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Pollen morphology of *Scorzonera* (Asteraceae) in Turkey

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Abstract

The pollen morphology of 45 taxa belonging to 15 sections of the genus *Scorzonera* distributed in Turkey were studied with light and electron microscopies. The pollen is generally 3-zonocolporate. Pollen grains are oblate-spheroidal with the polar axes 23.2–59.2 µm and the equatorial axes 27–62.5 µm. The outline is more or less circular to slightly elliptic in equatorial view and triangular or obtuse-hexagonal in polar view; amb semiangular to intersemiangular. Sculpturing is echinolophate. The spines are commonly concave-conical with a broad basis, sides are straight or slightly convex with a subacute tapered apical portion. Numerical analysis showed that polar axes, equatorial axes and exine thickness are valuable variables for separating the examined taxa.

Keywords: Asteraceae, Pollen, *Scorzonera*, Turkey

Introduction

Scorzonera L. with about 160 species is a genus in the subtribe Scorzonnerinae Dumort. of the tribe Cichorieae of the Asteraceae family. The genus, which is of ancient Mediterranean origin, is widespread in the more arid regions of Eurasia and northern Africa (Bremer 1987, Nazarova 1997, Coskuncelebi *et al.* 2015). The first thorough analysis of the genus *Scorzonera* was provided by Candolle (1805). Later, the genus was divided into various sections and subgenera based on morphological characters; four sections (*Podospermum* DC., *Scorzonera*, *Lasiospora* Less. and *Epilasia* (Bunge) Benth.) by Boissier (1875), 3 subgenera (*Podospermum*, *Pseudopodospermum* (Lipsch. & Krasch.) Lipsch., and *Scorzonera*) by Lipschitz (1935, 1939) and Kamelin & Tagaev (1986). More recent treatments recognised the polyphyletic nature of *Scorzonera* s.l. with further splitting of taxa at the level of genus (Nazarova 1997). Mavrodiev *et al.* (2004) proposed to treat *Scorzonera*, *Podospermum*, and *Lasiospora* as distinct genera. In addition, the phylogenetic reconstruction by Owen *et al.* (2006) revealed that *Lasiospora* represents a lineage separate from *Scorzonera* (Coskuncelebi *et al.* 2015).

In the *Flora of Turkey*, 42 species of *Scorzonera* were reported as present in Turkey (Chamberlain 1975). Currently, *Scorzonera* in its wide sense is represented by 52 species (59 taxa) in Turkey, of which 31 species are endemics (Coskuncelebi *et al.* 2012, Makbul *et al.* 2012, Coskuncelebi *et al.* 2015). In Coskuncelebi *et al.* (2015) an updated infrageneric and generic classification was proposed, together with a checklist and a new key for the species of *Scorzonera* distributed in Turkey. In this treatment, the genus was divided into three subgenera (*Scorzonera*, *Podospermum*, and *Pseudopodospermum*), whereas *S.* subgen. *Scorzonera* was further subdivided into 13 sections (*Anatolia*, *Foliosae*, *Incisae*, *Infrarosulares*, *Nervosae*, *Papposae*, *Parviflorae*, *Pulvinares*, *Scorzonera*, *Subaphyllae*, *Tuberosae*, *Turkestanicae*, and *Vierhapperia*).

Pollen morphology has provided a useful approach to systematic relationships among the genera of the Asteraceae (Wagenitz 1955, Stix 1960, Avetisjan 1964, Skvarla & Larson 1965, Blackmore 1982, 1990, Punt & Hoen 2009, Ceter *et al.* 2013). Wodehouse (1935) surveyed the pollen morphology of the Lactuceae, including several members of the Scorzonnerinae, and provided a new terminology for their complex pollen grains. Most Scorzonnerinae genera have pollen grains with elaborated systems of ridges and spines disposed around and between the apertures; this sculpturing pattern

was termed echinolophate by Wodehouse (1935) and fenestrated by Faegri & Iversen (1992). The pollen morphology of *S. hispanica*, *S. parviflora*, *S. humilis*, *S. graminifolia* L., *S. purpurea* L., and *S. nervosa* Trev. was studied using LM by Wodehouse (1935). Wageniz (1976) described three evolutionary trends in Asteraceae pollen morphology: reduction of spines, reduction and loss of inner columellae and formation of surface ridges (lophae or fenestrated pollen). Askerova (1969, 1970, 1976) conducted palynological investigation of the genus *Scorzonera* connected with questions of taxonomy. Inceoglu & Karamustafa (1977) described the pollen morphology of *S. eriophora* DC. and *S. tomentosa* L. Blackmore (1982) examined pollen samples of c. 130 species in seven genera of subtribe *Scorzonerinae* by light, scanning electron and transmission electron microscopy and described seven pollen types (*S. humilis*-type, *S. laciniata*-type, *S. hispanica*-type, *S. lanata*-type, *Tourneuxia*-type, and *Tragopogon*-type) on the basis of the number and arrangement of the lacunae. Ten species of *Scorzonera* (*S. humilis* L., *S. parviflora* Jacq., *S. aristata* Ramond & DC., *S. hirsuta* L., *S. albicans* Cosson, *S. laciniata* L., *S. reverchonii* Debeaux ex Hervier, *S. baetica* (Boiss.) Boiss., *S. hispanica* L. and *S. angustifolia* L.) from the Iberian Peninsula were studied by light microscopy and scanning electron microscopy by Guardia & Blanca (1985). The pollen morphology of *S. ekimii* A. Duran was described by Duran (2002). Nair & Lawrence (1985) described the pollen morphology of *S. divaricata* from India. Meo & Khan (2004) divided five species of *Scorzonera* sp. (*S. handae*, *S. picridioides*, *S. laciniata*, *S. virgata* and *S. ammophila*) into three groups on the basis of exine thickness. The pollen morphology of 46 Egyptian species representing 23 genera of the tribe Lactuceae was investigated using light and scanning electron microscopy. Seven pollen types were recognized: *Geropogon* pollen type, *Koelipinia* pollen type, *Lactuca* pollen type, *Launaea* pollen type, *Rhagadiolus* pollen type, *Scolymus* pollen type and *Scorzonera* pollen type; *Scorzonera alexandrina* Boiss. and *S. mollis* M. Bieb var. *longifolia* were placed into the *Scorzonera* pollen type (Osman 2006). The pollen morphology of *S. ammophila*, *S. picridioides*, *S. virgata*, *S. hondae* and *S. laciniata* was examined by Qureshi *et al.* (2008). The pollen morphology of the 13 taxa of *Scorzonera* (*S. laciniata* subsp. *laciniata*, *S. cana* var. *cana*, *S. armeniaca*, *S. suberosa*, *S. mollis* subsp. *mollis*, *S. inaequiscapa*, *S. insica*, *S. eriophora*, *S. cinerea*, *S. sericea*, *S. pseudolanata*, *S. sosnowskyi*, and *S. tomentosa*) from Turkey was investigated by Türkmen *et al.* (2010). The developmental origins of structural diversity in the pollen walls of *S. humilis* and *S. hispanica* were studied by Blackmore *et al.* (2010). The pollen morphology of *S. ketzkhovelii* Grossh. and *S. zorkunensis* Coskunc. & Makbul was described by Hamzaoglu *et al.* (2010) and Coskuncelebi *et al.* (2012), respectively. Makbul *et al.* (2012) investigated the palynological properties of *S. ahmet-duranii* sp. nov. Pollen morphology of *S. pygmaea* Sibth. & Sm. var. *pygmaea* and *S. pygmaea* var. *nutans* (Czeczott) O. Koyuncu & Yaylacı were studied by Koyuncu *et al.* (2014).

This study includes a detailed morphological pollen analysis of 45 taxa of *Scorzonera* which are distributed in Turkey by using LM and SEM in Table 1. All taxa in this study were examined for the first time, except *S. parviflora* Jacq., *S. pygmaea* Sibth. & Sm. subsp. *pygmaea*, *S. pygmaea* subsp. *nutans* (Czeczott) Chamberlain, and *S. ahmet-duranii* S. Makbul & Coskuncelebi. The study attempts to clarify the systematics of the Turkish *Scorzonera*.

TABLE 1. Voucher information for the species in this study.

Taxon	Locality	Voucher and specimen code
<i>S.</i> subgen. <i>Podospermum</i>		
<i>S. cana</i> (C. A. Mey) Hoffm. var. <i>alpina</i> (Boiss.) Chamberlain	A8 Rize: 2640 m, 28.07.2011	Makbul & Coskuncelebi 333 (RUB, KTUB)
<i>S. cana</i> (C. A. Mey) Hoffm. var. <i>jacquiniana</i> (W. Koch) Chamberlain	C3 Konya: 1359 m, 27.05.2010 A8 Rize: 2400 m	Makbul & Coskuncelebi 206 (RUB, KTUB) Makbul 028 (RUB, KTUB)
<i>S. cana</i> (C. A. Mey) Hoffm. var. <i>radicosa</i> (Boiss.) Chamberlain	C5 Niğde: 1690 m, 08.06.2010	Makbul & Coskuncelebi 219 (RUB, KTUB)
<i>S. laciniata</i> L. subsp. <i>calcitrapifolia</i> (Vahl) Marie	C3 Isparta: 1199 m, 24.05.2010	Makbul & Coskuncelebi 200a (RUB, TUB)
<i>S. hieracifolia</i> Hayek	B4 Konya: 912 m, 11.06.2009	Makbul & Coskuncelebi 138 (RUB, KTUB)
<i>S.</i> subgen. <i>Pseudopodospermum</i>		
<i>S. elata</i> Boiss.	C2 Muğla: 152 m, 25.05.2010	Makbul & Coskuncelebi 204 (RUB, KTUB)
<i>S. suberosa</i> C. Koch subsp. <i>cariensis</i> (Boiss.) Chamberlain	C6 Maraş: 1300 m, 16.05.2010	Makbul & Coskuncelebi 180a (RUB, KTUB)
<i>S. phaeohappa</i> (Boiss.) Boiss.	C6 Gaziantep: 1135 m, 15.05.2010	Makbul & Coskuncelebi 174 (RUB, KTUB)
<i>S. mollis</i> Bieb. subsp. <i>szowitzii</i> (DC.) Chamberlain	A7 Gümüşhane: 1595–1800 m, 21.05.2004	Makbul 36 (RUB, KTUB)
<i>S. semicana</i> DC.	A9 Kars: 1430 m, 12.06.2010	Makbul & Coskuncelebi 226 (RUB, KTUB)

...continued on the next page

TABLE 1. (Continued)

Taxon	Locality	Voucher and specimen code
S. subgen. <i>Scorzonera</i> sect. <i>Anatolia</i>		
<i>S. boissieri</i> Lipsch.	B6 Maraş: 2203 m, 14.07.2010	Makbul & Coskuncelebi 247 (RUB, KTUB)
<i>S. karabelensis</i> Parolly & N. Kilian	C2 Muğla: 1114 m, 22.05.2012	Makbul & Coskuncelebi 346 (RUB, KTUB)
<i>S. longiana</i> Sümbül	C3 Antalya: 1727 m, 25.07.2010	Makbul & Coskuncelebi 255 (RUB, KTUB)
<i>S. sandrasica</i> Hartvig & Strid	C2 Muğla: 2025 m, 23.06.2010	Makbul & Coskuncelebi 232 (RUB, KTUB)
<i>S. ulrichii</i> Parolly & N. Kilian	C4 Antalya: 1336 m, 05.07.2010	Makbul & Coskuncelebi 237 (RUB, KTUB)
<i>S. zorkunensis</i> Coskuncelebi & S. Makbul	C6 Osmaniye: 2073 m, 05.07.2010	Makbul & Coskuncelebi 242 (RUB, KTUB).
S. subgen. <i>Scorzonera</i> sect. <i>Foliosae</i>		
<i>S. acuminata</i> Boiss.	A4 Ankara: 968 m, 07.06.2010	Makbul & Coskuncelebi 215 (RUB, KTUB)
<i>S. davisii</i> Lipsch.	C10 Van: 1533 m, 19.07.2011	Makbul & Coskuncelebi 315 (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Incisae</i>		
<i>S. lacera</i> Boiss. & Bal.	B6 Maraş: 727 m, 08.06.2009	Makbul & Coskuncelebi 134 (RUB, KTUB)
<i>S. violacea</i> Chamberlain	C3 Antalya: 1727 m, 25.07.2010	Makbul & Coskuncelebi 256 (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Infrasulares</i>		
<i>S. acantholimon</i> Hand. & Mazz.	B6 Maraş: 2355 m, 14.07.2010	Makbul & Coskuncelebi 246 (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Nervosae</i>		
<i>S. argyrea</i> Boiss.	C2 Muğla: 1369 m, 26.07.2010	Makbul & Coskuncelebi 258 (RUB, KTUB)
<i>S. ketzkhovellii</i> Sosn. ex Grossh. & Sosn.	A9 Erzurum: 2180 m, 07.07.2010	Makbul & Coskuncelebi 270 (RUB, KTUB)
<i>S. mirabilis</i> Lipsch.	A8 Erzurum: 2190 m, 05.07.2010	Makbul & Coskuncelebi 264 (RUB, KTUB)
<i>S. veratrifolia</i> Fenzl	B9 Bitlis: 1965 m, 06.08.2010	Makbul & Coskuncelebi 267 (RUB, KTUB)
<i>S. latifolia</i> (Fisch. & Mey.) DC. var. <i>angustifolia</i> Prilipko.	A8 Erzurum: 2190 m, 05.07.2010	Makbul & Coskuncelebi 265 (RUB, KTUB)
<i>S. latifolia</i> (Fisch. & Mey.) DC. var. <i>latifolia</i> (Fisch. & Mey.) DC.	A8 Bayburt: 2150 m, 27.07.2005	Makbul 94 (RUB, KTUB)
<i>S. dzhawakhetica</i> Sosn. ex Grossh. & Sosn.	A8 Artvin: 2122 m, 04.07.2010	Makbul & Coskuncelebi 260 (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Papposae</i>		
<i>S. papposa</i> DC.	C6 Maraş: 747 m, 15.05.2010	Makbul 172 & Coskuncelebi (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Parviflorae</i>		
<i>S. parviflora</i> Jocq.	B6 Sivas: 1301 m, 06.06.2009	Makbul & Coskuncelebi 128 (RUB, KTUB)
	A8 Erzurum: 1630 m	Makbul 088 (RUB, KTUB)
<i>S. tuzgoluensis</i> A. Duran, B. Doğan & S. Makbul	B4 Konya: 908 m, 06.07.2011	Makbul & Coskuncelebi 140 (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Pulvinares</i>		
<i>S. amasiana</i> Hausskn. & Bornm.	A5 Amasya: 480 m, 22.05.2010	Makbul & Coskuncelebi 188 (RUB, KTUB)
<i>S. lasiocarpa</i> Chamberlain	C6 Hatay: 46 m, 30.04.2011	Makbul & Coskuncelebi 273 (RUB, KTUB)
<i>S. seidlitzii</i> Boiss.	A9 Artvin: 2150 m, 16.07.2003	Makbul 22 (RUB, KTUB)
<i>S. rigida</i> Aucher	B7 Erzincan: 2306 m, 11.07.2009	Makbul 156 (RUB, KTUB)
<i>S. pygmaea</i> Sibth. & Sm. subsp. <i>pygmaea</i> Sibth. & Sm.	A2 Bursa: 2159 m, 24.07.2010	Makbul & Coskuncelebi 271 (RUB, KTUB)
<i>S. pygmaea</i> Sibth. & Sm. subsp. <i>nutans</i> (Czeczott) Chamberlain	A4 Kastamonu: 2055 m, 02.08.2009	Makbul 165 (RUB, KTUB)
<i>S. yildirimlii</i> A. Duran & Hamzaoglu	C6 Osmaniye: 2073 m, 05.07.2010	Makbul & Coskuncelebi 243 (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Scorzonera</i>		
<i>S. ahmet-duranii</i> S. Makbul & Coskuncelebi	C2 Muğla: 1655 m, 23.06.2010	Makbul & Coskuncelebi 230 (RUB, KTUB)
<i>S. coriacea</i> A. Duran & Aksoy	C3 Konya: 1401 m, 12.06.2009	Makbul & Coskuncelebi 144 (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Subaphyllae</i>		
<i>S. aucheriana</i> DC.	B7 Erzincan: 1153 m, 25.06.2009	Makbul & Coskuncelebi 167 (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Tuberosae</i>		
<i>S. sublanata</i> Lipsch.	C2 Muğla: 1369 m, 19.05.2011	Makbul & Coskuncelebi 276 (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Turkestanicae</i>		
<i>S. renzii</i> Rech. f.	B9 Bitlis: 1965 m, 06.08.2010	Makbul & Coskuncelebi 266 (RUB, KTUB)
S. subgen. <i>Scorzonera</i> sect. <i>Vierhapperia</i>		
<i>S. pisidica</i> Hub.-Mor.	C2 Muğla: 1282 m, 23.06.2010	Makbul & Coskuncelebi 229 (RUB, KTUB)
<i>S. kotschyi</i> Boiss.	B6 Maraş: 1070 m, 07.06.2009	Makbul 133 (RUB, KTUB)

TABLE 2. Summary statistics for seven characters examined in 45 taxa of *Scorzonera*.

