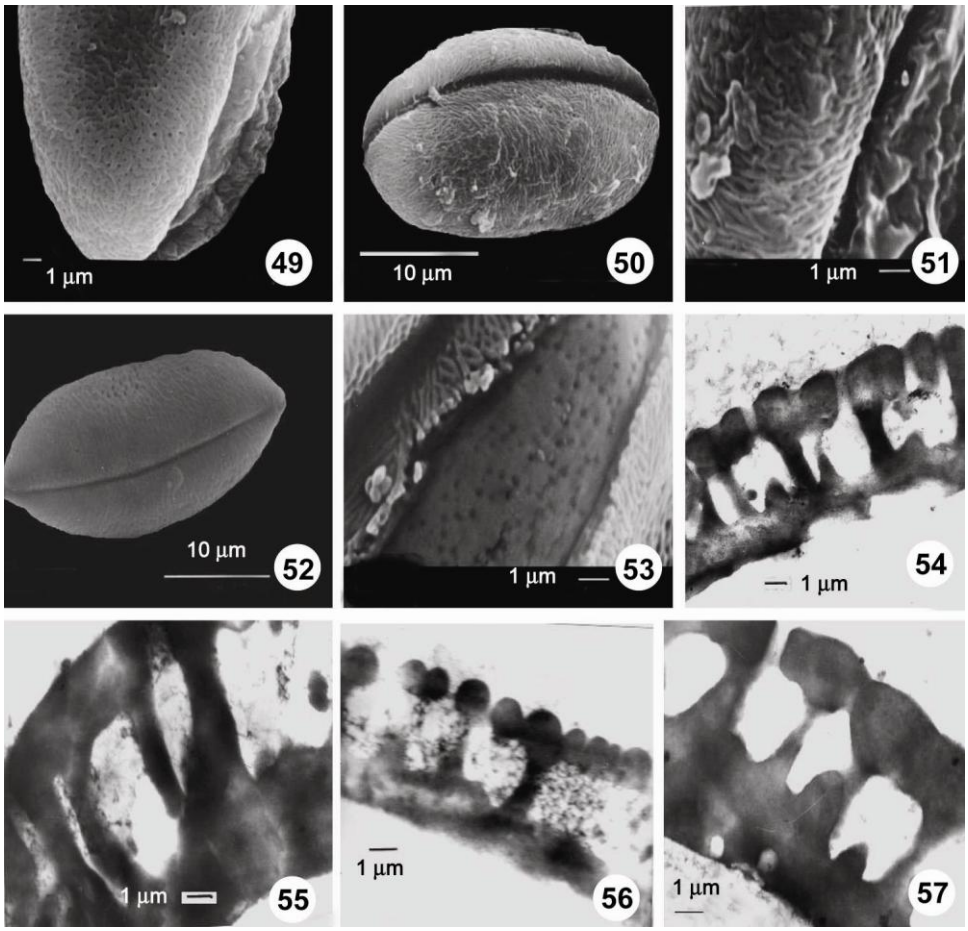
Figs 25-36: SEM photomicrographs. 25. *A. albidum* subsp. *caucasicum*, distal view with striate-perforate ornamen-tation. 26-27. *A. hymenorrhizum* (26. Distal view, 27. Psilate ornamentation on the sulcus membrane). 28-29. *A. kunthianum* (28. Distal view, 29. Striate-perforate ornamentation on the sulcus membrane). 30. *A. sipyleum*, distal view. 31. *A. wiedemannianum*, equatorial view with striate-rugulate-perforate ornamentation. 32-33. *A. rupicola* (32. Distal view, 33. Operculum covering the sulcus membrane). 34-35. *A. trachycoleum* (34. Distal view, 35. Rugulate ornamentation on the sulcus membrane). 36. *A. asperiflorum*, proximal view and sulcus ends.

A monosulcate aperture may be a strong palynological evidence for the common origin of monocotyledons and dicotyledons. Sulcate, colpate and colporate pollen apertures are the most common in biotically pollinated families and sulcate pollen has a much older pollen record than both porate and colpate pollen (Kuprianova 1969, 1979; Sporne 1972, Zavada 1983, Linder 2000).



