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Seed micromorphology and anatomy of 36 *Muscari* (Asparagaceae) taxa from Turkey with notes on their systematic importance

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Abstract – This study presents the first in-depth evaluation of the morphological and anatomical characters, as well as their taxonomic importance, of the seeds of 36 taxa in subgenera *Muscari*, *Leopoldia*, *Pseudomuscari* and *Botryanthus* of the genus *Muscari* in Turkey, where 24 of the taxa are endemic. The results indicate that the taxa generally differ from each other in terms of seed shape and dimension. Seed dimensions vary between 1.66 mm and 3.21 mm in length, and between 1.12 mm and 2.63 mm in width. The seed surface ornamentation is grouped into nine forms: ruminate, reticulate, reticulate-areolate, reticulate-foveate, alveolate, scalariform, rugose, verrucate and areolate. The most common type is ruminate, while areolate, reticulate-foveate and scalariform ornamentation forms were found to be taxon-specific. Testa structures of the taxa examined consist in general of two different layers: the epidermis and the subepidermis in scleranchymatous or parenchymatous structures. The subepidermis may be absent in some of taxa. The structure and thickness of the epidermis and the subepidermis are very important characteristics that disclose interspecific relations among the examined taxa. We also provide a key for the identification of the studied taxa based on seed features.

Keywords: crystal, morphology, *Muscari*, scanning electron microscopy, taxonomy, testa, Turkey

Introduction

The genus *Muscari* Mill. is found across the European continent, Mediterranean region and northwest Asia (Jafari and Maassoumi 2011). According to the latest checklist study, the genus is represented by 51 species worldwide (Govaerts 2019). According to other recent studies, *Muscari* includes 40 species belonging to four subgenera as *Muscari*, *Leopoldia* and *Botryanthus* and *Pseudomuscari* with controversial status in Turkey, 26 of which are endemic (Dizkırıcı et al. 2019, Eker 2019a,b, Demirci-Kayıran et al. 2019). The genus is characterized by its bulbs, basal leaves, inflorescences, pedicels, flower form and colour, filament placement relative to the tube, and capsule shape (Davis and Stuart 1984). Major taxonomic problems of the genus include the many synonyms among taxa, the fact that type specimens are often cultivated material of unknown origin, that widespread taxa show a lot of variation and the color difference between fresh and dried flowers (Davis and Stuart 1984). Moreover, reliable classification is impossible in the genus because morphological characteristics and karyological information are not complete or consistent enough to make uncontroversial taxonomic judgements (Dizkırıcı et al. 2019). The genus was placed in Hyacinthaceae until the Angiosperm Phylogeny Group (APG) re-evaluated its taxonomic position as a result of subsequent studies, and placed it within the family Asparagaceae (Reveal and Chase 2011, Guner et al. 2012, Demirci and Özhatay 2017).

Several morphological, anatomical, cytological, palynological and ecological studies on taxa belonging to various genera of Asparagaceae have been performed previously (Shoub and Halevy 1971, Bentzer et al. 1974, Küçüker 1990, Uysal 1999, Herrmann et al. 2006, Lynch et al. 2006, Uysal et al. 2007, Gürsoy and Şık 2010, Kahraman et al. 2010, Doğu and Bağcı 2009, Doğu et al. 2011, Sezer et al. 2013). However, the morphological and anatomical features of

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seeds have been largely ignored in the systematics of taxa in the family, except in a few new species descriptions (Yıldırım 2015, 2016, Doğu and Uysal 2019).

The purpose of this study is to: (i) examine the morphological and anatomical characteristics of seeds of 36 taxa in subgenera *Muscari*, *Leopoldia*, *Pseudomuscari* and *Botryanthus* of the genus *Muscari* in Turkey, and (ii) debate the taxonomic use of these characters. The study will also serve as a guide to further related studies on various genera in the family.

Material and methods

The plant specimens were collected from various phytogeographical regions of Turkey during the fruiting season and were deposited at VANF (Van Yüzüncü Yıl University Herbarium). Details are provided in Tab. 1.

Macromorphological features of the seeds including colour, shape and size were documented for 100 seeds of 10 individuals per species utilizing a Leica EZ4 binocular microscope with a HD camera (On-line Suppl. Fig. 1, Tab. 2). For the micromorphological features of surface ornamentation, anticlinal and periclinal cell walls, and the form of epidermal cells, the samples were studied with a Scanning Electron Microscope (On-line Suppl. Fig. 2, Tab. 3). Seeds were first placed on the stub with silver epoxy and coated with gold, then examined with a Zeiss LEO 440 SEM.

A survey of seed anatomical characters was done with dry herbarium materials. Cross-sections were taken from the middle of the seed with a fully automatic microtome (Thermo Shonda Met Finesse, Thermo). They were brought through a series of alcohol and xylene, dyed with hematoxylin and eosin-Y in a staining device (ASC 720 Medite) and mounted using Entellan (On-line Suppl. Fig. 3, Tab. 4) (Karaismailoğlu 2015, Karaismailoğlu and Erol 2018, Karaismailoğlu and Güner 2019). Anatomical characteristics were examined with an Olympus CX31 light microscope and Kameram Imaging Software (KAMERAM12 CCD, Argenit Micro System Ltd., Turkey).

The terminology used for seed morphological and anatomical characteristics is compatible with Stearn (1985).