Taxa/ characters	Polar axis (μm) mean	Equatorial axis (μm) mean	Exine (μm)	Perforation number at base	Number of spines ($10 \mu\text{m}^2$)	Abporal lacunae shape	Pollen type
S1	29.7	31.7	5.3	0	0	0	2
S2	30.1	32.2	5.4	0	0	0	2
S3	34	36.7	5.1	1	0	0	2
S4	30.1	31.4	5.6	0	0	0	2
S5	34.8	37.1	5.2	0	0	0	2
S6	57.6	61	8.5	0	1	1	1
S7	38.9	41.4	7.6	0	2	1	1
S8	30.4	32.3	7.8	0	1	1	1
S9	31.9	33.3	7.6	0	1	1	1
S10	33.1	35.7	9.5	0	2	1	1
S11	33.7	36.5	7	0	3	1	1
S12	28.3	30.7	6.6	0	3	0	0
S13	29	31.3	6.6	0	3	0	0
S14	28.1	30	6.2	0	3	0	0
S15	28.7	31.4	6.5	0	3	0	0
S16	33.9	36.7	6.2	1	3	0	0
S17	36.8	39.1	6.9	1	3	1	1
S18	32.2	35	6.6	1	3	1	1
S19	51.3	54.7	6.9	1	4	0	0
S20	31.6	33.8	6.9	1	3	0	0
S21	29.3	31.4	6.4	1	5	0	0
S22	30.2	30.7	5.5	1	5	0	0
S23	27.2	29.4	6.2	1	5	0	0
S24	33.9	35.9	6.3	1	5	0	0
S25	31.2	33.5	7.3	1	5	0	0
S26	31.1	34.2	5.9	1	5	0	0
S27	32.4	35.8	6.9	1	5	0	0
S28	29.2	32.4	6.3	1	5	0	0
S29	40.5	43.3	6.4	1	6	1	1
S30	49.2	51	7	0	5	1	1
S31	31	33.5	6.7	1	5	1	1
S32	28.3	30.6	6.2	1	5	0	0
S33	26.6	29	5.6	1	5	0	0
S34	29.3	31.1	6	1	5	0	0
S35	47.5	48.7	7.1	1	5	0	0
S36	28	30.1	6.1	1	5	0	0
S37	48.6	51.2	7.5	1	5	0	0
S38	28.5	31.9	6.3	1	5	0	0
S39	36.2	39	7.2	1	5	1	1
S40	35.9	38	7	1	5	1	1
S41	32.6	35.5	5.8	1	5	0	0
S42	34.4	37.1	5.7	1	5	0	0
S43	29.1	32	6	1	5	1	1
S44	33.9	36.7	6.2	1	5	0	0
S45	43.1	45	7.2	1	5	0	0

Materials and methods

Plant materials

Materials used for this study were collected at different periods of the year and from various locations in Turkey. Collectors and localities of the investigated specimens are given in Table 1. All vouchers are deposited in the Herbarium of the Karadeniz Technical University, Department of Biology (KTUB), and the Herbarium of the Recep Tayyip Erdoğan University, Department of Biology (RUB). The order of the species was adopted from Coskuncelebi *et al.* (2015).

Palynological

Pollen slides were prepared using the Erdtman (1960) acetolysed technique and further studied under the light microscope. Their photographs were taken with the Olympus BX51 digital photomicrograph system. Measurements were based on 30 or more pollen grains per specimen (Blackmore 1984, Blackmore & Persson 1996, Punt *et al.* 2007, 2009).

For scanning electron microscopy (SEM) studies, dried pollen grains were transferred on aluminum stubs and coated with gold for 4 min in a sputter-coater. Morphological observations were made in a Jeol JSM 6490LV scanning electron microscope at Turkish Petroleum International Company (TPAO) research center SEM laboratory, Ankara. Terminology was adopted from Blackmore (1984), Blackmore & Persson (1996) and Punt *et al.* (2007, 2009).

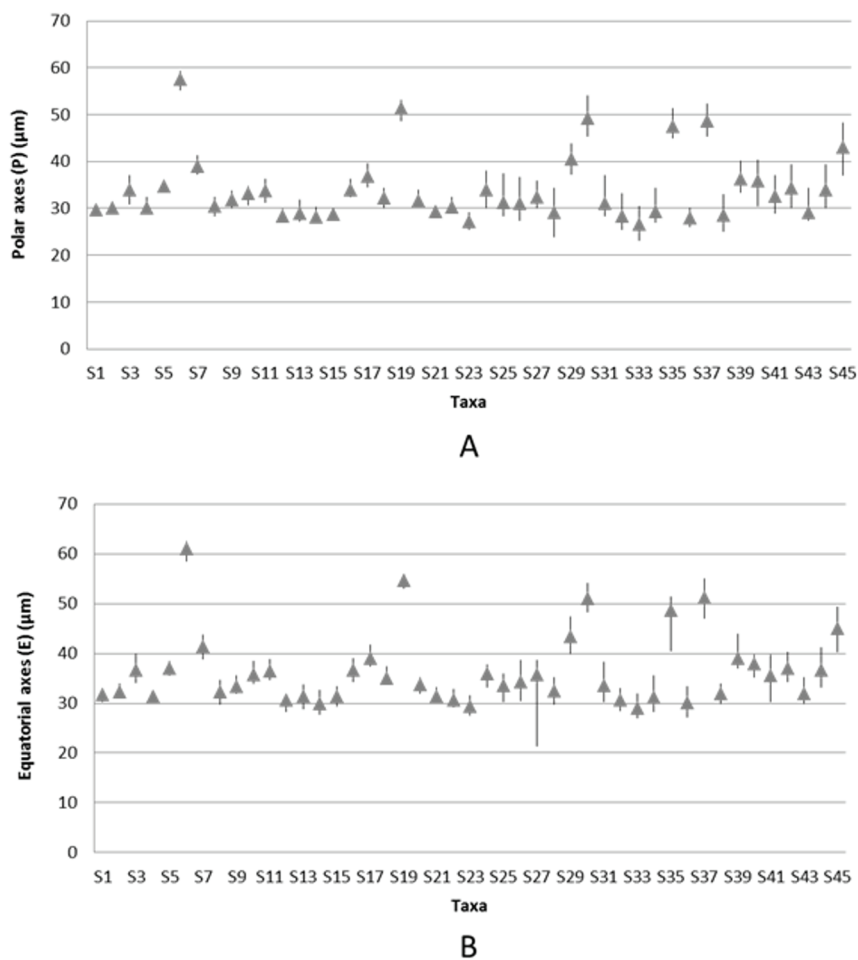


FIGURE 1. Simpson and Roe test for the taxa of *Scorzonera* examined in the present study. A. Polar axes (P), B. Equatorial axes (E).

Numerical analysis

The Simpson and Roe graphical test (Van der Pluym & Hideux 1997) was used for statistical calculations (Fig. 1). For the pollen characters of the 45 taxa coefficients of correlation were determined, and they were grouped using the clustering analysis method (UPGMA, dissimilarity, standardized variables). A total of 7 palynological characters comprising 5 quantitative and 2 qualitative characters were selected to distinguish 45 studied taxa of *Scorzonera* (Table 2). For the multivariate analysis, a primary matrix was created using 45 taxa and seven characters. The clustering analysis was based on Gower's (1971) general coefficient similarity (Sneath & Sokal 1973), which can be used directly with a mixture of character types (binary, qualitative and quantitative characters). UPGMA was selected because it is not only the most commonly used method but also appears to produce an accurate reflection similarity matrix as measured by the co-phenetic correlation coefficient of Sokal & Rohlf (1962) symmetrical hierarchical structure (McNeill 1979) and congruence with classification derived by traditional methods (Ward 1993). To interpret and summarize the data, Principle Component Analysis (PCA) was employed for identification of valuable pollen morphological characters used for taxonomy. PCA is the technique for obtaining low-dimensional representation of multivariate data. Untransformed, centred and standardised data were used to create a covariance matrix, and 3 eigenvectors were extracted. All computations were made by the MVSP 3.1 software.

Results

The main palynological features of the studied taxa of *Scorzonera* are summarized in Tables 3–5 and shown in Figs. 2–15.

Size, symmetry and shape

The pollen grains of *Scorzonera* are radially symmetrical and isopolar. Pollen grains are oblate-spheroidal with the polar axes 23.2–59.2 μm and the equatorial axes 27–62.5 μm . The dimensions are smaller in *S. laciocarpa* and *S. ketzkhovellii* and larger in *S. elata* and *S. lacera*. Their outlines are more or less circular to slightly elliptic in equatorial view and triangular or obtuse-hexagonal in polar view; amb semiangular to intersemiangular (Tables 3–5, Figs. 2–6, Figs. 7–15).

Apertures

The pollen grains of *Scorzonera* are 3-zonocolporate. The compound aperture consists a meridionally elongated colpus (Clg 13.4–29.4; Clt 3.5–8.3) which is distinctly divided into two abporal lacunae, a longate porus (Plg 4.2–10.1; Plt 3–7.9). The highest numbers of colpus were observed in *S. elata*, *S. lacera*, and *S. amasiana*, whereas *S. karabelensis* have the lowest numbers of colpus (Figs. 2–15).

Three pollen types were described based on their lacuna system. *Scorzonera acantholimon*, *S. amasiana*, *S. argyrea*, *S. aucheriana*, *S. dzhawakhetica*, *S. karabelensis*, *S. ketzkhovellii*, *S. kotschyi*, *S. laciocarpa*, *S. latifolia* var. *angustifolia*, *S. latifolia* var. *latifolia*, *S. longiana*, *S. mirabilis*, *S. pisidica*, *S. pygmaea* subsp. *nutans*, *S. pygmaea* subsp. *pygmaea*, *S. rigida*, *S. sandrasica*, *S. seidlitzii*, *S. sericea*, *S. sublanata*, *S. ulrichii*, *S. veratrifolia*, *S. yildirimlii* and *S. zorkunensis* were shown to have the *S. laciniata* type of lacuna system (6 abporal lacunae, 6 equatorial lacunae and 6 interapertural lacunae).

Scorzonera acuminata, *S. ahmet-duranii*, *S. boissieri*, *S. coriacea*, *S. davisii*, *S. elata*, *S. inaequiscapa*, *S. incisa*, *S. lacera*, *S. mollis* subsp. *szowitzii*, *S. parviflora*, *S. phaepappa*, *S. semicana*, *S. suberosa* subsp. *cariensis*, *S. tuzgoliensis* and *S. violacea* shown the *S. hispanica* type of lacuna system (similar to the *S. laciniata* type but with a large hexagonal lacuna at each pole).

Scorzonera cana var. *alpina*, *S. cana* var. *jacquiniana*, *S. cana* var. *radicosa*, *S. hieraciifolia*, *S. laciniata* subsp. *calcitrapiifolia* and *S. renzii* show the *S. lanata* type of lacuna system (similar to the *S. laciniata* type but with three pentagonal lacuna at each pole).

The abporal lacunae are large, angular and narrower towards the mesoaperture (*S.* subgen. *Pseudopodospermum*, *S. boissieri*, *S.* sect. *Foliosae*, *S.* sect. *Incisae*, *S.* sect. *Papposae*, *S.* sect. *Parviflorae*, *S.* sect. *Scorzonera*, *S.* sect. *Turkestanicae*) or the abporal lacunae are rounded and narrower towards the mesoaperture (Tables 3–5, Figs. 2–15).

TABLE 3. Pollen morphological measurements of the studied taxa of *Scorzonera* (S1–S20).