Figs 37-48: SEM photomicrographs. 37. *A. asperiflorum*, rugulate-perforate ornamentation. 38-39. *A. calyptratum*, proximal view and sulcus ends. 39. Rugulate-perforate ornamentation. 40-41. *A. curtum* (40. Distal view, 41. Striate-perforate ornamentation). 42. *A. artvinense*, distal view and sulcus ends. 43. *A. artvinense*, striate-perforate ornamentation. 44-45. *A. affine* (44. Distal view. 45. Rugulate ornamentation on the sulcus membrane). 46-47. *A. aucheri* (46. Distal view and sulcus ends. 47. Rugulate-perforate ornamentation). 48. *A. jubatum*, distal view).

Biggest pollen size was found in *A. calyptratum*, whereas the smallest was found in *A. karyeteini* (Table 2). The pollen size given for this genus are 19.3 µm × 55.2 µm (Radulescu 1973), 25.75 µm × 17.48 µm - 51.19 µm × 32.30 µm (Özhatay 1977), 25.50 µm × 18.44 µm - 44.52 × 26.80 µm (Güler and Pehlivan 2006). It is reasonably accepted that pollen grain size is positively correlated with chromosome number. However, in the present study it was observed that some taxa with bigger pollen grains have lower chromosome numbers (e.g. *A. kunthianum* and *A. asperiflorum* where, 2n = 16) and some taxa with bigger pollen size have higher chromosome number (e.g. *A. trachycoleum*, 2n = 32, 48).



Figs 49-53: SEM photomicrographs. 49. *A. jubatum* (49. Rugulate-perforate ornamentation). 50-51. *A. dictyoprasum* (50. Distal view, 51. Striate-rugulate-perforate ornamentation on the sulcus membrane). 52-53. *A. karyeteini* (52. Distal view, 53. Perforate ornamentation on sulcus membrane).
Figs 54-57: TEM photomicrographs of exine structure (54. *A. albidum* subsp. *caucasicum.* 55. *A. trachycoleum.* 56. *A. curtum.* 57. *A. jubatum*).

It was recognized that the sulcus extends from distal to proximal end in all the taxa investigated. The proximal extension of the sulcus ranged from 7.07 - 15.79(N) to 7.73 - 18.12 (A) µm (Table 2). The extended sulcus type has been observed on *Allium* and the family Liliaceae (Güler and Pehlivan 2006, Özler and Pehlivan 2007). Chanda *et al*. (1979) explained that an extended sulcate-type of aperture was not common but, it was found occasionally in both dicotyledons and monocotyledons. The sulcus ends were sharp in *A. albidum* subsp. *caucasicum*, *A. kunthianum*, *A. sipyleum*, *A. wiedemannianum*, and *A. rupicola*, whereas the sulcus ends were truncate in *A. affine*. The sulcus ends were rounded in the other investigated taxa (Figs 1-24, 36, 38, 42, 46). The longest sulcus extension dimension was measured in *A. calyptratum*, whereas the shortest dimension was observed in *A. hymenorrhizum*. The widest sulcus dimension was seen in *A. wiedemannianum*. The longest length dimension of sulcus was seen in *A. calyptratum* and the shortest dimension was seen in *A. albidum* subsp. *caucasicum* (Table 2). Several researchers have emphasized that the sulcus features and the presence of operculum may be a taxonomic value in