Grouping of taxa was performed using the clustering analysis method (UPGMA) in MultiVariate Statistical Package (MVSP) in accordance with the 44 characters in Tables 2-4 (Fig. 1). Characters used in statistical analysis were: seed colour (1); shape: orbicular (2), ovate (3), oblong (4), elliptic (5), lanceolate (6); sizes: length (7), width (8), L/W (9); surface ornamentation: reticulate (10), alveolate (11), areolate (12), verrucate (13), ruminate (14), foveate (15), rugose (16), scalariform (17); anticlinal cell walls: sunken (18), raised (19), unclear (20); periclinal cell walls: convex (21), concave (22), unclear (23); epidermal cell structure: polygonal (24), alveolar (25), rectangular (26), flat (27), unclear (28); anatomical structure of the epidermis: flat (29), rectangular (30), crushed (31), polygonal (32), scleranchymatous cells (33), parenchymatous cells (34); anatomical structure of the subepidermis: crushed (35), flat (36), orbicular (37), square (38), polygonal (39), rectangular (40), scleranchymatous cells (41), parenchymatous cells (42); testa thickness (43); presence of crystals (44). The dissimilarity matrix of the studied taxa was created with MVSP (Kovach 2007) (On-line Suppl. Tab. 1). A dendrogram was created. Also, the cophenetic correlation coefficient is designed to explain the relation between the dendrogram and similarity matrix (On-line Suppl. Tab. 1, Fig. 1).

Results

This work assesses macromorphologically the seed features of the studied taxa, including colour, shape and dimensions. All of the taxa examined have the same seed color (black) but the shape and size of seeds vary considerably. Seeds examined can be divided into 7 shapes; orbicular, ovate-orbicular, ovate, oblong-ovate, oblong-elliptic, elliptic

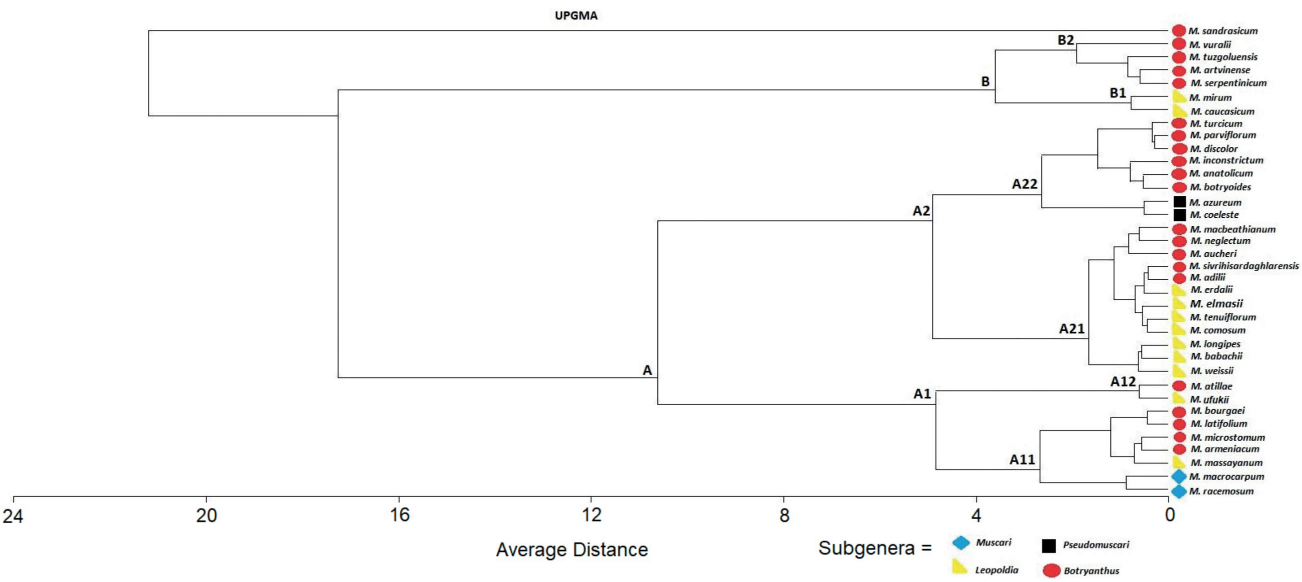

Fig. 1. Cluster analysis of the studied taxa.

and elliptic-lanceolate. Orbicular is the most common type (found in 20 taxa). However, oblong-ovate, oblong-elliptic and elliptic-lanceolate are characteristic types for *Muscari mirum*, *M. longipes* and *M. macbeathianum*, respectively. Seed dimensions range from 1.66 mm to 3.21 mm in length, and from 1.12 mm to 2.63 mm in width. While *M. erdalii* and *M. racemosum* have the largest seeds, *M. macbeathianum* has the smallest seeds (Tab. 2, On-line Suppl. Fig. 1).

The surface ornamentation, anticlinal and periclinal cell walls, and epidermal cell structures of the seeds have been micromorphologically evaluated in this study. Seed surface ornamentation is grouped into nine types: ruminate, reticulate, reticulate-areolate, reticulate-foveate, alveolate, scalariform, rugose, verrucate and areolate. The most common form is ruminate, while areolate, reticulate-foveate and scalariform ornamentation forms were found to be taxon-specific (Tab. 3, On-line Suppl. Fig. 2). The reticulate-foveate (in *M. elmasii*), areolate (*M. neglectum*), and scalariform (*M. azureum*) ornamentation types are each displayed by only one taxon. The anticlinal cell walls in the studied taxa are raised, sunken or unclear. While sunken cell walls are widely seen in the alveolate, verrucate, areolate, reticulate-areolate and scalariform ornamentation types, the reticulate and reticulate-foveate ornamentation types are found where epidermal cells are enclosed by raised walls. Rugose and ruminate types are associated with unclear form (Tab. 3). No clear relationship exists between convex or concave periclinal cell walls and surface ornamentation types; however, ruminate and rugose types are found only with unclear periclinal cells. The shape of epidermal cells on the seed surface has also showed diversity and may be grouped into polygonal, alveolar, rectangular and unclear categories. The most common cell type is unclear, while rectangular and alveolar are fairly rare (Tab. 3).