Taxa	Chromosome number (2n)*	Polar axes (P) (µm)		Equatorial axes (E) (µm)			P/E	Pollen shape	Exine (µm)	Aperture type	Colpus (µm)		Pore (µm)		Pollen type	
		Min	Max	Mean	Min	Max					Mean	Clt	Clg	Plt		Pig
Subgenus Podospermum																
<i>S. cana</i> var. <i>alpina</i> (S1)	2n=14	28.8	30.6	29.7	30.2	33	31.7	0.94	Oblate-spheroidal	5.3	3-zonocolporate	4.3	16	3.7	4.6	2
<i>S. cana</i> var. <i>jacquiniana</i> (S2)	2n=14	29	31.5	30.1	31.1	34	32.2	0.93	Oblate-spheroidal	5.4	3-zonocolporate	4.8	16.2	3.9	4.7	2
<i>S. cana</i> var. <i>radicosa</i> (S3)	2n=14	30.8	37.1	34	34.1	40	36.7	0.93	Oblate-spheroidal	5.1	3-zonocolporate	4.8	17.5	4.4	5.4	2
<i>S. laciniata</i> subsp. <i>calcitrapifolia</i> (S4)	2n=14	28.9	32.4	30.1	30.3	32.5	31.4	0.96	Oblate-spheroidal	5.6	3-zonocolporate	4.4	16.3	3.5	4.7	2
<i>S. hieracifolia</i> (S5)	2n=14	33.3	36.1	34.8	35.5	38.5	37.1	0.93	Oblate-spheroidal	5.2	3-zonocolporate	4.9	16.9	4.2	5.4	2
Subgenus Pseudopodospermum																
<i>S. elata</i> (S6)	2n=14	55.2	59.2	57.6	58.5	62.5	61	0.94	Oblate-spheroidal	8.5	3-zonocolporate	8.3	29.4	7.9	10.1	1
<i>S. suberosa</i> subsp. <i>cariensis</i> (S7)	2n=14	37.3	41.3	38.9	38.8	43.8	41.4	0.94	Oblate-spheroidal	7.6	3-zonocolporate	6.2	21.4	4.6	6.1	1
<i>S. phaeohappa</i> (S8)	2n=28	28.4	32.4	30.4	29.7	34.7	32.3	0.94	Oblate-spheroidal	7.8	3-zonocolporate	4.7	17.8	3.5	5	1
<i>S. mollis</i> subsp. <i>szowitzii</i> (S9)	2n=14	30.1	33.8	31.9	32	35.5	33.3	0.96	Oblate-spheroidal	7.6	3-zonocolporate	5	17.5	3.6	5	1
<i>S. semicana</i> (S10)	2n=28	30.6	34.7	33.1	33.9	38.5	35.7	0.93	Oblate-spheroidal	9.5	3-zonocolporate	6.1	20.2	5	6.5	1
Subgenus Scorzonera sect. Anatolia																
<i>S. boissieri</i> (S11)	2n=14	31.3	36.3	33.7	34.7	38.9	36.5	0.92	Oblate-spheroidal	7	3-zonocolporate	4.9	19.5	3.7	5.1	1
<i>S. karabelensis</i> (S12)	2n=12	27.5	29.9	28.3	28.3	31.3	30.7	0.92	Oblate-spheroidal	6.6	3-zonocolporate	4.9	15.2	3.5	4.3	0
<i>S. longiana</i> (S13)	2n=14	27.1	31.8	29	28.8	33.8	31.3	0.93	Oblate-spheroidal	6.6	3-zonocolporate	4.6	15.7	3.5	4.5	0
<i>S. sandrasica</i> (S14)	2n=12	27.3	30.2	28.1	27.7	32.7	30	0.94	Oblate-spheroidal	6.2	3-zonocolporate	6	16	3	4.9	0
<i>S. ulrichii</i> (S15)	2n=12	27.7	30	28.7	29.4	33.3	31.4	0.91	Oblate-spheroidal	6.5	3-zonocolporate	4.5	16.4	3.6	4.4	0
<i>S. zorkanensis</i> (S16)	2n=28	32.5	36.2	33.9	34.3	39.1	36.7	0.92	Oblate-spheroidal	6.2	3-zonocolporate	4.6	16.3	3.7	4.6	0
Subgenus Scorzonera sect. Foliosae																
<i>S. acuminata</i> (S17)	2n=12	34.5	39.6	36.8	37.3	41.8	39.1	0.94	Oblate-spheroidal	6.9	3-zonocolporate	5.6	20.6	5.1	6.2	1
<i>S. davisii</i> (S18)	2n=12	30.1	34.4	32.2	33.7	37.3	35	0.92	Oblate-spheroidal	6.6	3-zonocolporate	5.3	17.8	3.5	5.1	1
Subgenus Scorzonera sect. Incisae																
<i>S. lacera</i> (S19)	2n=14	48.6	53.1	51.3	53.1	56	54.7	0.94	Oblate-spheroidal	6.9	3-zonocolporate	7.9	25.5	6.3	8	1
<i>S. violacea</i> (S20)	2n=14	30.2	34	31.6	32	35.1	33.8	0.93	Oblate-spheroidal	6.9	3-zonocolporate	5	18.1	3.7	5	1

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TABLE 3 (Continued, S21–S40).

Taxa	Chromosome number (2n)*	Polar axes (P) (µm)			Equatorial axes (E) (µm)			P/E	Pollen shape	Exine (µm)	Aperture type	Colpus (µm)		Pore (µm)		Pollen type
		Min	Max	Mean	Min	Max	Mean					Clc	Clg	Plt	Plg	
Subgenus <i>Scorzonera</i> sect. <i>Infrarosulatales</i>																
<i>S. acantholimon</i> (S21)		28	30.5	29.3	30.2	33.2	31.4	0.93	Oblate-spheroidal	6.4	3-zonocolporate	4.4	16.5	3.6	4.3	0
Subgenus <i>Scorzonera</i> sect. <i>Nervosae</i>																
<i>S. argyrea</i> (S22)	2n=12	29.5	32.5	30.2	29.1	32.8	30.7	0.98	Oblate-spheroidal	5.6	3-zonocolporate	6.4	17.1	3.3	5.1	0
<i>S. ketzkhovetii</i> (S23)	2n=14	25.4	29.2	27.2	27.6	31.5	29.4	0.93	Oblate-spheroidal	6.2	3-zonocolporate	4.1	15.3	3.4	4.3	0
<i>S. mirabilis</i> (S24)		30	38.1	33.9	33.1	37.8	35.9	0.94	Oblate-spheroidal	6.3	3-zonocolporate	5.4	18.6	4.4	5	0
<i>S. veratrifolia</i> (S25)		28.3	37.4	31.2	30.3	35.9	33.5	0.93	Oblate-spheroidal	7.3	3-zonocolporate	4.7	17.9	3.7	4.9	0
<i>S. latifolia</i> var. <i>angustifolia</i> (S26)		27.4	36.7	31.1	30.4	38.7	34.2	0.91	Oblate-spheroidal	5.9	3-zonocolporate	6.6	16.6	3.6	4.8	0
<i>S. latifolia</i> var. <i>latifolia</i> (S27)	2n=24	30.1	35.8	32.4	21.3	38.7	35.8	0.91	Oblate-spheroidal	6.9	3-zonocolporate	8.2	18.5	3.7	5.8	0
<i>S. dzhawakhetica</i> (S28)	2n=12	23.9	34.4	29.2	29.8	35.2	32.4	0.9	Oblate-spheroidal	6.3	3-zonocolporate	5.1	16.2	3.8	4.7	0
Subgenus <i>Scorzonera</i> sect. <i>Papposae</i>																
<i>S. papposa</i> (S29)	2n=14	37.3	43.8	40.5	40	47.4	43.3	0.94	Oblate-spheroidal	6.4	3-zonocolporate	5.6	21.4	5	6.6	1
Subgenus <i>Scorzonera</i> sect. <i>Parviflorae</i>																
<i>S. parviflora</i> (S30)	2n=14	45.3	54.1	49.2	48.3	54.2	51	0.96	Oblate-spheroidal	7	3-zonocolporate	7.9	23.1	5	7	1
<i>S. tuzgoluensis</i> (S31)	2n=12	28.4	37	31	30.2	38.3	33.5	0.93	Oblate-spheroidal	6.7	3-zonocolporate	5	16.7	3.4	4.9	1
Subgenus <i>Scorzonera</i> sect. <i>Pulvinariae</i>																
<i>S. amastiana</i> (S32)	2n=14	25.4	33.1	28.3	28.4	33	30.6	0.92	Oblate-spheroidal	6.2	3-zonocolporate	4.3	15.6	3.5	4.4	0
<i>S. lasiocarpa</i> (S33)	2n=12	23.2	30.5	26.6	27	31.9	29	0.92	Oblate-spheroidal	5.6	3-zonocolporate	4.8	14.3	3.2	4.2	0
<i>S. seidlitzii</i> (S34)	2n=12	27	34.3	29.3	28.2	35.6	31.1	0.94	Oblate-spheroidal	6	3-zonocolporate	5.4	14.9	3.4	4.5	0
<i>S. rigida</i> (S35)	2n=12	45	51.3	47.5	40.4	51.4	48.7	0.98	Oblate-spheroidal	7.1	3-zonocolporate	6.5	22.9	5.5	6.3	0
<i>S. pygmaea</i> subsp. <i>pygmaea</i> (S36)	2n=12	26	30	28	27.2	33.3	30.1	0.93	Oblate-spheroidal	6.1	3-zonocolporate	3.5	13.4	3.2	4.2	0
<i>S. pygmaea</i> subsp. <i>nutans</i> (S37)		45.3	52.3	48.6	47	55.1	51.2	0.95	Oblate-spheroidal	7.7	3-zonocolporate	6.4	23.3	6.8	7	0
<i>S. yildirimlii</i> (S38)		25.1	33	28.5	30	34	31.9	0.89	Oblate-spheroidal	6.3	3-zonocolporate	4.4	15.9	3.5	4.4	0
Subgenus <i>Scorzonera</i> sect. <i>Scorzonera</i>																
<i>S. ahmet-duranii</i> (S39)	2n=14	33.3	40.1	36.2	37.1	44	39	0.93	Oblate-spheroidal	7.2	3-zonocolporate	6.4	18.7	5.6	6.4	1
<i>S. corticea</i> (S40)		30.5	40.4	35.9	35.2	39.8	38	0.94	Oblate-spheroidal	7	3-zonocolporate	7	21	3.7	6.3	1

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TABLE 3 (Continued, S41–S45).

Taxa	Chromosome number (2n)*	Polar axes (P) (µm)			Equatorial axes (E) (µm)			P/E	Pollen shape	Exine (µm)	Aperture type	Colpus (µm)			Pollen type	
		Min	Max	Mean	Min	Max	Mean					Clt	Clg	Plt		Pig
Subgenus <i>Scorzonera</i> sect. <i>Subaphyllae</i>																
<i>S. aucheriana</i> (S41)	2n=12	29	37.1	32.6	30.2	39.7	35.5	0.92	Oblate-spheroidal	5.8	3-zonocolporate	5.1	17.3	4.3	5.1	0
Subgenus <i>Scorzonera</i> sect. <i>Tuberosae</i>																
<i>S. sublanata</i> (S42)	2n=12	30.1	39.4	34.4	34.2	40.3	37.1	0.93	Oblate-spheroidal	5.7	3-zonocolporate	5.3	19	4.6	5.5	0
Subgenus <i>Scorzonera</i> sect. <i>Turkestanicae</i>																
<i>S. renzii</i> (S43)	2n=14	27.3	34.3	29.1	30	35.1	32	0.91	Oblate-spheroidal	6	3-zonocolporate	4.8	15.5	3.7	4.5	1
Subgenus <i>Scorzonera</i> sect. <i>Vierhapperia</i>																
<i>S. pisidica</i> (S44)	2n=12	30	39.4	33.9	33.1	41.2	36.7	0.92	Oblate-spheroidal	6.2	3-zonocolporate	4.8	16.6	3.9	4.6	0
<i>S. kotschyi</i> (S45)	2n=12	37	48.3	43.1	40.3	49.4	45	0.96	Oblate-spheroidal	7.2	3-zonocolporate	7.2	23	5.8	6.5	0

Clt – colpus length, Clg – colpus width, Plt – pore width, Pig – pore length

0 = *S. laciniata* type; 1 = *S. hispanica* type; 2 = *S. lanata* type

*Altmordu *et al.* (2015), Coskuncellebi *et al.* (2015), Martin *et al.* (2012, 2015)

TABLE 4. Further pollen morphological measurements of the studied taxa of *Scorzonera* (S1–S20).

Taxa	Ornamentation		Spine		Lacunae		Ridges/lacunae			
	Length(µm)	Width at base (µm)	Perforation number at base	Number of spines (10µm ²)	Diameter (µm)	Ornamentation	Apical lacunae shape	Thick (µm)	High (µm)	Ornamentation
S. subgen. <i>Podospermum</i>										
<i>S. cana</i> var. <i>alpina</i> (S1)	4.9 (±0.35)	1.1 (±0.14)	10-15	26-30	6.2 (±0.33)	Perforate	Rounded	3.4 (±0.29)	3-4	Perforate
<i>S. cana</i> var. <i>jacquiniana</i> (S2)	5.1 (±0.39)	1.3 (±0.22)	10-15	26-30	6.8 (±0.52)	Perforate	Rounded	3.5 (±0.25)	2-3.5	Perforate
<i>S. cana</i> var. <i>radicosa</i> (S3)	4.9 (±0.49)	1.2 (±0.13)	15-20	26-30	8.6 (±0.87)	Perforate	Rounded	4 (±0.44)	3.5-4	Perforate
<i>S. laciniata</i> subsp. <i>calcitrapifolia</i> (S4)	4.5 (±0.46)	1.04 (±0.16)	10-15	26-30	6.9 (±0.38)	Perforate	Rounded	3.3 (±0.26)	4-5.5	Perforate
<i>S. hieracifolia</i> (S5)	5 (±0.43)	1.3 (±0.13)	10-15	26-30	8.8 (±0.97)	Perforate	Rounded	4.1 (±0.42)	4-5.5	Perforate
S. subgen. <i>Pseudopodospermum</i>										
<i>S. elata</i> (S6)	7 (±0.71)	1.5 (±0.27)	10-15	32-37	12.5 (±1.08)	Perforate	Angular	5.7 (±0.32)	4-4.5	Perforate
<i>S. suberosa</i> subsp. <i>cariensis</i> (S7)	5 (±0.61)	1.3 (±0.09)	10-15	32-40	9.9 (±0.9)	Perforate	Angular	4.2 (±0.38)	3.75-4.25	Perforate
<i>S. phaeohappa</i> (S8)	5.3 (±0.35)	1.22 (±0.13)	10-15	32-37	7.2 (±0.49)	Perforate	Angular	3.5 (±0.32)	4-4.5	Perforate
<i>S. mollis</i> subsp. <i>szowitzii</i> (S9)	5.5 (±0.77)	1.29 (±0.3)	10-15	32-37	7 (±0.78)	Perforate	Angular	3.3 (±0.2)	2-2.5	Perforate
<i>S. semicana</i> (S10)	7.7 (±0.99)	1.6 (±0.31)	10-15	35-40	9.4 (±1.26)	Perforate	Angular	5 (±0.56)	4-4.5	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Anatolia</i>										
<i>S. boissieri</i> (S11)	5.9 (±0.5)	1.3 (±0.11)	10-15	20-24	7.7 (±0.67)	Perforate	Angular	3.7 (±0.22)	4.5-5	Perforate
<i>S. karabelensis</i> (S12)	5.1 (±1.23)	1.25 (±0.08)	10-15	20-24	6.1 (±0.48)	Perforate	Rounded	3 (±0.62)	2-2.5	Perforate
<i>S. longiana</i> (S13)	5.4 (±0.54)	1.27 (±0.11)	10-15	20-24	6.6 (±0.64)	Perforate	Rounded	3.5 (±0.36)	3-3.5	Perforate
<i>S. sandrasica</i> (S14)	4.7 (±0.91)	1.5 (±0.26)	10-15	20-24	6.1 (±0.81)	Perforate	Rounded	2.7 (±0.42)	3-3.5	Perforate
<i>S. ulrichii</i> (S15)	5.2 (±0.67)	1.4 (±0.16)	10-15	20-24	6.6 (±0.52)	Perforate	Rounded	3.5 (±0.28)	3-3.5	Perforate
<i>S. zorkunensis</i> (S16)	5 (±0.4)	1.2 (±0.11)	15-20	20-24	7.7 (±0.81)	Perforate	Rounded	3.6 (±0.34)	4-4.5	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Foliosae</i>										
<i>S. acuminata</i> (S17)	6 (±0.59)	1.3 (±0.15)	15-20	20-24	8.3 (±1.05)	Perforate	Angular	3.9 (±0.41)	5-5.5	Perforate
<i>S. davisii</i> (S18)	5.5 (±0.48)	1.2 (±0.16)	15-20	20-24	7 (±0.5)	Perforate	Angular	3.6 (±0.26)	5-5.5	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Incisae</i>										
<i>S. lacera</i> (S19)	7.1 (±0.77)	1.41 (±0.26)	15-20	25-30	12.1 (±0.51)	Perforate	Angular	5.5 (±0.28)	4-4.5	Perforate
<i>S. violacea</i> (S20)	5.7 (±0.46)	1.3 (±0.13)	15-20	20-24	7 (±0.52)	Perforate	Angular	3.3 (±0.62)	4-4.5	Perforate

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TABLE 4 (Continued, S21–S38).