some families (Schulze 1980, 1982, Kosenko 1991a, 1991b, 1999, Halbritter and Hesse 1993, Friis *et al*. 1997, Güler and Pehlivan 2006). In SEM photomicrographs, sulcus membranes are psilate in *A. hymenorrhizum*, *A. sipyleum*, *A. wiedemannianum*, *A. artvinense*, *A. aucheri*, and *A. jubatum*. Striate - reticulate sulcus membrane ornamentation was seen in *A. albidum* subsp. *caucasicum*, *A. kunthianum*, and *A. rupicola*. Rugulate sulcus membrane ornamentation was found in *A. trachycoleum*, *A. asperiflorum*, *A. calyptratum*, *A. curtum*, *A. affine* and *A. dictyoprasum*. A perforate sulcus membrane was found in *A. karyeteini* (Figs 25-53). Similarly, Güler and Pehlivan (2006) reported that sulcus membrane ornamentatios were psilate, psilate-perforate and rugulate-perforate in *Allium* taxa. An operculum was seen in *A. albidum* subsp. *caucasicum* (Section *Rhizirideum*), *A. rupicola* (Section *Codonoprasum*), and *A. asperiflorum* (Section *Allium*). The operculum was found to be fragmented on the sulcus membrane (Figs 3, 9, 13) or sometimes completely covering it (Figs 3, 9, 13, 33). In the other similar study of this genus, the operculum was determined only in *A. pallens subsp. pallens*, *A. bassitense* and *A. hirtovaginum* under the Section *Codonoprasum* (Güler and Pehlivan 2006). According to Kosenko (1991a, 1991b, 1992), a non-operculate exine is a plesiomorphic peculiarity. In the present investigation, *A. albidum* subsp. *caucasicum*, *A.rupicola*, and *A.asperiflorum*, which posses an operculum are more advanced than other taxa examined.

In the present investigated taxa (such as *A. albidum* subsp. *caucasicum*, *A. curtum*, *A. trachycoleum*, and *A. jubatum*), the exine was semitectate and the tectum with perforate. Perforate pollen wall in the monocotyledons is a plesiomorphic character and the endexine is rarely seen in the monocotyledones (Zavada 1983, 1984). Palaeopalynological studies have shown that, in early period of angiosperm evolution, a tectate–perforate and semitectate exine is seen predominantly (Walker 1974a, b, Crane 1989, Hughes and Audrey 1994). Although the endexine was very thin with interruptions in *A. trachycoleum* and *A. curtum*, it was very thin without interruptions in *A. albidum* subsp. *caucasicum* and *A. jubatum* (Figs 54-57). The thickest exine dimension was found in *A. jubatum* and the thinnest exine dimension was found in *A. hymenorrhizum* (Table 2). In the present survey, the number of perforations in 1 μm^2 was between 3 and 11 at the sulcus side or at the lateral surface. The diameter of a perforation was approximately 0.08-0.75 μm. The diameter of perforation was observed to be the highest in *A. asperiflorum* (Fig. 37). The number of perforations in 1 μm^2 was more in *A. albidum* subsp. *caucasicum* (Fig. 25).

According to SEM survey, the exine sculpture was striate-perforate, striate-rugulate-perforate and rugulate-perforate (Table 2, Figs 25-53). However, in *A. wiedemannianum*, one of the lateral surfaces of the pollens is striate-rugulate-perforate and the other surface of the pollen grains was striate-perforate (Fig. 31). Therefore, this pollen grain is para-isopolar. Perforate-striate, perforate-rugulate and perforate-striate-rugulate exine structure have been reported in previous investigations (He *et al*. 2000, Güler and Pehlivan 2006). Radulescu (1973) described that the tribe *Allieae* pollen had reticulate mostly microreticulate exine sculpturing and grouped *Allieae* pollen grains according to the density of the microreticulum.

The present study revealed that *Allium* taxa possess three types ornamentational characteristics as follows:

(i) Striate - perforate: *A. albidum* subsp. *caucasicum*, *A. kunthianum*, *A. rupicola*, *A. curtum*, *A. artvinense*, *A. affine* and *A. karyeteini.*

(ii) Striate - rugulate-perforate: *A. hymenorrhizum*, *A. sipyleum*, *A. wiedeman-nianum*, *A. dictyoprasum* and *A. trachycoleum.*

(iii) Rugulate - perforate: *A. asperiflorum*, *A. calyptratum*, *A. aucheri* and *A. jubatum.*

The *A. sipyleum* and *A. karyeteini* had thickest intine while *A. hymenorrhizum* had thinnest one (Table 2).