The results of the examination of the anatomical structures of the seeds are indicated in On-line Suppl. Fig. 3 and Tab. 4. Testa structures of the seeds of the examined taxa generally consisted of 2 main layers, the epidermis and the subepidermis, formed in either the scleranchymatous or parenchymatous tissue. The epidermis layer displays important variations in cell form, consisting of flat, rectangular, crushed, or polygonal cells, in 1-3 layers, and has undulated or straight wall structure. The most frequent form is flat, while the rarest ones are the rectangular and polygonal types (Tab. 4, On-line Suppl. Fig. 3). The subepidermis layer consists of crushed, orbicular, rectangular, square, flat or polygonal cells in 1-10 layers. The most commonly seen types are crushed and polygonal, whereas the rarest ones are the orbicular and square types. The subepidermis layer is not found in some of the examined taxa (*M. discolor*, *M. inconstrictum*, *M. parviflorum*, *M. botryoides* and *M. turcicum*) (Tab. 4). The thickness of the epidermis layers varies between 16.64 µm (in *M. turcicum*) and 128.46 µm (in *M. longipes*). Raphide crystals are seen in the epidermis or subepidermis layers of seeds in *M. comosum*, *M. tenuiflorum*, *M. babachii*, *M. discolor* and *M. vuralii* (Tab. 4, On-line Suppl. Fig. 3).

A dendrogram indicating differences and similarities among the studied taxa was created by numerical analyses of the seed morphological and anatomical characters, based on the variation of 44 characteristics in 36 taxa. The cophenetic correlation between the similarity matrix and dendrogram has been computed as 0.59, representing a good match. Cluster A2 includes the highest number of taxa when compared to other clusters. *Muscari sandrasicum* forms a clade separate from these clusters in the dendrogram (Fig. 1). *M. discolor* and *M. parviflorum* are the most closely related taxa (with a dissimilarity coefficient of 1.01), the most distantly related taxa recorded are *M. sandrasicum* and *M. turcicum* (with a dissimilarity coefficient of 136.31) (On-line Suppl. Tab. 1).

Discussion

The morphological features of seeds offer valuable information about evolutionary relationships among flowering plants (Corner 1976, Karaismailoğlu and Erol 2018). However, seed morphological and anatomical features have so far not been extensively used to elucidate inter-species relationships within genera of the family Asparagaceae. This is the first study to reveal the morphological and anatomical features of the seeds of a genus in the family, and it will be a model for subsequent studies on various genera.

The macromorphological characters of seeds display variation among the examined *Muscari* taxa, with the exception of seed colour, which is consistently black. The general appearance among populations, including floristic characters and capsule structures, of *M. macrocarpum* and *M. racemosum* in subgenus *Muscari*, *M. caucasicum* and *M. weissii* in subgenus *Leopoldia*, *M. aucheri* and *M. armeniacum* in subgenus *Botryanthus* are very similar, but they can be easily distinguished using seed shape and size.

Comparison of the surface micromorphological structure of seeds is of taxonomical importance (Karaismailoğlu and Erol 2018). Heywood (1971) discusses the significance and efficiency of scanning electron microscopy in elucidating taxonomic problems and distinguishing taxa. However, there are few studies on the importance of seed micromorphology in the family Asparagaceae (Yıldırım 2015, 2016). This study on 36 *Muscari* taxa shows that seed microstructures are useful characteristics in separating the taxa within the family. Almost all of the studied taxa have been examined in this way for the first time, with the exceptions of *M. elmasii* (smooth) and *M. atillae* (smooth) (Yıldırım 2015, 2016). We recorded nine seed surface ornamentation types in this study. In the genus, the most common seed ornamentation types are ruminate and reticulate. In contrast to this study, reticulate and reticulate-areolate types have been commonly seen among taxa from various angiosperm families (Tantawy et al. 2004, Karaismailoğlu 2015, Karaismailoğlu and Erol 2018). Two closely related taxa in the subgenus *Muscari*, *M. macrocarpum* and *M. racemosum*, have the same reticulate surface ornamentation type; however, *M. macrocarpum* has different secondary cuticular

Tab. 1. The examined taxa and their locations (*=endemic taxon).