Taxa	Ornamentation		Spine		Lacunae		Ridges lacuna	
	Length(μm)	Width at base (μm)	Perforation number at base	Diameter (μm)	Ornamentation	Thick (μm)	High Ornamentation (μm)	
S. subgen. <i>Scorzonera</i> sect. <i>Infrarosulares</i>								
<i>S. acantholimon</i> (S21)	5.3 (± 0.5)	1.2 (± 0.09)	10-15	6.4 (± 0.39)	Perforate	3.5 (± 0.26)	3.5-4	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Nervosae</i>								
<i>S. argyrea</i> (S22)	4.9 (± 0.79)	1.5 (± 0.32)	10-15	5.9 (± 1.19)	Perforate	2.7 (± 0.33)	3.5-4	Perforate
<i>S. ketzkhovellii</i> (S23)	5 (± 0.62)	1.23 (± 0.08)	10-15	6 (± 0.69)	Perforate	3.1 (± 0.45)	3.5-4	Perforate
<i>S. mirabilis</i> (S24)	5.1 (± 0.5)	1.28 (± 0.15)	10-15	7.2 (± 0.72)	Perforate	3.6 (± 0.29)	3.5-4	Perforate
<i>S. veratrifolia</i> (S25)	6 (± 0.72)	1.4 (± 0.12)	10-15	7.4 (± 0.7)	Perforate	3.7 (± 0.24)	5-5.5	Perforate
<i>S. latifolia</i> var. <i>angustifolia</i> (S26)	4.9 (± 0.58)	1.09 (± 0.13)	15-20	6.8 (± 0.83)	Perforate	2.9 (± 0.42)	3-3.5	Perforate
<i>S. latifolia</i> var. <i>latifolia</i> (S27)	5.5 (± 0.84)	1.52 (± 0.36)	15-20	7.4 (± 0.78)	Perforate	2.9 (± 0.37)	5-5.5	Perforate
<i>S. dzhawakhetica</i> (S28)	5.1 (± 0.64)	1.3 (± 0.08)	15-20	6 (± 0.79)	Perforate	3.5 (± 0.59)	4-4.5	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Papposae</i>								
<i>S. papposa</i> (S29)	5.2 (± 0.52)	1.22 (± 0.1)	15-20	9.8 (± 0.62)	Perforate	4.5 (± 0.52)	4-4.5	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Parviflorae</i>								
<i>S. parviflora</i> (S30)	6.3 (± 0.73)	1.37 (± 0.2)	10-15	11.5 (± 0.98)	Perforate	5.1 (± 0.47)	3-3.5	Perforate
<i>S. tuzgoluensis</i> (S31)	5.6 (± 0.43)	1.3 (± 0.14)	15-20	6.1 (± 1.4)	Perforate	3.3 (± 0.34)	3-3.5	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Pubivnares</i>								
<i>S. amasiana</i> (S32)	5 (± 0.37)	1.2 (± 0.11)	15-20	6.1 (± 0.38)	Perforate	3.3 (± 0.27)	3-3.5	Perforate
<i>S. lasiocarpa</i> (S33)	4.3 (± 1.04)	1.15 (± 0.12)	15-20	6 (± 0.52)	Perforate	2.9 (± 0.32)	3-3.5	Perforate
<i>S. seidlitzii</i> (S34)	4.7 (± 0.6)	1.3 (± 0.37)	15-20	6.5 (± 1.17)	Perforate	2.8 (± 0.5)	3-3.5	Perforate
<i>S. rigida</i> (S35)	6.3 (± 1.05)	1.4 (± 0.13)	15-20	11.3 (± 1.07)	Perforate	5 (± 0.74)	3-3.5	Perforate
<i>S. pygmaea</i> subsp. <i>pygmaea</i> (S36)	4.7 (± 0.76)	1.3 (± 0.14)	15-20	5.5 (± 0.76)	Perforate	3 (± 0.49)	3-3.5	Perforate
<i>S. pygmaea</i> subsp. <i>nutans</i> (S37)	6.3 (± 0.64)	1.42 (± 0.2)	15-20	11.6 (± 0.8)	Perforate	5.5 (± 0.37)	3-3.5	Perforate
<i>S. yildirimlii</i> (S38)	5.1 (± 0.54)	1.2 (± 0.12)	15-20	6.7 (± 0.39)	Perforate	3.5 (± 0.32)	3-3.5	Perforate

... continued on the next page

TABLE 4 (Continued, S39–S45).

Taxa	Ornamentation			Spine		Lacunae			Ridges lacuna		
	Length(μm)	Width at base(μm)	Perforation number at base	Diameter (μm)	Ornamentation	Thick (μm)	High (μm)	Ornamentation			
S. subgen. <i>Scorzonera</i> sect. <i>Scorzonera</i>											
<i>S. ahmet-duranii</i> (S39)	7.9 (± 0.75)	1.5 (± 0.23)	15-20	9.6 (± 0.55)	Perforate	4.5 (± 0.31)	3-3.5	Perforate	4.5 (± 0.31)	3-3.5	Perforate
<i>S. coriacea</i> (S40)	5.6 (± 0.84)	1.5 (± 0.42)	15-20	8.6 (± 1.51)	Perforate	3.7 (± 0.46)	3-3.5	Perforate	3.7 (± 0.46)	3-3.5	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Subaphyllae</i>											
<i>S. aucheriana</i> (S41)	4.8 (± 0.4)	1.1 (± 0.1)	15-20	8.7 (± 0.86)	Perforate	3.7 (± 0.39)	3-3.5	Perforate	3.7 (± 0.39)	3-3.5	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Tuberosae</i>											
<i>S. sublanata</i> (S42)	4.5 (± 0.6)	1.4 (± 0.71)	15-20	6.6 (± 0.57)	Perforate	3.5 (± 0.37)	3-3.5	Perforate	3.5 (± 0.37)	3-3.5	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Turkestanicae</i>											
<i>S. renzii</i> (S43)	5 (± 0.33)	1.1 (± 0.19)	15-20	6.6 (± 0.53)	Perforate	3.5 (± 0.28)	3-3.5	Perforate	3.5 (± 0.28)	3-3.5	Perforate
S. subgen. <i>Scorzonera</i> sect. <i>Vierhapperia</i>											
<i>S. pisidica</i> (S44)	5.1 (± 0.47)	1.2 (± 0.09)	15-20	8 (± 0.84)	Perforate	3.7 (± 0.42)	3-3.5	Perforate	3.7 (± 0.42)	3-3.5	Perforate
<i>S. kotschyi</i> (S45)	6.2 (± 0.8)	1.28 (± 0.17)	15-20	11.2 (± 1.09)	Perforate	4.5 (± 0.6)	3-3.5	Perforate	4.5 (± 0.6)	3-3.5	Perforate

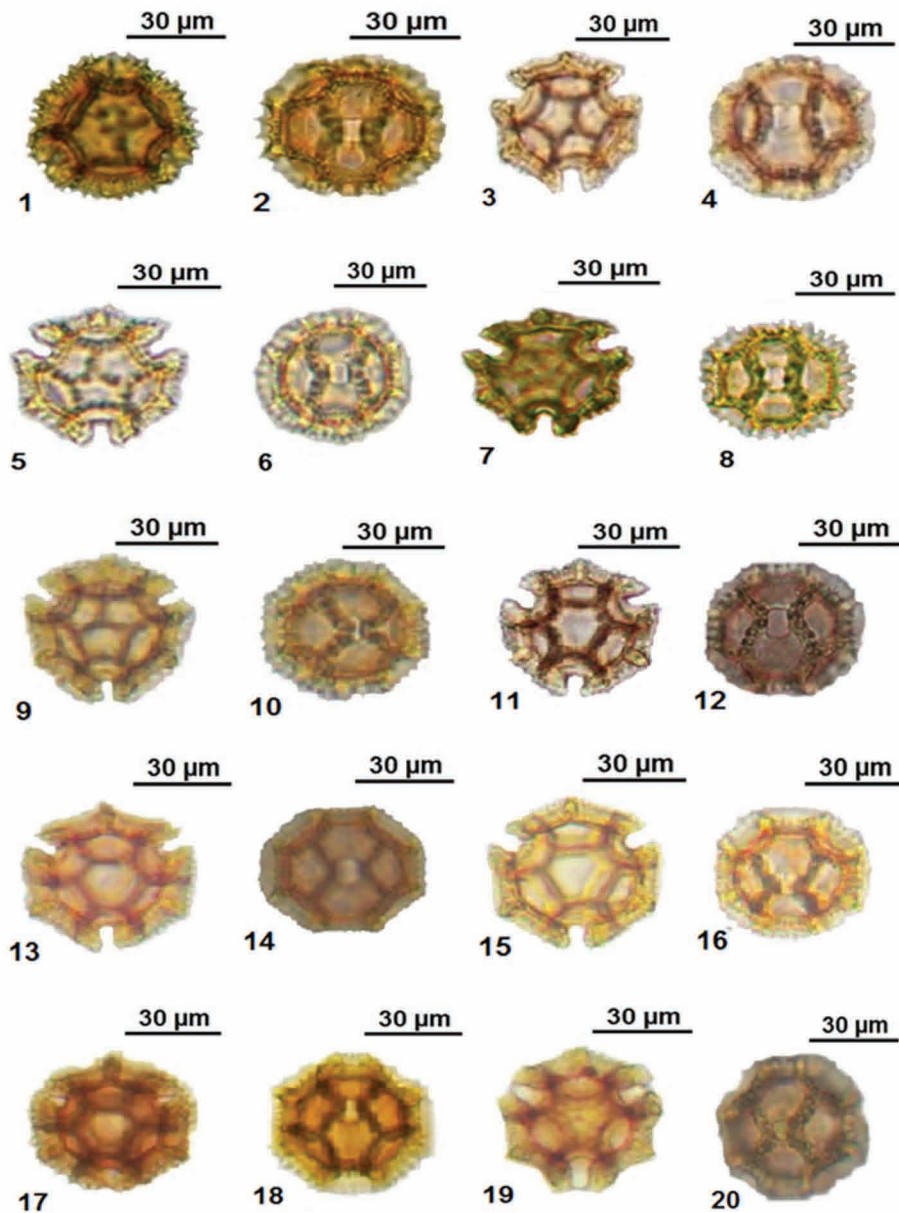


FIGURE 2. Pollen morphology of *Scorzonera* examined by light microscope (LM). 1, 2. *S. cana* var. *alpina*; 3, 4. *S. cana* var. *jacquiniana*; 5, 6. *S. cana* var. *radicosa*; 7, 8. *S. laciniata* subsp. *calcitrapifolia*; 9, 10. *S. hieraciifolia*; 11, 12. *S. elata*; 13, 14. *S. suberosa* subsp. *cariensis*; 15, 16. *S. phaeohappa*; 17, 18. *S. mollis* subsp. *szowitzii*; 19, 20. *S. semicana*.

TABLE 5. PCA variable loadings for the first 3 components.

Variables	PC 1	PC 2	PC 3
Exine thickness (V1)	0.389	0.251	-0.513
Pollen type (V2)	-0.330	0.417	0.033
Abporal lacunae shape (V3)	-0.292	0.517	-0.249
Perforation number at base (V4)	0.340	-0.434	0.139
Number of spines (V5)	0.416	0.006	-0.590
Polar axes (V6)	0.430	0.388	0.395
Equatorial axes (V7)	0.426	0.397	0.388
Eigenvalues	2.738	2.234	0.982
Percentage	39.109	31.911	14.029
Cumulative percentage	39.109	71.020	85.049

Exine

The stratified exine has an overall thickness that ranges from 5.1 μm in *S. cana* var. *radicosa* to 9.5 μm in *S. semicana* when the spines are excluded. Foraminated sexine is about three times as thick as nexine with cavea and without costae. Branching columellae spanning a very restricted cavea is below the ridges. Ornamentation is echinolophate. The spines are commonly concave-conical with a broad basis, sides are straight or slightly convex with a subacute tapered apical portion. The number of spines at 10 μm^2 is 15–40. The spine length varies between 1.25–2.5 μm and the width of spines varies between 1.1–1.6 μm . The base of the spines in almost all species has irregularly 2 seriate perforations with the smaller holes are often found distally. The number of perforations are 10–15 or 15–20 (Tables 3–5; Figs. 2–6, Figs. 7–15). Lacunae diameter is 5–12.1 μm , thickness of ridges lacuna is 2.6–5.7 μm , depth of ridges lacuna is 2–5.5 μm , and ornamentation of ridges is perforate.

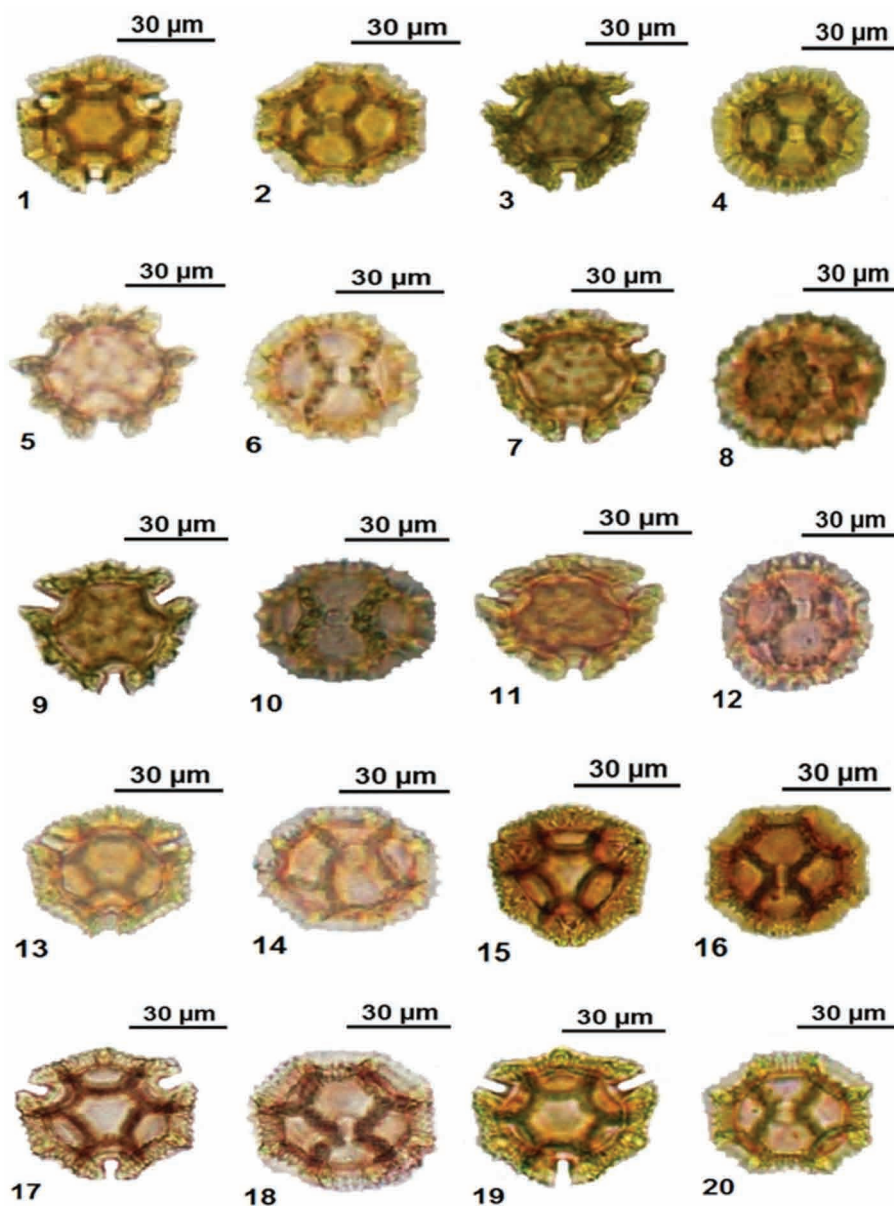


FIGURE 3. Pollen morphology of *Scorzonera* examined by light microscope (LM). 1, 2. *S. boissieri*; 3, 4. *S. karabelensis*; 5, 6. *S. longiana*; 7, 8. *S. sandrasica*; 9, 10. *S. ulrichii*; 11, 12. *S. zorkunensis*; 13, 14. *S. acuminata*; 15, 16. *S. davisii*; 17, 18. *S. lacera*; 19, 20. *S. violacea*.