Section *Rhizirideum* has been proved as non monophyletic based on moleculer results. There is close genetic relationship between subgenera *Allium* and *Rhizirideum*. (Dubouzet and Shinoda 1998, He *et al*. 2000). The results revealed that further molecular and morphological studies are needed to solve the problems related to taxonomy of this genus.

Acknowledgements

The authors thank collectors, especially Professor Mehmet Koyuncu from the Faculty of Pharmacy of Ankara University, for allowing to use their specimens.

References

Chanda S, K. Gosh and S. Nillson. 1979. On the polarity and tetrad arrangement in some mono and diaperturate angiosperm pollen grains. Grana **18**: 21-31.

Crane P.R. 1989. Paleobotanical evidence on the early radiation of nonmagnoliid dicotyledones. Plant Sys. Evol. **162**: 165-191.

Davis P.H., R.R. Mill and K. Tan. 1984. Flora of Turkey and the East Eagean Islands. Edinburgh Univ. Press, Edinburgh.

Davis P.H., R.R. Mill and K. Tan. 1988. Flora of Turkey and the East Eagean Islands (Supplement). Edinburgh Univ. Press, Edinburgh.

Dubouzet J.G. and K. Shinoda. 1998. Phylogeny of *Allium* L. subgen. *Melanocrommyum* (Webb et Berth.) Rouy based on DNA sequence analysis of the internal transcribed spacer region of nrDNA. Theor. Appl. Genet. **97**: 541-549.

Erdtman G. 1960. The acetolysis method: A revised description. Sven. Bot. Tidskr. **54**: 561-564.

Faegri K, P.E. Kallland and K.J. Knzywinski (Eds). 1989. Textbook of pollen analysis. Wiley & Sons, New York.

Friis E.M., P.R. Crane and K.R. Pedersen. 1997. *Anacostia*, a new basal angiosperm from the early Cretaceous of North America and Portugal with trichotomocolpate/monocolpate pollen. Grana **36**: 225-244.

Gurushidze M., R.M. Fritsch and F.R. Blattner. 2008. Phylogenetic analysis of *Allium* sung. Melanocrommyum infers cryptic species and demands a new sectional classification. Science direct-Moleculer phylogenetics and evolution (www.sciencedirect.com/science).

Güler Ü. and S. Pehlivan. 2006. Pollen morphology of some species belonging to *Codonoprasum* and *Allium* sections of *Allium* (Liliaceae-Alliaceae) genus. Biologia Bratislava **61**: 449-455.

Güner A., N. Özhatay, T. Ekim and K.H. Canbaşer. 2000. Flora of Turkey and the East Eagean Islands (Supplement. 2). Edinburgh Univ. Press, Edinburgh.

Halbritter, H. and M. Hesse. 1993. Sulcus morphology in some monocot families. Grana **32**: 87-99.

Harley M.M. and M.S. Zavada. 2000. Pollen of the monocotyledons: Selecting characters for cladistic analysis. *In*: Monocots: Systematics and Evolution, K.L. Wilson and D.A Morrison (Eds), pp. 194-213. CSIRO, Melbourne.

He X., S. Ge, J. Xu and D. Hong. 2000. Phylogeny of Chinese *Allium* (Liliaceae) using PCR-RFLP analysis. Science in China (Series C) **43**(5): 454-463.

Hughes N.F. and B. Audrey. 1994. Search for antecedents of early creataceous monosulcate columellate pollen. Rev. Palaeobot. Palynol. **83**: 175-183.

Kollmann F. 1984. *Allium* L. *In*: Flora of Turkey and the East Eagean Islands, P.H. Davis, R.R. Mill and K.Tan (Eds), p. 99. Edinburgh Univ. Press, Edinburgh.

Kosenko V.N. 1991a. Pollen morphology of the genus *Fritillaria* (Liliaceae). Bot. Zh. **76**: 1696-1706.