No	Subgenus	Taxa	Location	Voucher
1	*Muscari*	*Muscari macrocarpum* Sweet	C1 Muğla; between Marmaris and Emecik, after Balık Pass, rocky valley, 36° 46' 27" N, 27° 59' 36" E, 324 m, 01.03.2016	H. Eroğlu 1215
2		**M. racemosum* Mill.	C2 Denizli; Çameli, Denizli-Fethiye road, 5 km to Aliveren Village, *Pinus* yards, serpentine fields, 37° 13' 39" N, 29° 26' 52" E, 1264 m, 04.05.2017.	H. Eroğlu 1317
3	*Leopoldia*	*M. caucasicum* (Griseb.) Baker	B9 Van; Erek Mountain, south of Sarmaç Village, steppe, 38° 29' 16" N, 43° 29' 26" E, 2200 m, 24.05.2016.	H. Eroğlu 1281
4		*M. weissii* Freyn	Antalya: Serik, Kumköy, *Pinus pinea* forest near the sea, dunes under the woood, 36° 52' 07" N, 30° 56' 36" E, 3 m, 02.04.2016.	H. Eroğlu 1220
5		*M. comosum* (L.) Mill.	C2 Muğla, Marmaris, between Marmaris and Datça, Hisarönü Bay, roadside, 36° 47' 59" N, 28° 05' 31" E, 70 m, 16.04.2017.	H. Eroğlu 1301
6		*M. tenuiflorum* Tausch	B6 Adana; Feke, Esendere Canyon, *Pinus* yards, 37° 45' 44" N, 35° 55' 03" E, 651 m, 15.06.2016.	H. Eroğlu 1288
7		**M. babachii* Eker & Koyuncu	C6 Hatay, Antakya, Kisecik Village, Radar road, scrub yards, 36° 18' 15" N, 36° 02' 59" E, 1430 m, 12.06.2016.	H. Eroğlu 1286
8		**M. erdalii* N.Özhatay & S.Demirci	C4 İçel; Mut, south of İbrahimli Village, scrub yards, 36° 40' 55" N, 33° 39' 23" E, 900 m, 02.05.2016.	H. Eroğlu 1255
9		*M. longipes* Boiss.	B6 Sivas; Hafik, west of Durulmuş Village, marly hills, 39° 50' 08" N, 37° 18' 20" E, 1312 m, 30.05.2017.	H. Eroğlu 1327
10		**M. massayanum* C.Grunert	C5 Adana; Pozantı, upwards of Hamidiye Village, serpentine slopes, 37° 32' 27" N, 35° 00' 51" E, 1357 m, 01.05.2016.	H. Eroğlu 1253
11		**M. mirum* Speta	C2 Denizli; Çameli, Denizli-Fethiye road, 4 km to Aliveren Village, serpentine slopes, 37° 12' 41" N, 29° 26' 17" E, 1475 m, 04.05.2016.	H. Eroğlu 1259
12		**M. elmasii* Yıldırım	C2 Muğla; Dalaman, above Gürleyik Village, Çal Mountain, *Pinus* yards, 36° 52' 49" N, 29° 07' 10" E, 1271 m, 14.05.2016.	H. Eroğlu 1270
13		**M. ufukii* E.Kaya & Demirci	B9 Van; Çatak, between Çatak-Bilgi Village, steppe, 38° 03' 48" N, 43° 11' 49" E, 1670 m, 17.07.2017.	H. Eroğlu 1341
14	*Pseudomuscari*	**M. coeleste* Fomin	B9 Van; Erek Mountain, side of Keşiş Lake, humid meadows, 38° 27' 43" N, 43° 34' 51" E, 2564 m, 18.05.2017.	H. Eroğlu 1319
15		**M. azureum* Fenzl	C5 Niğde; Ulukışla, Karagöl, humid meadows, 37° 24' 16" N, 34° 33' 38" E, 2599 m, 01.05.2016.	H. Eroğlu 1251
16	*Botryanthus*	**M. aucheri* (Boiss.) Baker	A9 Kars; Sarıkamış to Handere 5. km, meadows, 40° 18' 33" N, 42° 30' 43" E, 2196 m, 08.06.2016.	H. Eroğlu 1285
17		*M. armeniacum* Leichtlin ex Baker	C4 Karaman; Sarıveliler, Atmeydanı place, steppe, 36° 41' 44" N, 32° 31' 00" E, 1665 m, 01.05.2017	H. Eroğlu 1306

18	*_M. sivrihisardaghlarensis_ Yıld. & B.Selvi	B3 Eskişehir; Sivrihisar, between Kuzuören and Karacaören villages, stony-rocky streamside, 39° 18’ 52” N, 31° 42’ 42” E, 1416 m, 02.05.2017.	H. Eroğlu 1309
19	_M. neglectum_ Guss. ex Ten.	B3 Eskişehir; Sivrihisar, Günyüzü cross, steppe, 39° 29’ 42” N, 31° 36’ 41” E, 1009 m, 17.04.2016.	H. Eroğlu 1242
20	*_M. anatolicum_ Cowley & Özhatay	C5 İçel; Toroslar, Arslanköy, above Dümbelek Geçidi rocky slopes, 37° 03’ 56” N, 34° 17’ 53” E, 2212 m, 11.05.2018.	H. Eroğlu 1382
21	*_M. tuzgoluensis_ Yıld.	B4 Aksaray, Eskil, 1 km towars Tuzgölü from Eskil, steppe, 38° 24’ 43” N, 33° 27’ 20” E, 922 m, 13.04.2016.	H. Eroğlu 1233
22	*_M. discolor_ Boiss. & Hausskn. ex Boiss.	C8 Mardin; Artuklu, Mardin-Diyarbakır road, Akresta pass, stony streamside, 37° 22’ 57” N, 40° 39’ 09” E, 1138 m, 07.04.2017.	H. Eroğlu 1297
23	_M. inconstrictum_ Rech.f.	C6 Kilis; south of Kocabeyli Village, stony-rocky fields, 36° 48’ 07” N, 36° 54’ 59” E, 450 m, 28.02.2016.	H. Eroğlu 1212
24	*_M. latifolium_ J.Kirk	B2 Çanakkale; Bayramiç, Ayazma promenade, under the forest, humid areas, 39° 44’ 45” N, 26° 50’ 47” E, 476 m, 03.05.2017.	H. Eroğlu 1313
25	*_M. adilii_ M.B.Güner & H.Duman	A3 Ankara, Beypazarı, above Hırkatepe Village, arounds of Koçahmet Fountain, marly valleys, 40° 11’ 43” N, 31° 46’ 39” E, 1000 m, 02.05.2017.	H. Eroğlu 1308
26	*_M. bourgaei_ Baker	C4 Karaman; Sarıveliler, Atmeydanı Place, meadows, streamside, 36° 41’ 25” N, 32° 32’ 41” E, 1603 m, 01.05.2017.	H. Eroğlu 1304
27	*_M. sandrasicum_ Karlén	C2 Muğla; Köyceğiz, Sandras Mountain, Sandras Highland, Değirmenbozuğu Place, stony streamside, 37° 05’ 36” N, 28° 53’ 23” E, 1356 m, 11.04.2016.	H. Eroğlu 1226
28	_M. microstomum_ P.H.Davis & D.C.Stuart	B5 Kayseri; Bünyan, between Bünyan and Pınarbaşı 4. km, humid meadows, 38° 49’ 40” N, 35° 54’ 24” E, 1389 m, 19.05.2016.	H. Eroğlu 1277
29	*_M. macbeathianum_ Kit Tan	B6 Adana; Tufanbeyli, 2 km from Güzelim Village to Tufanbeyli, dune under _Pinus_, 38° 09’ 24” N, 36° 10’ 45” E, 1442 m, 09.05.2018.	H. Eroğlu 1374
30	*_M. vuralii_ Bağcı & Doğu	C4 Karaman; Sarıveliler, Atmeydanı place, meadows, 36° 41’ 25” N, 32° 32’ 01” E, 1603 m, 14.04.2016.	H. Eroğlu 1234
31	_M. parviflorum_ Desf.	C5 İçel; Yenişehir, between Emirler and Turunçlu villages, garden edges, 36° 50’ 10” N, 34° 28’ 42” E, 288 m, 28.09.2016.	H. Eroğlu 1291
32	*_M. serpentinicum_ Yıldırım, Altıoğlu & Pirhan	C2 Muğla; Köyceğiz, Sandras Mountain, Sandras Highland, Değirmenbozuğu Place, stony streamside, 37° 05’ 36” N, 28° 53’ 23” E, 1356 m, 11.04.2016.	H. Eroğlu 1224
33	_M. botryoides_ (L.) Mill.	B9 Ağrı; Tutak, between Aşağıköşk and Doğanüstün villages, meadows, 39° 24’ 21” N, 42° 45’ 36” E, 1669 m, 10.05.2016.	H. Eroğlu 1262
34	*_M. artvinense_ Demirci & E.Kaya	A9 Artvin; Murgul, above Korucular Village, meadows, 41° 18’ 00” N, 41° 38’ 58” E, 762 m, 13.05.2016.	H. Eroğlu 1266
35	*_M. atillae_ Yıldırım	B7 Malatya, Akçadağ, Levent Canyon, marly-movement slopes, 38° 26’ 03” N, 37° 55’ 56” E, 1197 m, 07.04.2017.	H. Eroğlu 1296
36	*_M. turcicum_ Uysal, Ertugrul & Dural	C4 Konya; Bozkır, above Avdan Highland, snowpatches, steppe, 37° 01’ 15” N, 32° 10’ 41” E, 1978 m, 11.05.2018.	H. Eroğlu 1379