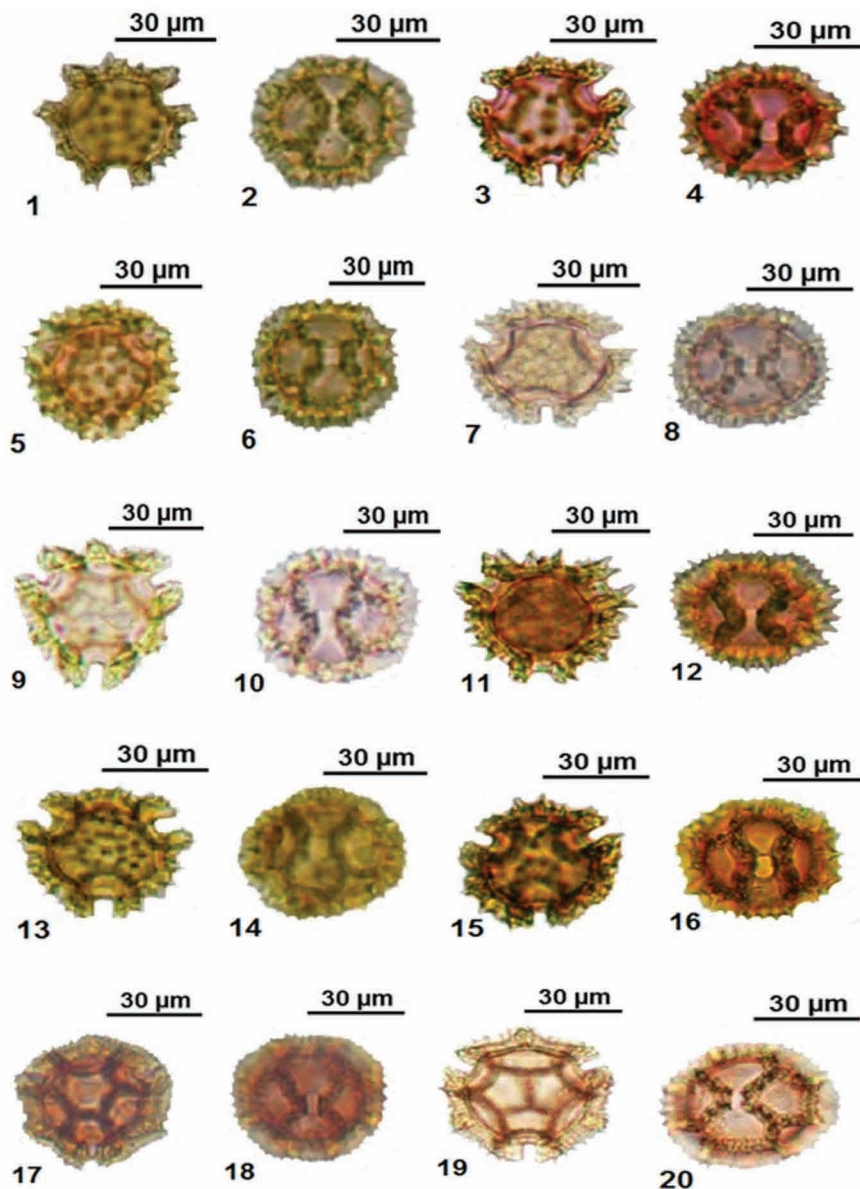


FIGURE 4. Pollen morphology of *Scorzonera* examined by light microscope (LM). 1, 2. *S. acantholimom*; 3, 4. *S. argyrea*; 5, 6. *S. ketzkhoveli*; 7, 8. *S. mirabilis*; 9, 10. *S. veratrifolia*; 11, 12. *S. latifolia* var. *angustifolia*; 13, 14. *S. latifolia* var. *latifolia*; 15, 16. *S. dzhawakhetica*; 17, 18. *S. papposa*; 19, 20. *S. parviflora*.

Numerical analysis of the palynological character states

A dendrogram resulting from the cluster analysis based on seven palynological variables of 45 taxa of *Scorzonera* is presented in Fig. 16. The dendrogram constructed by UPGMA revealed three main groups with 65 % level of similarity; the first one comprises members of *S.* subgen. *Podospermum* (S1–S5), the second one comprises members of *S.* subgen. *Pseudopodospermum* (S6–S10) and also S11 from *S.* subgen. *Scorzonera*, and the last one refers to *S.* subgen. *Scorzonera* (S11–S45, except S11). From the dendrogram and PCA analysis, it is evident that *S. boissieri* (S11) and the species of *S.* subgen. *Pseudopodospermum* are closely associated. In the first group, *S. cana* var. *alpina*, *S. cana* var. *jacquiniana*, *S. laciniata* subsp. *calcitrapifolia* and *S. hieraciifolia* are closely related, with 98 % similarity. *S. cana* var. *radicosa* fell in a different group with 85 % similarity due to a difference in the perforation number at the base. In the second group, *S. phaeohappa* and *S. mollis* subsp. *szowitzii* are quite similar with a level of 98 %, and *S. elata* and *S. suberosa* subsp. *cariensis* are also closely related with 96 % similarity. Cluster analysis showed that the last main group is a very large group which consists of three clusters, described further as Clusters A, B and C. Cluster A includes *S. karabalensis*, *S. longiana*, *S. sandrasica* and *S. ulrichii*. Cluster B includes three subgroups, namely B1, B2 and B3. Cluster B1 includes *S. zorkunensis* and *S. violacea* which are closely related, with 97 % similarity. Cluster B2

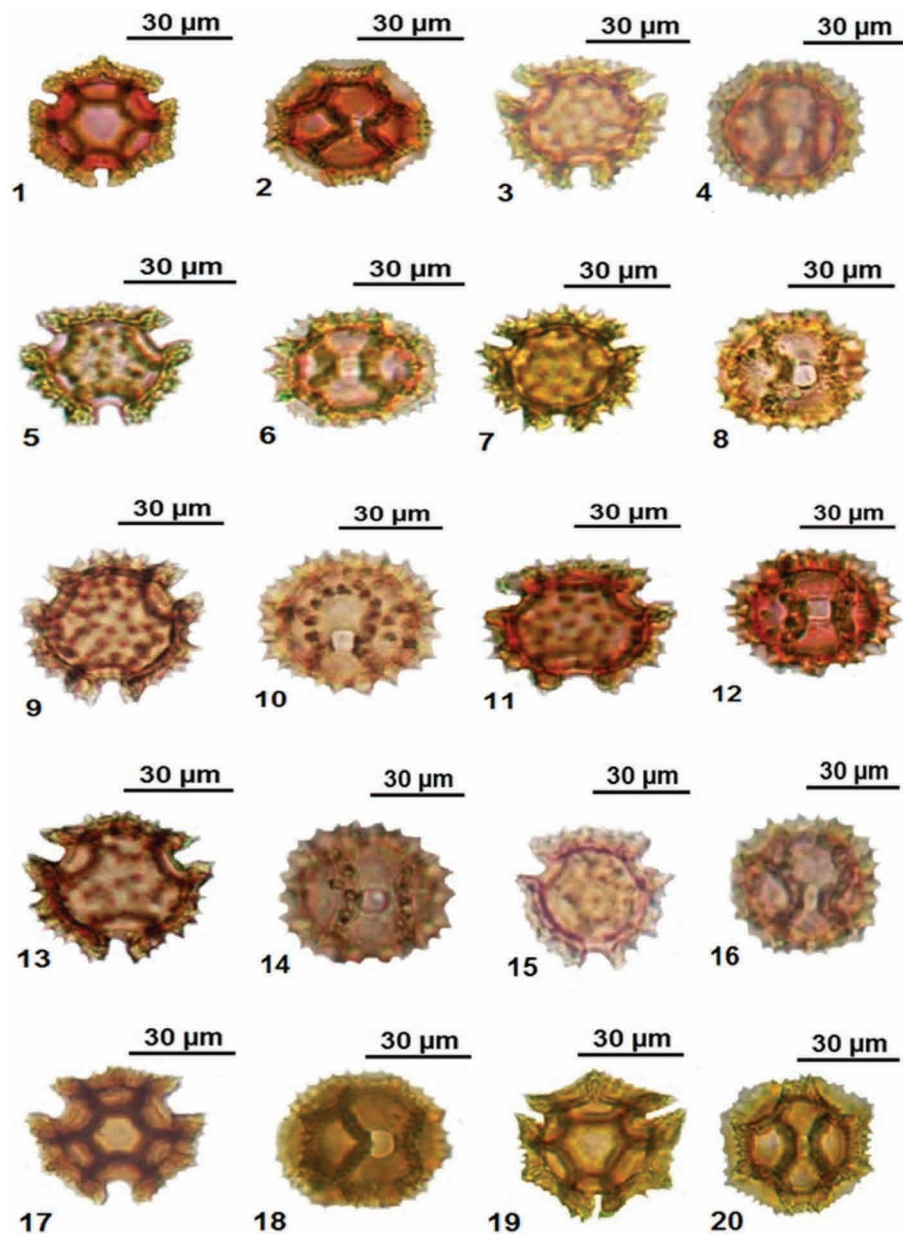


FIGURE 5. Pollen morphology of *Scorzonera* examined by light microscope (LM). 1, 2. *S. tuzgoluensis*; 3, 4. *S. amasiana*; 5, 6. *S. lasiocarpa*; 7, 8. *S. seidlitzii*; 9, 10. *S. rigida*; 11, 12. *S. pygmaea* subsp. *pygmaea*; 13, 14. *S. pygmaea* subsp. *nutans*; 15, 16. *S. yildirimlii*; 17, 18. *S. ahmet-duranii*; 19, 20. *S. coriacea*.

includes also two subgroups, namely B2a and B2b. Cluster B1a includes *S. acantholimon*, *S. amasiana*, *S. yildirimlii*, *S. ketzkhovellii*, *S. dzhawakhetica*, *S. pygmaea* subsp. *pygmaea*, *S. mirabilis*, *S. pisidica*, *S. latifolia* var. *angustifolia*, *S. seidlitzii*, *S. lasiocarpa* and *S. argyrea*. These are quite similar, with more than a 95 % degree of similarity. Cluster B1b includes *S. veratrifolia*, *S. latifolia* var. *latifolia*, *S. rigida*, *S. kotschyi* and *S. pygmaea* subsp. *nutans*. They are closely related, with 96 % similarity. Cluster B3 includes *S. lacera*, *S. aucheriana* and *S. sublanata*. They are quite similar with a degree of 90 % similarity. Cluster C includes three subgroups, referred to as C1, C2 and C3. Cluster C1 includes *S. acuminata*, *S. papposa*, *S. ahmet-duranii*, *S. coriacea* and *S. renzii*. In this cluster *S. ahmet-duranii* and *S. coriacea* are more similar (96 % similarity) to each other than the others. *Scorzonera acuminata* and *S. papposa* can also be initially separated from the others at first. Cluster C2 includes *S. davisii* and *S. tuzgoluensis*. Lastly, Cluster C3 includes only *S. parviflora*. *Scorzonera parviflora* is fairly closely related with the other taxa of Cluster C with 80 % similarity.

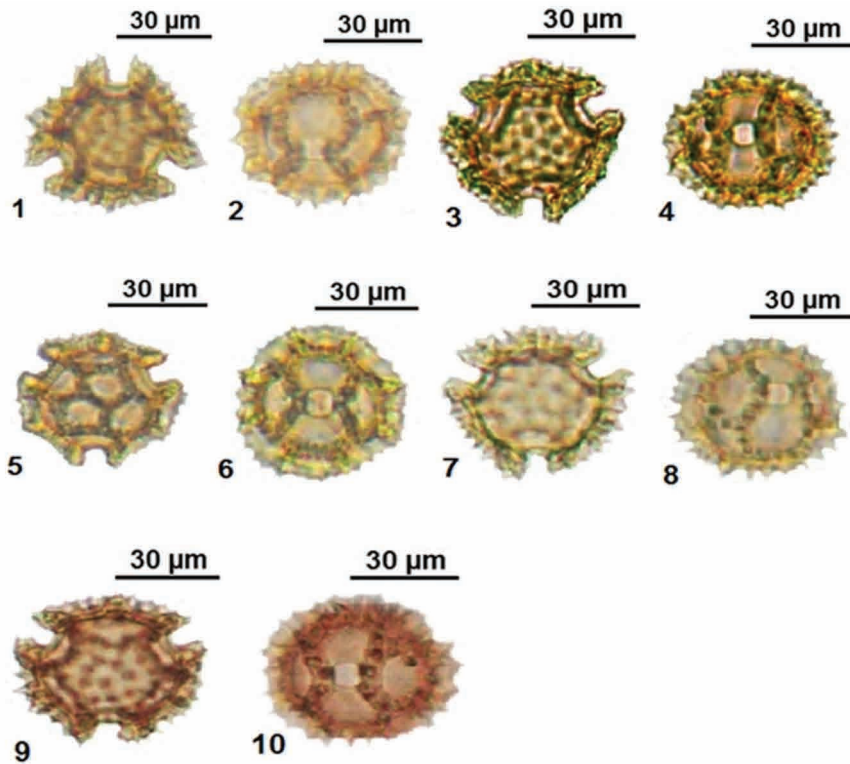


FIGURE 6. Pollen morphology of *Scorzonera* examined by light microscope (LM). 1, 2. *S. aucheriana*; 3, 4. *S. sublanata*; 5, 6. *S. renzii*; 7, 8. *S. pisidica*; 9, 10. *S. kotschyi*.

PCA analysis was performed to determine which variables are important in explaining the total variation among the examined 45 taxa. PCA case scores are given in Fig. 17. The PCA loadings and the eigenvalues are given in Table 5. Due to their eigenvalues, only the first three components were taken into account for most of the variance in the data. This is specifically because out of the seven possible components only three can explain 85.049 % of the total variation. The first principal component explains 39.109 % of the total variation in the examined taxa. Polar axes, equatorial axes and number of spines are the most significant variables in the first principal component since they have the highest relative variation rate (Table 5). The abporal lacunae, the pollen type and equatorial axes provided the strongest influence on the taxa in the second principal component. These explain 31.911 % of the total variation. The third principal component explains 14.029 % of the total variation, mainly through the variables of polar axes, equatorial axes and perforation number at base.

Discussion

The pollen grains of the taxa of *Scorzonera* were placed in the *S. humilis*-type, *S. laciniata*-type, *S. hispanica*-type, *S. lanata*-type of Blackmore (1982) and the *Scorzonera* type of Osman (2006) according to the lacunar system features. Meo & Khan (2004) divided the genus into three palynogroups (I, II and III) based on the exine thickness.