Kosenko V.N. 1991b. Pollen morphology of the family Liliaceae s. str. Bot. Zh. **76**: 1201-1210.

Kosenko V.N. 1992. Pollen morphology and systematic problems of the Liliaceae family. Bot. Zh. **77**: 1-15.

Kosenko V.N. 1999. Contributions to the pollen morphology and taxonomy of the Liliaceae. Grana **38**: 20-30.

Kuprianova L.A. 1969. On the evolutionary levels in the morphology of the pollen grains and spores. Pollen et Spores **11**: 333-351.

Kuprianova L.A. 1979. On the possibility of the development of tricolpate pollen from monosulcate. Grana. **18**: 1-4.

Linder H.P. 2000. Pollen morphology and wind pollination in angiosperms. *In:* Pollen and Spores: Morphology and Biology, M.M. Harley, C.M. Morton and S. Blackmore (Eds). pp. 73-88. Royal Botanic Gardens, Kew.

Özhatay N. 1977. Trakya bölgesi ve İstanbul çevresi Alliaceae familyası üzerinde taksonomik, sitolojik ve palinolojik araştırmalar. İ.Ü. Eczacılık Fakültesi Farmasötik Botanik kürsüsü, Doçentlik Tezi.

Özler H. and S. Pehlivan. 2007. Comparison of pollen morphological structures of some taxa belonging to *Asparagus* L. and *Fritillaria* L. (Liliaceae) from Turkey. Bangladesh J.Bot. **36**(2): 111-120.

Pehlivan S. and H. Özler. 2003. Pollen morphology of some species of *Muscari* Miller (Liliaceae-Hyacinthaceae) from Turkey. Flora **198**: 200-210.

Punt W.S. Blackmore, S. Nilsson and A. Le Thomas. 1994. Glossary of Pollen and Spore Terminology. LPP Foundation, Uttecht.

Radulescu D. 1973. Recherches morpho-palynologiques sur la famille Liliaceae. Acta Bot. Horti. Bucur. 133-248.

Reynold E.S. 1963. The use of lead citrate at high pH as an electron opaque stain in electron microscopy. Stain. Tech. **43**: 139-144.

Schulze W. 1980. Beiträge zur taxonomie der Liliifloren VI. Der umfang der Liliaceae. Math. Nat. **29**: 607-636.

Schulze W. 1982. Beiträge zur taxonomie der Liliifloren × Asparagaceae. Math. Nat. **31**: 309-330.

Seçmen Ö., Y. Gemici, G. Görk, L. Bekât and E. Leblebici. 1998. Tohumlu bitkiler sistematiği. Ege Üniversitesi Basımevi, Bornova, İzmir. s. 396.

Skvarla J.J. and B.L. Turner. 1966. Systematic implications from electron microscopic studies of Compositae pollen. Ann. Mo. Bot. Gard. **53**: 220-256.

Sporne K.N. 1972. Some observations on the evolution of pollen types in dicotyledons. New Phytol. **71**:181-185.

Walker J.W. 1974a. Evolution of exine structure in the pollen of primitive angiosperms. Am. J. Bot. **61**: 891-902.

Walker J.W. 1974b. Aperture evolution in the pollen of primitive angiosperms. Am. J. Bot. **61**: 1112-1136.

Walker J.W. 1976. Evolutionary significance of the exine in the pollen of primitive angiosperms. *In*: The Evolutionary Significance of the Exine, I.K. Ferguson and J. Muller (Eds). pp. 251-308. Linnean Soc. Symp. Series 1. Academic Press, London.

Wodehouse R.P. 1935. Pollen grains. MacGraw Hill, New York. 574 pp.

Zavada M.S. 1983. Comparative morphology of monocot pollen and evolutionary trends of apertures and wall structures. Bot. Rev. **49**: 331-378.

Zavada M.S. 1984. Angiosperm origins and evolution based on dispersed fossil pollen ultrastructure. Ann. Miss. Bot. Gard. **71**: 444-463.

(Manuscript received on 27 May 2009; revised on 12 September 2009)