Tab. 2. Macromorphological characters of the seeds of the studied taxa (mean values ± standard deviation, L=length, W=width).

Subgenus	Taxa	Shape	Seed dimensions		
			L (mm)	W (mm)	L/W
Muscari	*Muscari macrocarpum*	orbicular	2.98 ± 0.32	2.61 ± 0.29	1.14
	M. racemosum	broadly ovate-orbicular	3.16 ± 0.22	2.63 ± 0.30	1.20
Leopoldia	*M. caucasicum*	broadly ovate	2.34 ± 1.18	1.85 ± 0.11	1.26
	M. weissii	orbicular	2.08 ± 0.14	1.76 ± 0.12	1.18
	M. comosum	orbicular	2.23 ± 0.13	2.03 ± 0.11	1.10
	M. tenuiflorum	broadly ovate-orbicular	2.45 ± 1.15	2.17 ± 0.14	1.13
	M. babachii	broadly ovate	2.70 ± 0.19	2.22 ± 0.15	1.22
	M. erdalii	broadly ovate	3.21 ± 0.25	2.43 ± 0.15	1.32
	M. longipes	oblong-elliptic	2.42 ± 0.24	2.01 ± 0.12	1.20
	M. massayanum	broadly ovate	3.13 ± 0.23	2.56 ± 0.18	1.22
	M. mirum	oblong-ovate	2.82 ± 0.22	2.34 ± 0.17	1.20
	M. elmasii	broadly ovate	2.81 ± 0.25	2.25 ± 0.20	1.24
	M. ufukii	broadly ovate	3.06 ± 0.17	2.61 ± 0.13	1.17
Pseudomuscari	*M. coeleste*	orbicular	2.18 ± 0.16	1.52 ± 0.09	1.43
	M. azureum	orbicular	2.06 ± 0.10	1.35 ± 0.09	1.52
Botryanthus	*M. aucheri*	orbicular	2.11 ± 0.13	1.37 ± 0.08	1.54
	M. armeniacum	broadly ovate-orbicular	1.96 ± 0.16	1.71 ± 0.11	1.14
	M. sivrihisardaghlarensis	broadly ovate-orbicular	2.18 ± 0.17	1.69 ± 0.12	1.28
	M. neglectum	broadly elliptic	2.06 ± 0.15	1.64 ± 0.10	1.25
	M. anatolicum	orbicular	2.09 ± 0.15	1.72 ± 0.19	1.21
	M. tuzgoluensis	orbicular	1.94 ± 0.13	1.65 ± 0.13	1.17
	M. discolor	orbicular	2.23 ± 0.26	1.73 ± 0.11	1.28
	M. inconstrictum	orbicular	1.99 ± 0.12	1.80 ± 0.12	1.10
	M. latifolium	ovate-orbicular	2.39 ± 0.20	1.98 ± 0.13	1.20
	M. adilii	orbicular	2.45 ± 0.16	2.20 ± 0.17	1.11
	M. bourgaei	orbicular	1.82 ± 0.09	1.42 ± 0.11	1.28
	M. sandrasicum	orbicular	1.94 ± 0.17	1.53 ± 0.16	1.26
	M. microstomum	orbicular	1.87 ± 0.13	1.55 ± 0.16	1.20
	M. macbeathianum	broadly elliptic-lanceolate	1.66 ± 0.13	1.12 ± 0.09	1.48
	M. vuralii	orbicular	2.15 ± 0.14	1.60 ± 0.12	1.34
	M. parviflorum	orbicular	1.90 ± 0.16	1.62 ± 0.17	1.17
	M. serpentinicum	orbicular	1.72 ± 0.11	1.51 ± 0.10	1.13
	M. botryoides	broadly ovate	1.80 ± 0.14	1.36 ± 0.11	1.32
	M. artvinense	orbicular	1.70 ± 0.12	1.41 ± 0.10	1.21
	M. atillae	orbicular	2.25 ± 0.10	1.87 ± 0.11	1.20
	M. turcicum	orbicular	1.76 ± 0.13	1.34 ± 0.09	1.31