While pollen grains of the genus *Scorzonera* are heterogeneous and exhibit a considerable variation in size (P and E), pollen shape (P/E) is the same in all taxa (Table 3; Fig. 1). Blackmore (1982) and Meo & Khan (2004), on the other hand, suggested that pollen sizes (P and E) showed numerous similarities among the taxa. Meo & Khan (2004) said that there was a great range of variation in exine thickness which was proved useful for classification at the species level, and they divided the taxa into three palynogroups (I, II and III) based on exine thickness. The exine thickness of group I had the lowest values (2.1–2.4 µm), group II had intermediate values (4.3 µm) and group III had the highest exine value (6.5–10.2 µm). The exine thickness of the taxa examined was determined at 5.1–9.5 µm. We evaluated that the exine thickness of *S. subgen. Podospermum* was the lowest (5.1–5.4 µm), *S. subgen. Pseudopodospermum* had the

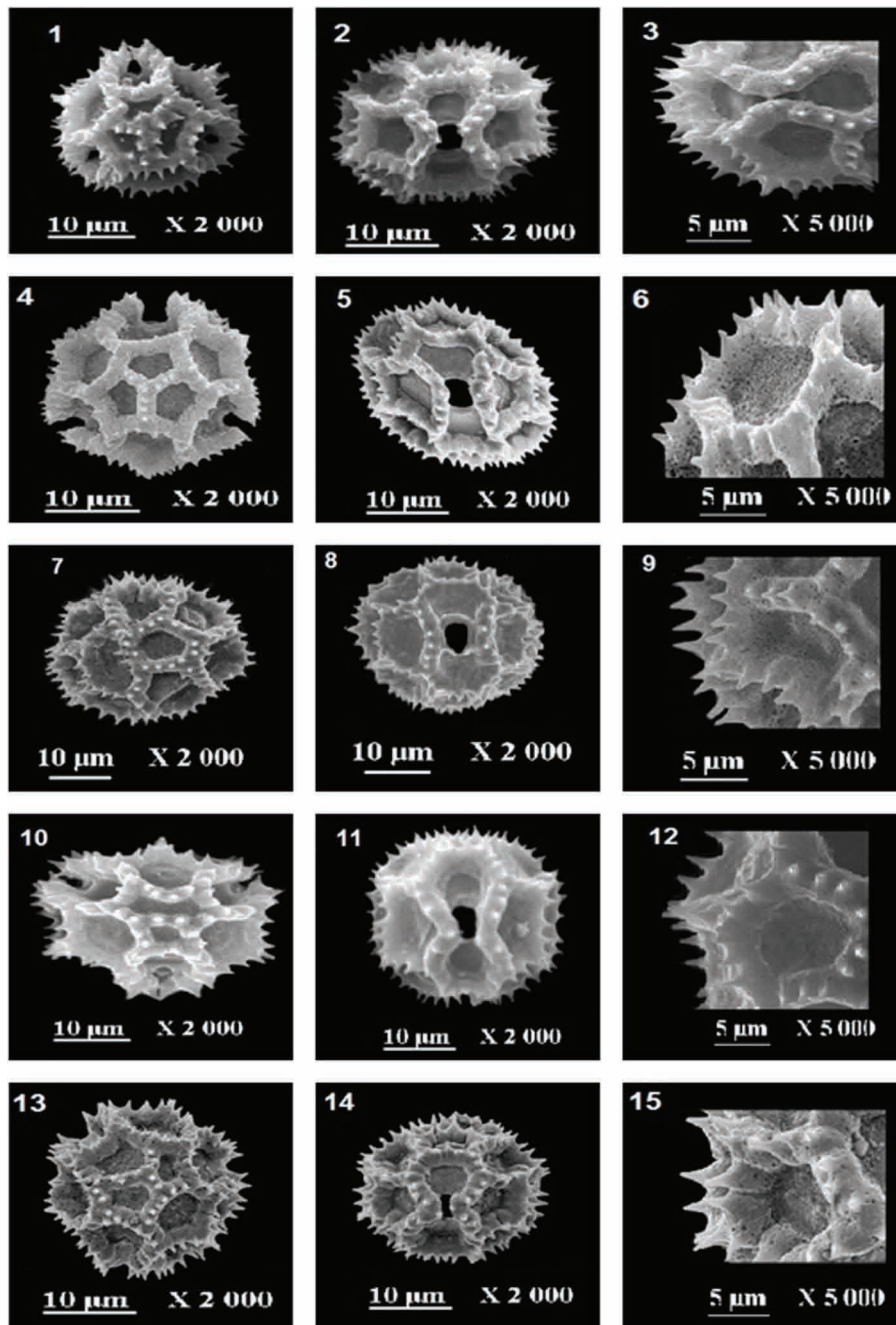


FIGURE 7. Pollen morphology of *Scorzonera* examined by scanning electron microscope (SEM). 1–3. *S. cana* var. *alpina*; 4–6. *S. cana* var. *jacquiniana*; 7–9. *S. cana* var. *radicosa*; 10–12. *S. laciniata* subsp. *calcitrapifolia*; 13–15. *S. hieraciifolia*.

highest exine thickness (7.6–9.5 µm) and *S.* subgen. *Scorzonera* has an intermediate thickness (5.6–7.5 µm) (Table 3). Also, Makbul *et al.* (2011) found that the general anatomical traits of the stem are very similar, and some anatomical characters, such as presence and distribution of secretory cells and channels, arrangement and composition of vascular bundles, cavities in pith, and hairs on epidermis were found to be important in delimiting the taxa examined.

Some of the taxa of *Scorzonera* have $2n = 12, 14$ and 28 chromosome numbers (Martin *et al.* 2012, 2015, Altınordu *et al.* 2015, Coskuncelebi *et al.* 2015). Also, Chaturvedi *et al.* (1990), Brochmann (1992) and Pınar *et al.* (2001) said that pollen size and pollen types have been shown to strongly correlate with the polyploid level, but the data presented here does not show such a correlation. Mean values for P and E and aperture types of diploid and polyploid *Scorzonera* species are very similar (Table 3–5). Similarly, a positive correlation was not reported by Ceter *et al.* (2013) for the values of P and E in diploid, triploid and tetraploid species *Tripleurospermum* Sch. Bip. and *Matricaria* L.

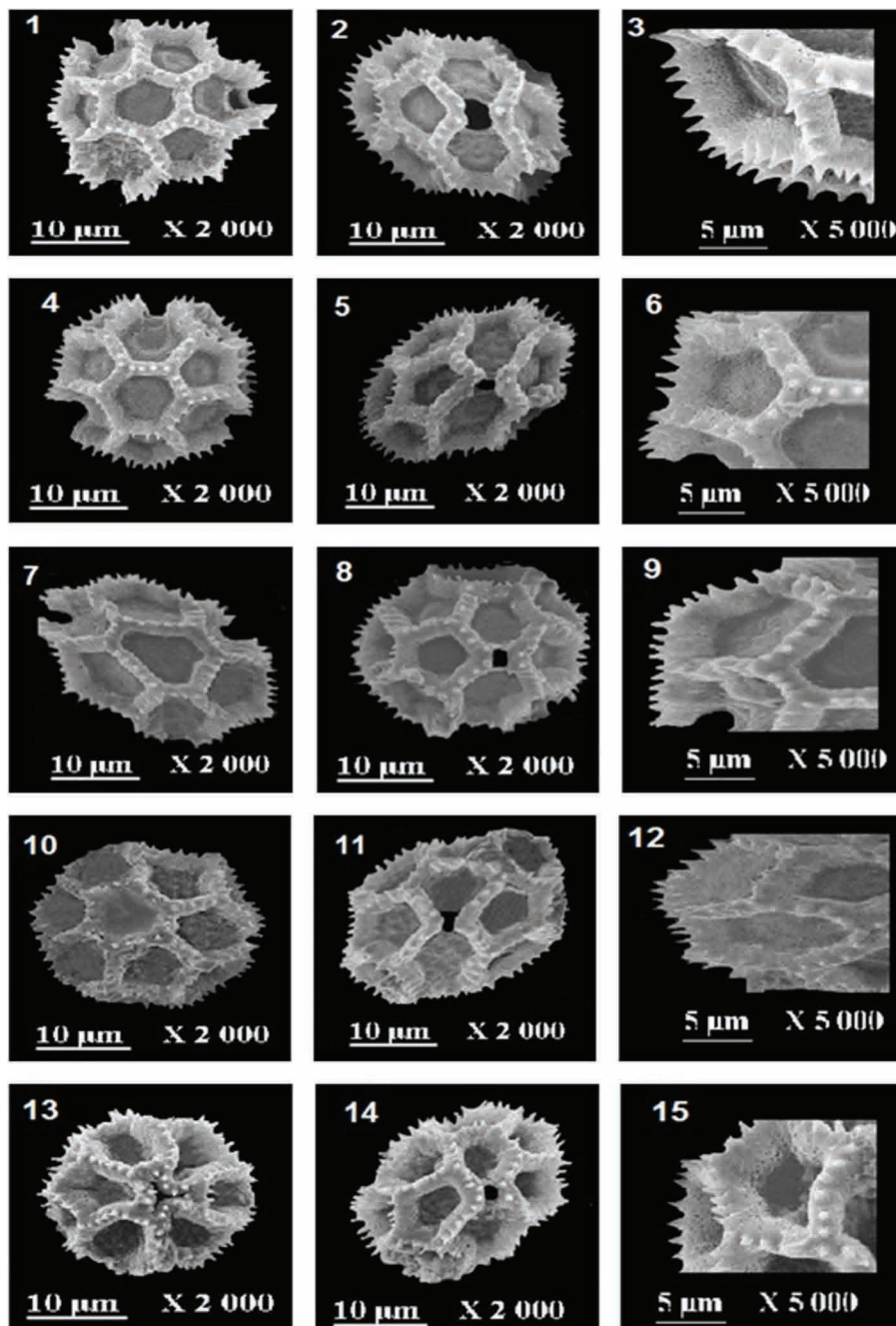


FIGURE 8. Pollen morphology of *Scorzonera* examined by scanning electron microscope (SEM). 1–3. *S. elata*; 4–6. *S. suberosa* subsp. *cariensis*; 7–9. *S. phaeohappa*; 10–12. *S. mollis* subsp. *szowitzii*; 13–15. *S. semicana*.

In the studies of *Lactuceae* pollen grains it has been noted that the evolution is taking place from echinate pollen to echinolophate (Nazarova 1997). Stix (1960), Skvarla *et al.* (1977), Salgado-Labouriau (1982), Mesfin *et al.* (1995), Pınar & Dönmez (2000) and Ceter *et al.* (2013) claimed that subapical perforations in the spine base in Asteraceae are a good taxonomic character for discriminating taxa. Even though perforations at the spine base have various size, but this study has revealed that the number of them are similar in each taxa. Mesfin *et al.* (1995), Kodak *et al.* (2012) and Ceter *et al.* (2013) stated that the ornamentations between spines are important characters in Asteraceae. However, we only observed perforate ornamentation between spines. Tomb *et al.* (1974) utilized spine length as an important diagnostic character in Cichorieae. Wageniz (1976) described how reductions of the spine length are an important evolutionary trend in Asteraceae pollen morphology. Wang *et al.* (2009) reported that the plesiomorphic state seems to generate spines less than 3 µm high. Spines of 2.5–3 µm occur in *S.* subgen. *Podospermum*, 1.25–1.4 µm in *S.* subgen. *Pseudopodospermum*, and 1.25–2.25 µm in *S.* subgen. *Scorzonera*. The number of spines also varies from species to species. The largest numbers of spines were found in *S.* subgen. *Pseudopodospermum*.

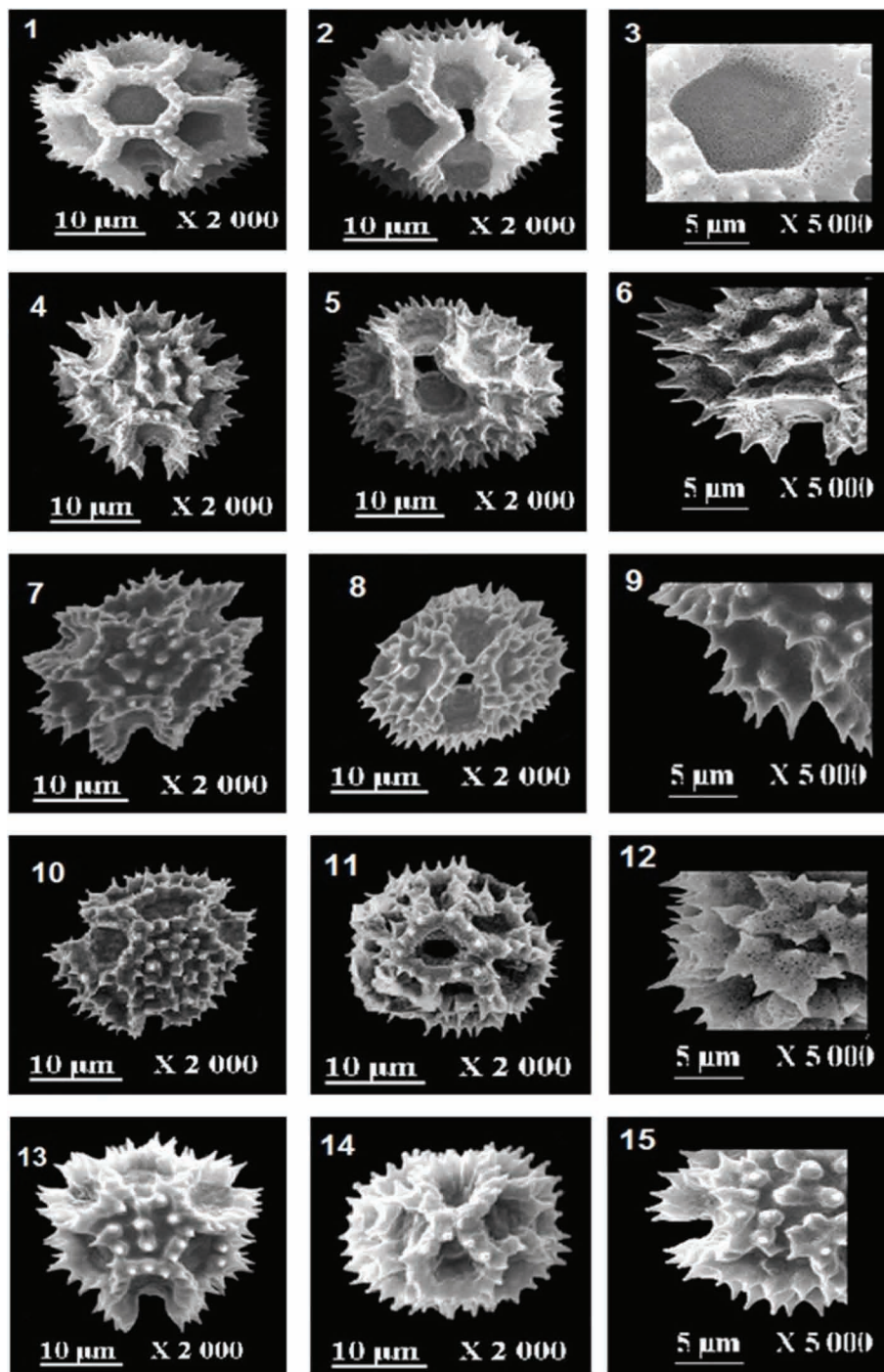


FIGURE 9. Pollen morphology of *Scorzonera* examined by scanning electron microscope (SEM). 1–3. *S. boissieri*; 4–6. *S. karabelensis*; 7–9. *S. longiana*; 10–12. *S. sandrasica*; 13–15. *S. ulrichii*.

The pollen grains in the Turkish *Scorzonera* with compound apertures are 3-zonocolpororate. However, several authors have used different terminology for the aperture types found in *Scorzonera*. Blackmore (1982) and Osman (2006) reported 3-zonocolpororate aperture types, as did Guardia & Blanca (1985) and Türkmen *et al.* (2010), whereas Inceoglu & Karamustafa (1977) reported triporate aperture types.