protrusions. Seed surface ornamentation is a useful character in distinguishing the taxa of the subgenus *Leopoldia*, which exhibits five ornamentation types in 11 taxa. In the subgenus *Pseudomuscari*, *M. coeleste* and *M. azureum* taxa are very similar in terms of population appearance, flowers and fruit capsule characteristics; however, they are distinctly different in terms of seed ornamentation types: ruminate and scalariform, respectively. In the subgenus *Botryanthus*, ornamentation types are diverse (seven types), and the distinct surface ornamentation in nearly identical taxa, such as *M. armeniacum-M. aucheri*, *M. armeniacum-M. bourgaei*, *M. armeniacum-M. microstomum* is proof of the taxonomical significance of this characteristic in the subgenus.

Earlier seed surface studies have indicated that the views and structures of anticlinal and periclinal cell walls are good diagnostic characters in the establishment of inter-species relationships (Barthlott 1981, Karaismailoğlu 2015, 2016). The types of anticlinal and periclinal cell walls, and epidermal cell structures of the examined taxa vary among the taxa, except for those of the subgenus *Muscari*.

Tab. 3. Micromorphological characters of the seeds of the studied taxa.

Subgenus	Taxa	Seed surface ornamentation	Anticlinal cell wall	Periclinal cell wall	Epidermal cell structure
Muscari	*Muscari macrocarpum*	reticulate	raised	concave	polygonal cells
	M. racemosum	reticulate	raised	concave	polygonal cells
Leopoldia	*M. caucasicum*	alveolate	sunken	concave	alveolar cells
	M. weissii	alveolate	sunken	concave	alveolar cells
	M. comosum	verrucate	sunken	convex	unclear
	M. tenuiflorum	reticulate-areolate	sunken	convex	polygonal cells
	M. babachii	reticulate-areolate	sunken	convex	polygonal cells
	M. erdalii	ruminate	unclear	unclear	unclear
	M. longipes	ruminate	unclear	unclear	unclear
	M. massayanum	ruminate	unclear	unclear	unclear
	M. mirum	reticulate-areolate	sunken	convex	polygonal cells
	M. elmasii	reticulate-foveate	raised	convex	polygonal and alveolar cells
	M. ufukii	ruminate	unclear	unclear	unclear
Pseudomuscari	*M. coeleste*	ruminate	unclear	unclear	unclear
	M. azureum	scalariform	sunken	convex	rectangular and polygonal cells
Botryanthus	*M. aucheri*	ruminate	unclear	unclear	unclear
	M. armeniacum	reticulate-areolate	sunken	concave	polygonal cells
	M. sivrihisardaghlarensis	rugose	unclear	Unclear	unclear
	M. neglectum	areolate	Sunken	concave	polygonal cells
	M. anatolicum	rugose	Unclear	unclear	unclear
	M. tuzgoluensis	ruminate	Unclear	unclear	unclear
	M. discolor	ruminate	Unclear	unclear	unclear
	M. inconstrictum	slightly reticulate	raised	concave	polygonal cells
	M. latifolium	ruminate	unclear	unclear	unclear
	M. adilii	ruminate	unclear	unclear	unclear
	M. bourgaei	ruminate	unclear	unclear	unclear
	M. sandrasicum	ruminate	unclear	unclear	unclear
	M. microstomum	verrucate	sunken	convex	unclear
	M. macbeathianum	ruminate	unclear	unclear	unclear
	M. vuralii	ruminate	unclear	unclear	unclear
	M. parviflorum	ruminate	unclear	unclear	unclear
	M. serpentinicum	verrucate	sunken	convex	unclear
	M. botryoides	rugose	unclear	unclear	unclear
	M. artvinense	rugose	unclear	unclear	unclear
	M. atillae	ruminate	unclear	unclear	unclear
	M. turcicum	ruminate	unclear	unclear	unclear

Revisions of the anatomy of the testa of the various angiosperm families are influential in solving systematic problems (Vaughan et al. 1976, Karaismailoğlu and Erol 2018). Koul et al. (2000) have shown that testa structures may be utilized as a valuable characteristic in the separation of the taxa and the clarification of their phylogenetic relationships.

The seed anatomical characters are frequently as useful as morphological characters for plant taxonomy, and they are valuable in the discrimination of closely correlated taxa in various families and genera (Karamian et al. 2012, Karaismailoğlu and Erol 2018, Karaismailoğlu et al. 2018). A detailed review of the literature has not found a previous study aiming at the exploration of phylogenetic relationships among the taxa with a comparative investigation of anatomical structures of the testa in members of the family Asparagaceae. This work is the first such study for the family and is the precursor to subsequent investigations. In this study, we found that the testae mostly consist of two layers,

Tab. 4. Testa anatomical features of the studied taxa (mean values ± standard deviation, + =presence, - =absence).

Subgenus	Taxa	Epidermis layers			Presence/ absence of crystals
		Epidermis structures	Subepidermis structures	Thickness (µm)	
Muscari	*M. macrocarpum*	1 layer, scleranchymatic flat cells	6-7 layers, scleranchymatic crushed cells	59.75 ± 2.48	–
	M. racemosum	1 layer, scleranchymatic rectangular cells	3-4 layers, scleranchymatic crushed cells	54.23 ± 3.09	–
Leopoldia	*M. caucasicum*	1 layer, scleranchymatic large flat cells	3-4 layers, parenchymatic orbicular or flat cells	105.44 ± 2.37	–
	M. weissii	1 layer, scleranchymatic rectangular cells	3 layers, scleranchymatic large flat cells	46.71 ± 1.82	–
	M. comosum	1 layer, scleranchymatic large flat cells	1 layer, parenchymatic rectangular or square cells	38.45 ± 3.63	+
	M. tenuiflorum	1 layer, scleranchymatic large flat cells	2-3 layers, scleranchymatic crushed cells	116.59 ± 3.88	+
	M. babachii	1 layer, scleranchymatic flat cells	2-3 layers, scleranchymatic crushed cells	121.10 ± 5.64	+
	M. erdalii	1 layer, scleranchymatic flat cells	3-4 layers, scleranchymatic crushed cells	40.37 ± 4.21	–
	M. longipes	1 layer, scleranchymatic flat cells	5-7 layers, scleranchymatic crushed cells	128.46 ± 4.23	–
	M. massayanum	1 layer, scleranchymatic flat cells	2 layers, scleranchymatic flat or crushed cells	68.83 ± 3.47	–
	M. mirum	1-2 layers, scleranchymatic crushed cells	5-6 layers, scleranchymatic crushed cells	108.54 ± 2.88	–
	M. elmasii	1 layer, scleranchymatic rectangular cells	4-5 layers, scleranchymatic crushed cells	44.16 ± 2.72	–
	M. ufukii	2-3 layers, scleranchymatic large flat cells	1 layer, scleranchymatic flat cells	85.35 ± 2.41	–
Pseudomuscari	*M. coeleste*	1 layer, scleranchymatic rectangular cells	2-3 layers, scleranchymatic flat cells	33.62 ± 3.13	–
	M. azureum	1 layer, scleranchymatic flat cells	2-3 layers, parenchymatic flat or polygonal cells	39.77 ± 2.54	–
Botryanthus	*M. aucheri*	2 layers, scleranchymatic large flat cells	1 layer, parenchymatic polygonal cells	38.76 ± 1.85	–
	M. armeniacum	1-2 layers, scleranchymatic flat cells	2 layers, parenchymatic flat or polygonal cells	71.19 ± 4.06	–
	M. sivrihisardaghlarensis	1 layer, scleranchymatic flat cells	3-4 layers, scleranchymatic crushed cells	37.84 ± 3.71	–

Subgenus	Taxa	Epidermis layers			Presence/ absence of crystals
		Epidermis structures	Subepidermis structures	Thickness (µm)	
	M. neglectum	1 layer, scleranchymatic flat cells	2 layers, parenchymatic flat cells	41.67 ± 3.24	–
	M. anatolicum	2 layers, scleranchymatic flat cells	2-3 layers, scleranchymatic crushed cells	23.08 ± 3.92	–
	M. tuzgoluensis	2 layers, scleranchymatic flat cells	1 layer, scleranchymatic polygonal cells	48.33 ± 2.18	–
	M. discolor	2 layers, scleranchymatic crushed cells	-	18.41 ± 2.38	+
	M. inconstrictum	2-3 layers, scleranchymatic crushed cells	-	22.05 ± 1.14	–
	M. latifolium	1 layer, scleranchymatic large flat cells	2-3 layers, parenchymatic flat cells	66.15 ± 3.52	–
	M. adilii	1 layer, scleranchymatic large flat cells	2-3 layers, scleranchymatic crushed cells	31.17 ± 1.84	–
	M. bourgaei	1 layer, scleranchymatic large flat cells	2 layers, scleranchymatic flat cells	64.26 ± 2.29	–
	M. sandrasicum	1 layer, scleranchymatic large flat cells	2-3 layers, parenchymatic flat cells	71.22 ± 2.31	–
	M. microstomum	1 layer, scleranchymatic flat or polygonal cells	2-3 layers, scleranchymatic polygonal cells	69.98 ± 3.53	–
	M. macbeathianum	2 layer, scleranchymatic large flat or rectangular cells	1 layer, scleranchymatic polygonal cells	41.13 ± 2.36	–
	M. vuralii	1 layer, scleranchymatic flat or polygonal cells	2-3 layers, scleranchymatic polygonal cells	44.86 ± 1.71	+
	M. parviflorum	1 layer, scleranchymatic large flat cells	-	18.08 ± 0.86	–
	M. serpentinicum	1 layer, scleranchymatic large rectangular cells	1 layer, scleranchymatic rectangular cells	39.73 ± 3.15	–
	M. botryoides	2-3 layers, scleranchymatic flat cells	-	25.81 ± 2.03	–
	M. artvinense	1 layer, scleranchymatic polygonal cells	8-10 layers, scleranchymatic crushed and orbicular cells	117.46 ± 3.55	–
	M. atillae	3 layers, scleranchymatic flat cells	2-3 layers, scleranchymatic polygonal cells	82.19 ± 2.68	–
	M. turcicum	1 layer, scleranchymatic crushed cells	-	16.64 ± 3.22	–

the epidermis and the subepidermis, in the sclerotic or parenchymatous structure. The epidermis type differs among the taxa. This 1-3 layered epidermis may consist of flat, rectangular, crushed, or polygonal cells. The most frequent form is flat, while the rarest are the rectangular and polygonal types. The structure of the subepidermis layer, which is mostly a compressed tissue under the epidermis layers, also displays significant differences among the taxa. The subepidermis layer consists of crushed, orbicular, rectangular, square, flat or polygonal cells in 1-10 layers, except for *M. discolor*, *M. inconstrictum*, *M. parviflorum*, *M. botryoides* and *M. turcicum*, which do not have a subepidermis layer. Testa characters such as the structures of the epidermis and subepidermis, thickness of the testa, and the presence or absence of crystals are fairly effective and beneficial in discriminating almost all of the studied taxa, especially in the pairs of closely correlated taxa *M. macrocarpum-M. racemosum*, *M. caucasicum-M. weissii*, *M. coeleste-M. azureum*, and *M. aucheri-M. armeniacum*. This can be interpreted as follows: the anatomy of the testa is a useful additional character in the *Muscari*, and it can aid in the classification of this huge genus. The results obtained are also in agreement with similar previous studies performed on seed structure of some taxa of the genera *Crocus* L. and *Romulea* Maratti in the closely related family Iridaceae, in terms of the differences observed at interspecific level in testa anatomical structures such as epidermis cell types and thickness of the testa (Grilli Caiola et al. 2010, Karaismailoğlu 2015, Karaismailoğlu et al. 2018).