Exine stratification and aperture configuration vary little within the subtribe Scorzonerinae, whereas the arrangement of lacunae is diverse and provides a number of useful taxonomic characters (Henning 1965, 1966, Blackmore 1982). The three pollen types described in this paper are based on the number and arrangement of the lacunae. *Scorzonera laciniata*-type, *S. hispanica*-type, *S. lanata*-type, and *S. laciniata*-type have been recorded in *S. sect. Anatolia*, *S. sect. Infrarosulares*, *S. sect. Nervosae* and *S. sect. Pulvinares*; *S. hispanica*-type in *S. subgen. Pseudopodospermum*, *S. sect. Foliosae*, *S. sect. Incisae*, *S. sect. Papposae*, *S. sect. Palviflorae*, *S. sect. Scorzonera*

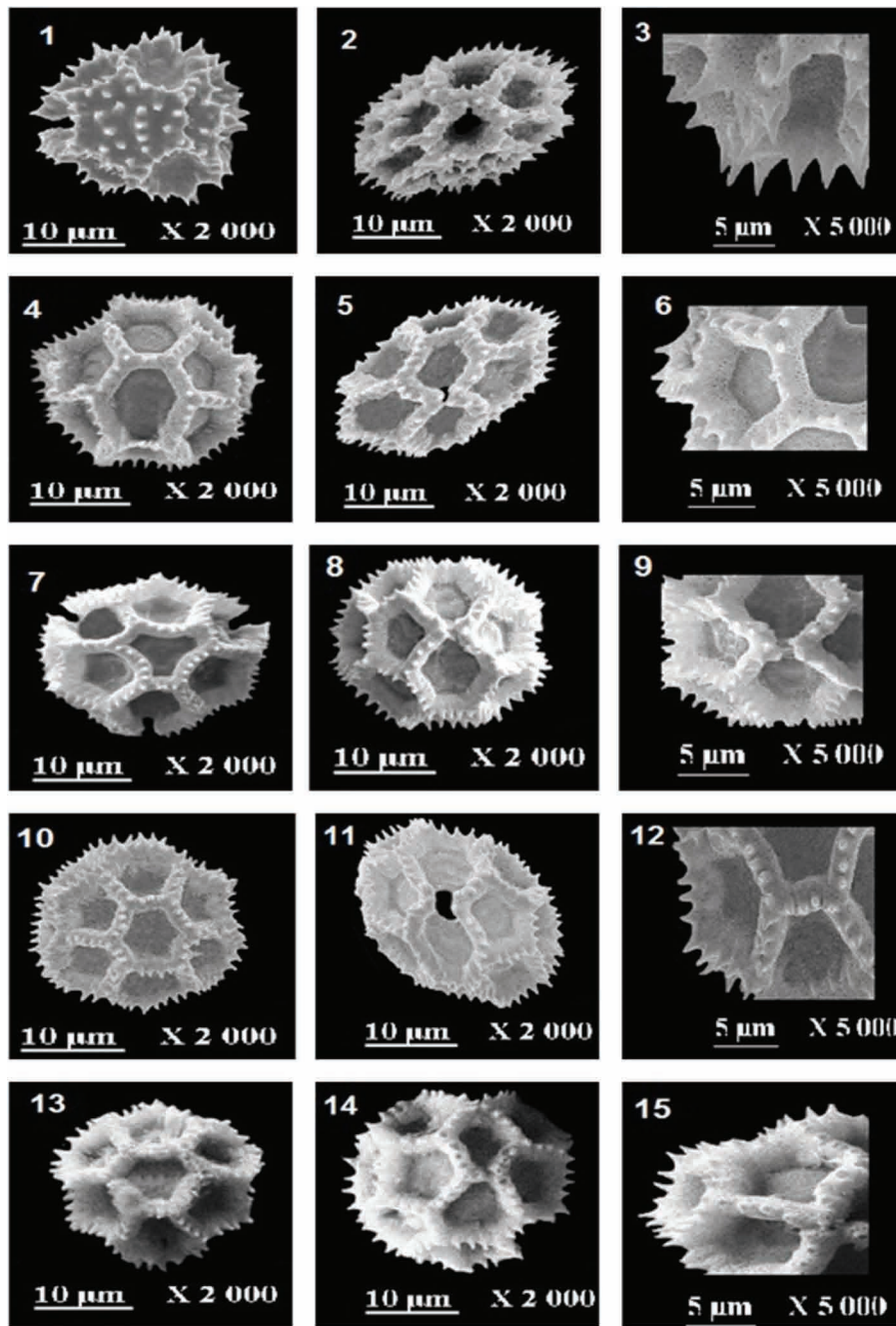


FIGURE 10. Pollen morphology of *Scorzonera* examined by scanning electron microscope (SEM). 1–3. *S. zorkunensis*; 4–6. *S. acuminata*; 7–9. *S. davisii*; 10–12. *S. lacera*; 13–15. *S. violacea*.

and *S. sect. Turkestanicae*; *S. laciniata*-type only in *S. subgen. Podospermum*. Pollen type is very constant within members of *S. subgen. Podospermum*. This finding supports the view of Mavrodiev *et al.* (2004) and Owen *et al.* (2006) who proposed that *S. subgen. Podospermum* should be recognized as a separate genus in spite of the lack of sufficient molecular data. *Scorzonera sect. Anatolia* including 6 taxa endemic to Turkey (*S. boissieri*, *S. karabelensis*, *S. longiana*, *S. sandrasica*, *S. ulrichii* and *S. zorkunensis*) was described by Coskuncelebi *et al.* (2015). According to our findings, nearly all members of *S. sect. Anatolia* have the *S. laciniata*-type pollen (excluding *S. boissieri* which has the *S. hispanica*-type). The pollen of *Crepidinae* and *Lactucinae* have six abporal lacunae, which may be angular and rounded (Wang *et al.* 2009). *Scorzonera subgen. Pseudopodospermum*, *S. boissieri*, *S. sect. Foliosae*, *S. sect. Incisae*, *S. sect. Papposae*, *S. sect. Parviflorae*, *S. sect. Scorzonera*, *S. sect. Turkestanicae* have been shown to have angular abporal lacunae types.

In the PCA analysis, the first three components underlined the fact that the most valuable palynological variables in separating the taxa of *Scorzonera* examined in this study are polar axes, equatorial axes and abporal lacunae shape.

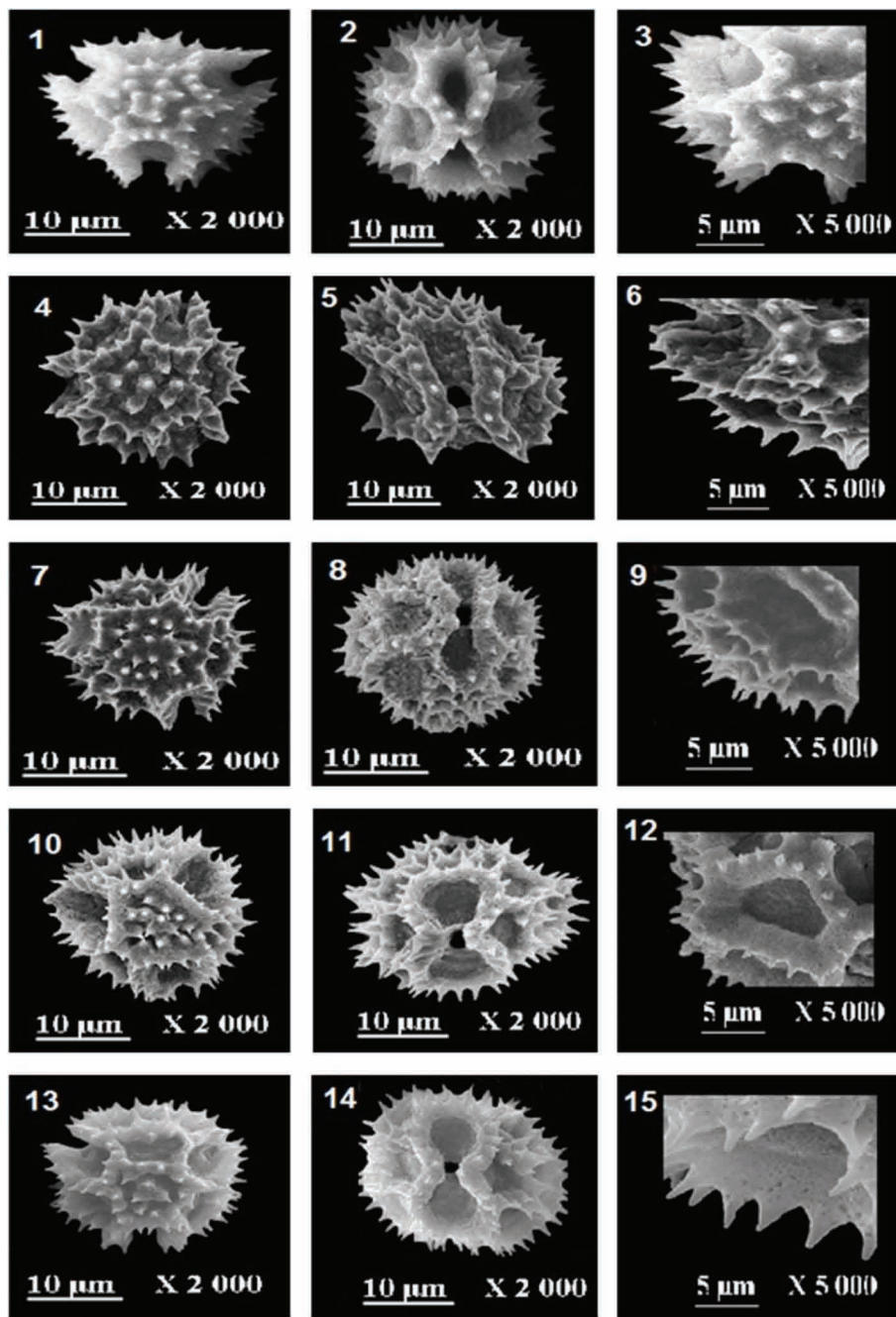


FIGURE 11. Pollen morphology of *Scorzonera* examined by scanning electron microscope (SEM). 1–3. *S. acantholimon*; 4–6. *S. argyrea*; 7–9. *S. ketzkhoveli*; 10–12. *S. mirabilis*; 13–15. *S. veratrifolia*.

The results of our cluster analysis show that members of *S.* subgen. *Podospermum* and *S.* subgen. *Pseudopodospermum* are most distinctly differentiated from the rest of the investigated taxa. However, members of *S.* subgen. *Scorzonera* were not well clustered at the sectional level. Some taxa were found to be more similar to members belonging to another section.

As given in the numerical analyses, the patterns of variation were confirmed among the taxa studied, and the variables or palynological characters should be evaluated together with the other morphological characters in order to separate the taxa of *Scorzonera*. The results of our analysis are quite similar in respect of clustering according to the pollen morphological characters to those in the study by Türkmen *et al.* (2010).

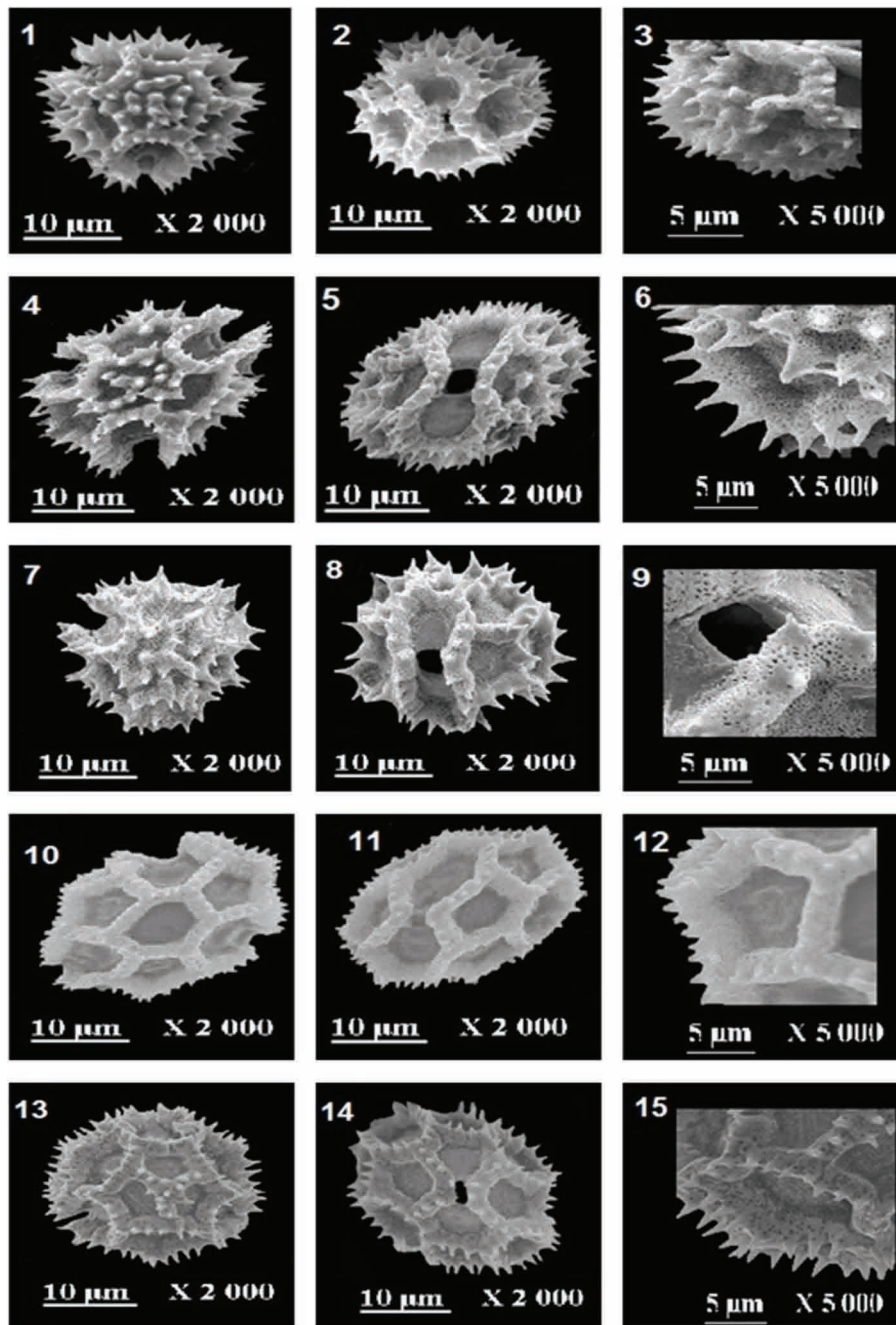


FIGURE 12. Pollen morphology of *Scorzonera* examined by scanning electron microscope (SEM). 1–3. *S. latifolia* var. *angustifolia*; 4–6. *S. latifolia* var. *latifolia*; 7–9. *S. dzhawakhetica*; 10–12. *S. papposa*; 13–15. *S. parviflora*.

Conclusions

The pollen morphology of 45 species belonging to 15 sections of *Scorzonera* were investigated with light microscopy and scanning electron microscopy. Thirteen qualitative or quantitative morphological characteristics of pollen were evaluated in these studies, which included radially symmetrical, isopolar and oblate-spheroidal characteristics. Pollen size and spine length proved to be the most useful character of systematic value in *Scorzonera*. Three pollen types, distinguished primarily by the number and position of their lacunae have been described. Cluster analysis revealed that the pollen taxa can be divided into three main groups based on pollen morphology. PCA analysis based on palynological traits showed that polar axis, equatorial diameter, exine thickness, lacuna type and spine length are the most important characters in explaining the total variation among the taxa examined. It has been concluded that a detailed analysis of the pollen characters is very useful in classification of the taxa studied.

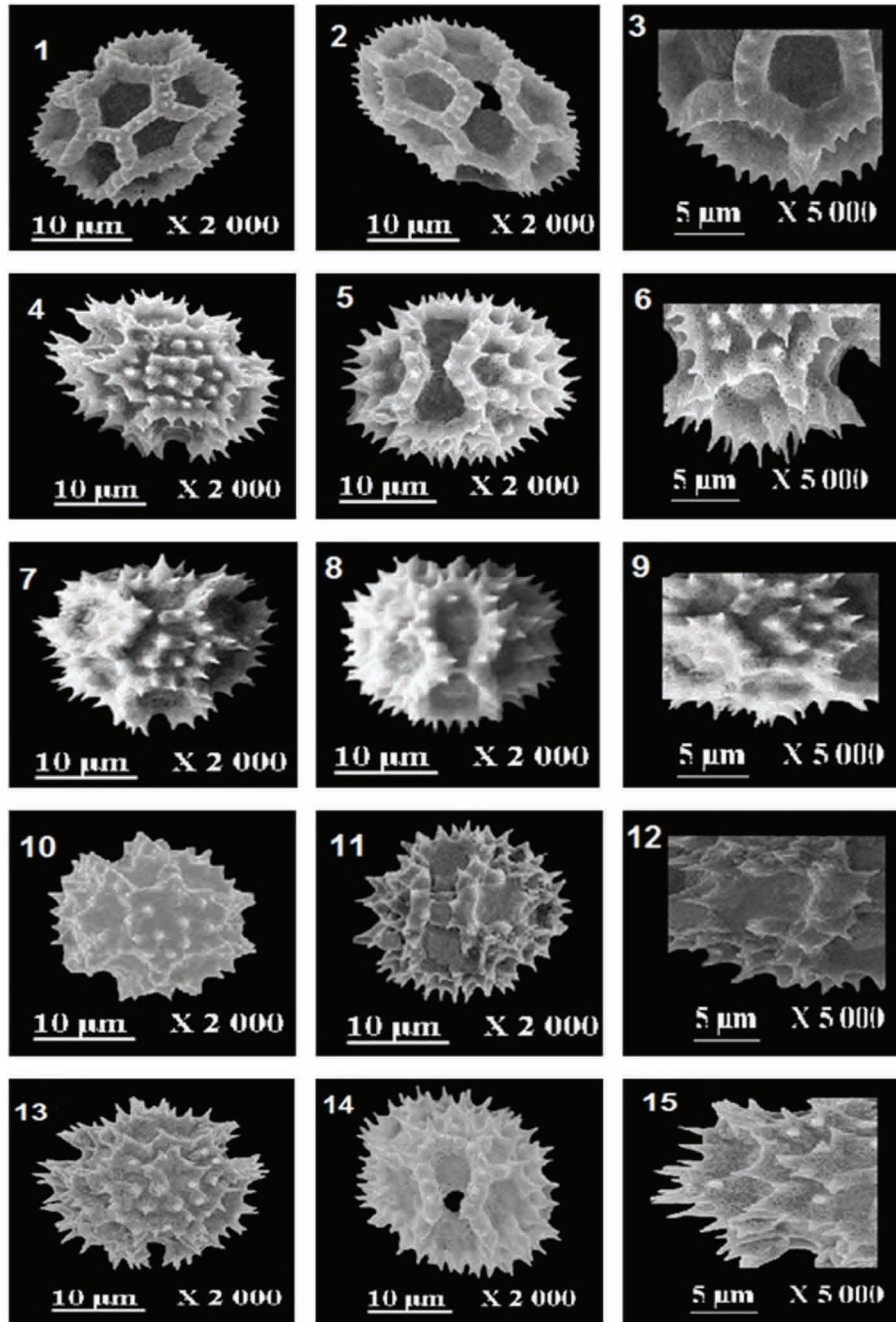


FIGURE 13. Pollen morphology of *Scorzonera* examined by scanning electron microscope (SEM). 1–3. *S. tuzgoluensis*; 4–6. *S. amasiana*; 7–9. *S. lasiocarpa*; 10–12. *S. seidlitzii*; 13–15. *S. rigida*.

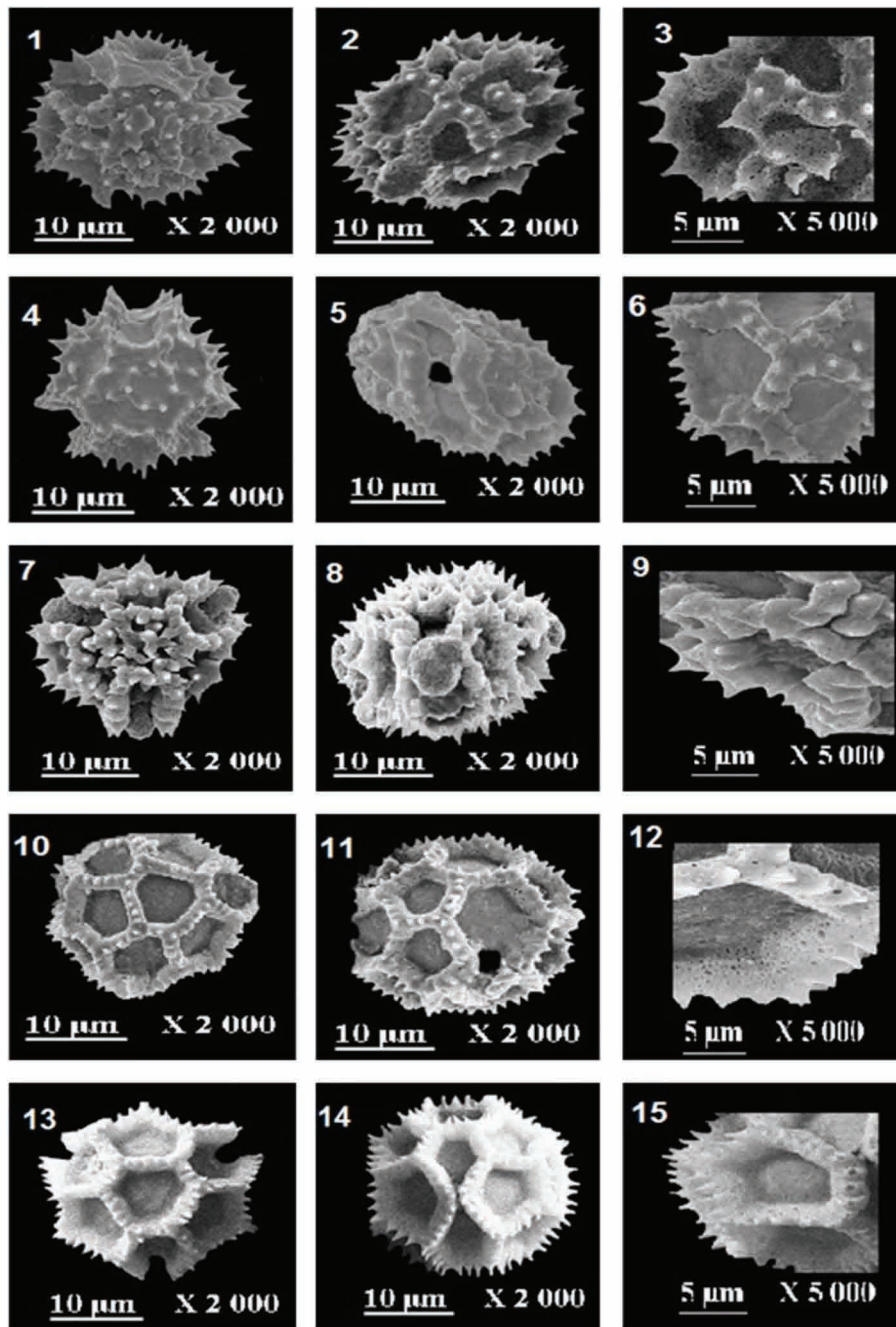


FIGURE 14. Pollen morphology of *Scorzonera* examined by scanning electron microscope (SEM). 1–3. *S. pygmaea* subsp. *pygmaea*; 4–6. *S. pygmaea* subsp. *nutans*; 7–9. *S. yildirimlii*; 10–12. *S. ahmet-duranii*; 13–15. *S. coriacea*.

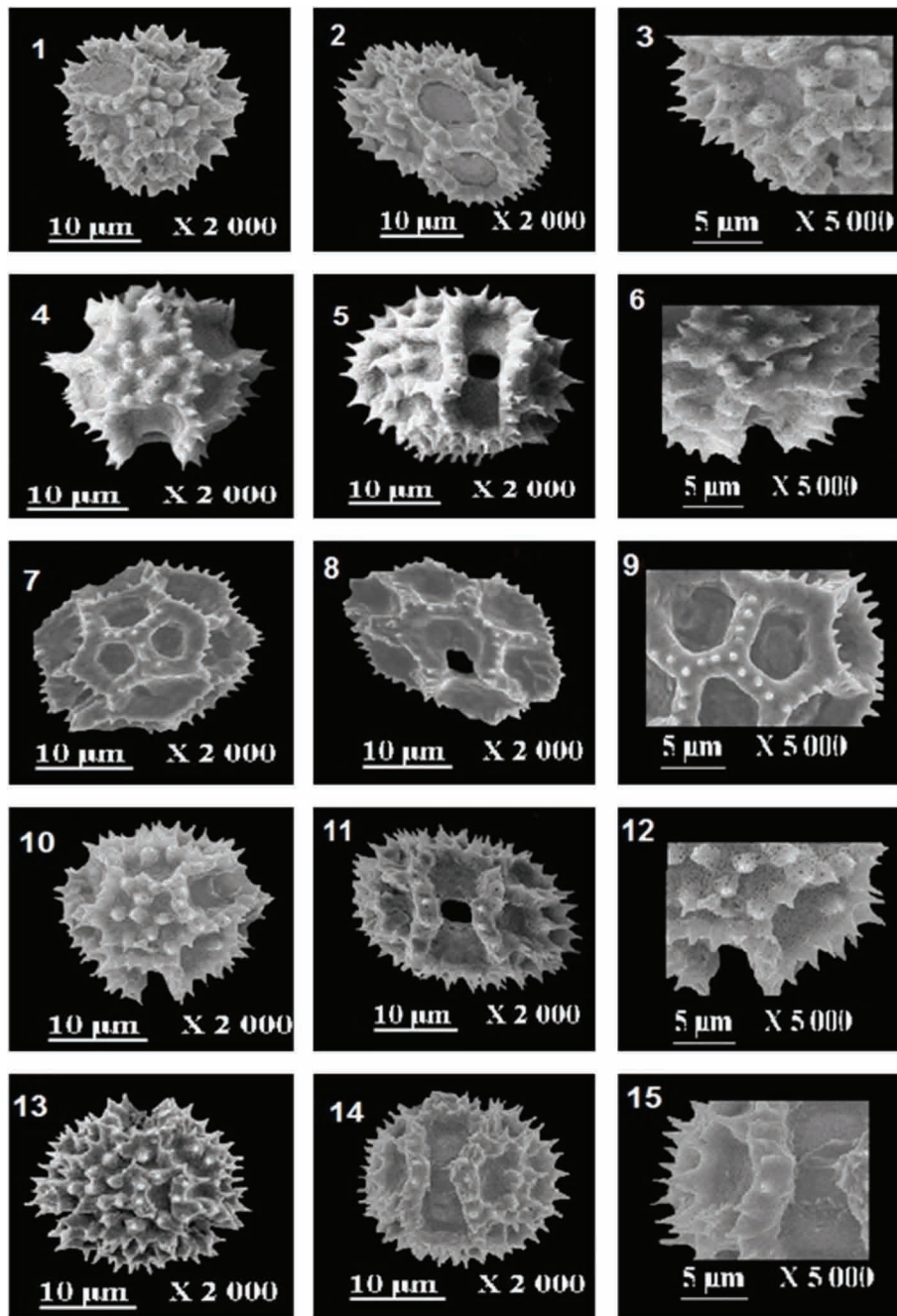


FIGURE 15. Pollen morphology of *Scorzonera* examined by scanning electron microscope (SEM). 1–3. *S. aucheriana*; 4–6. *S. sublanata*; 7–9. *S. renzii*; 10–12. *S. pisidica*; 13–15. *S. kotschyi*.

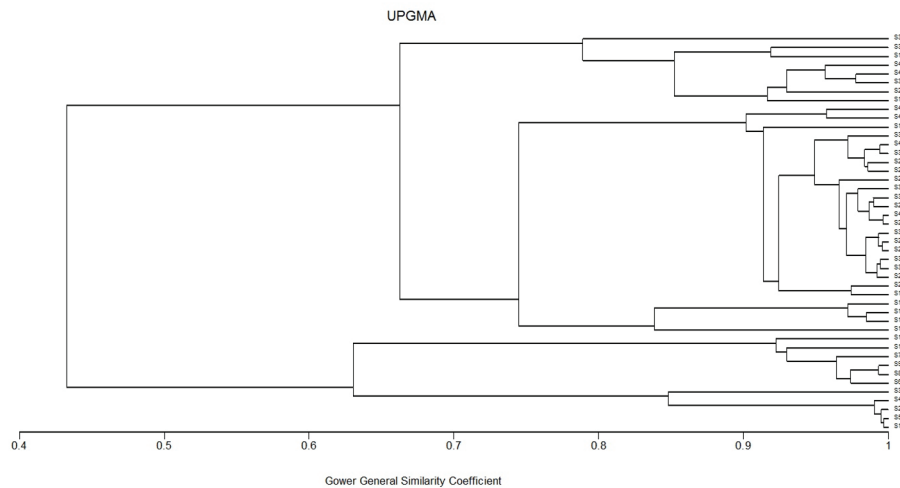


FIGURE 16. Dendrogram showing similarity distance of the examined taxa of *Scorzonera*.

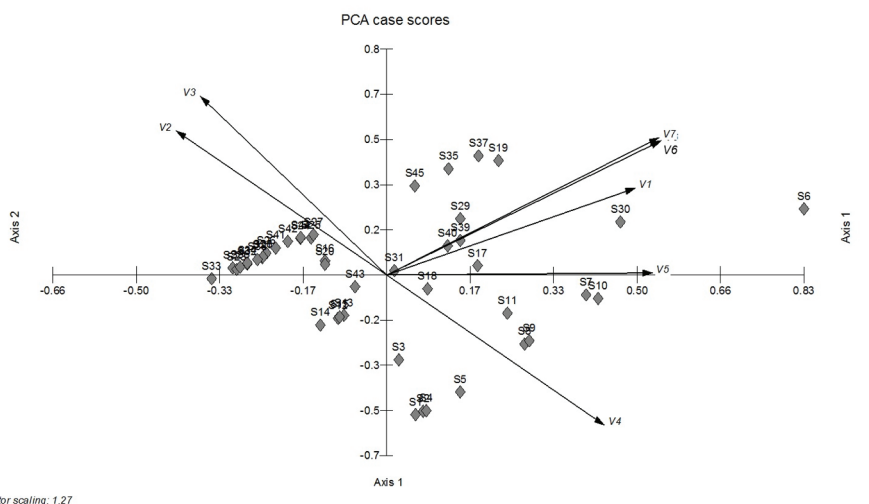


FIGURE 17. Principal component analysis of 45 taxa and 7 variables projected onto the first 2 axes. The signal (\blacklozenge) is for taxa and variables are showed as vectors.

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