The dendrogram showing two main clusters largely agree with the results of Davis and Stuart (1984). The seed morphological and anatomical variations have been observed at the species level and subgenus level, especially in shapes, ornamentation types, dimensions, and thicknesses and structures of epidermis and subepidermis layers. The proximity between taxa belonging to subgenera *Muscari* and *Pseudomuscari* has been preserved; however, there are taxon transitions between *Leopoldia* and *Botryanthus* subgenera. While *M. atillae*, *M. latifolium*, *M. microstomum* and *M. armeniacum* taxa are among the taxa belonging to *Botryanthus* subgenus, *M. mirum* and *M. caucasicum* taxa are located between *Leopoldia* taxa.

In conclusion, the study of morphological and anatomical seed characteristics of the studied *Muscari* taxa offers important insights into the systematics of taxa within the genus.

Key to studied *Muscari* taxa, based on seed characteristics

1. Seed shape is orbicular 2
1. Seed shape is ovate, ovate-orbicular, oblong-elliptic, oblong-ovate, elliptic, elliptic-lanceolate 21
2. Seed ornamentation is reticulate 3
2. Seed ornamentation is alveolate, verrucate, ruminate, scalariform or rugose 4
3. Outer epidermis of testa consists of crushed cells, with 2-3 layers . . . .*M. inconstrictum*
3. Outer epidermis of testa consists of flat cells, with 1 layers . . . . *M. macrocarpum*
4. Seed ornamentation is alveolate or scalariform 5
4. Seed ornamentation is verrucate, ruminate or rugose . . 6
5. Seed ornamentation is alveolate . . . . *M. weissii*
5. Scalariform . . . . *M. azureum*
6. Seed ornamentation is verrucate or rugose 7
6. Ruminate 11
7. Anticlinal cell walls are sunken 8
7. Anticlinal cell walls are unclear 10
8. Outer epidermis of testa consists of flat or polygonal cells 9
8. Outer epidermis of testa consists of rectangular cells . . . .*M. serpentinicum*
9. Subepidermis of testa consists of rectangular cells . . . .*M. comosum*
9. Subepidermis of testa consists of polygonal cells . . . .*M. microstomum*
10. Outer epidermis of testa consists of flat cells . . . . *M. anatolicum*
10. Outer epidermis of testa consists of polygonal cells . . . . *M. artvinense*
11. Outer epidermis is 1 layer 12
11. Outer epidermis is 2 or 3 layers 19
12. Outer epidermis of testa consists of crushed or rectangular cells 13
12. Outer epidermis of testa consists of flat or polygonal 14
13. Outer epidermis of testa consists of crushed . . . . *M. turcicum*
13. Rectangular . . . . *M. coeleste*
14. Subepidermis layer is absent . . . . *M. parviflorum*
14. Subepidermis layer is present 15
15. Subepidermis is in parenchymatous structure . . . .*M. sandrasicum*
15. Subepidermis is in scleranchymatous structure . . . 16
16. Subepidermis consists of crushed cells . . . . . *M. adilii*
16. Subepidermis consists of flat or polygonal cells 17
17. Subepidermis consists of flat . . . . *M. bourgaei*
17. Polygonal 18
18. Crystals are present in the epidermis or subepidermis layers . . . . *M. vuralii*
18. Crystals are absent . . . .*M. microstomum*
19. Outer epidermis is 3 layers . . . .*M. atillae*
19. 2 layers 20
20. Subepidermis is in parenchymatous structure . . . . *M. aucheri*
20. Subepidermis is in scleranchymatous structure . . . . *M. tuzgoluensis*
21. Seed shape is elliptic or oblong 22

21. Seed shape is ovate or ovate-orbicular 25
22. Seed shape is elliptic 23
22. Oblong 24
23. Seed shape is elliptic-lanceolate . *M. macbeathianum*
23. Broadly elliptic . . . . *M. neglectum*
24. Seed shape is oblong-ovate . . . . *M. mirum*
24. Oblong-elliptic . . . . *M. longipes*
25. Seed shape is ovate 26
25. Seed shape is ovate-orbicular 32
26. Seed surface ornamentation is alveolate or reticulate 27
26. Seed surface ornamentation is ruminate or rugose . 29
27. Seed surface ornamentation is reticulate 28
27. Alveolate . . . . *M. caucasicum*
28. Seed surface ornamentation is reticulate-foveate . . . . *M. elmasii*
28. Reticulate-areolate . . . . *M. babachii*
29. Seed surface ornamentation is rugose . . *M. botryoides*
29. Ruminate 30
30. Outer epidermis of testa is 2-3 layers . . . . *M. ufukii*
30. Outer epidermis of testa is 1 layer 31
31. Subepidermis is 3-4 layers . . . . *M. erdalii*
31. Subepidermis is 2 layers . . . . *M. massayanum*
32. Seed ornamentation is ruminate or rugose 33
32. Seed ornamentation is reticulate or reticulate-areolate 34
33. Seed surface ornamentation is ruminate . . *M. latifolium*
33. Rugose . . . . *M. sivrihisardaghlarensis*
34. Seed surface ornamentation is reticulate . . . . *M. racemosum*
34. Reticulate-areolate 35
35. Crystals are present in the epidermis or subepidermis layers . . . . *M. tenuiflorum*
35. Crystals are absent . . . . *M. armeniacum*

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