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Pollen morphology of *Quercus* (subgenus *Quercus*, section *Quercus*) in Iran and its systematic implication

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Abstract

For the first time, pollen morphology of 9 (4 spp. and 5 subspp.) taxa representing lobed leaved oaks of Iran in the family of Fagaceae has been examined and illustrated using light microscopy and scanning electron microscopy of acetolysed material. Detailed pollen morphological characteristics are given for *Quercus* section. The pollen grains are single, isopolar, radially symmetrical, tricolpate, tricolporoidate or tricolporate. Pollens were studied to show all possible characteristics like shape, size, apertures, wall thickness, etc., with special reference to the specific features of each pollen type such as structural, sculptural and suprasculptural patterns. There is considerable variation in pollen morphology between taxa so that, three types of pollen shape, five types of structural pattern, two types of sculptural pattern, five types of suprasculptural pattern and three types of perfora distribution are defined. Furthermore, the relationship between pollen morphology and taxonomy is discussed. Overall, pollen characters are shown to be a useful and informative tool for assessing taxonomic position within *Quercus* section in Iran.

Keywords: Quercus, pollen morphology, taxonomy, SEM, LM, Iran

Introduction

Quercus is the largest genus in the family of Fagaceae, comprising more than 400 species in some classification [1,2], but modern taxonomic treatments will probably reduce that number [3]. Members of the genus have a wide geographical range, occupying vast territories of the North Hemisphere in North America, Europe and Asia [4]. Genus Quercus has a problematic taxonomy [5] because of its immense size and wide distribution [6], heterophylly, widespread hybridization between the infrageneric taxa and changes in morphological features (e.g. [7,8]). Most of the information about the classification of Quercus has come from taxonomic studies where the emphasis is on foliar and fruit characteristics. Based on consideration of the species characteristics as a whole, most specialists have disagreed on specific nomenclature for subgenera, species, varieties and forms [1,2,9-11].

Quercus is the most frequent genus of Fagaceae in forests of Iran [12]. Several species of oaks grow abundantly in Zagros, Arasbaran and Hyrcanian Forests exhibiting remarkable morphological variation. From a geographical point of view,

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Zagros Forests with an area of more than 5 million ha account for almost 40 percent of Iran's forests. These forests cover a vast area of Zagros mountain ranges stretching from Piranshahr in the northwest to the vicinity of Firouzabad in the south of Iran. Arasbaran Forest constitutes a limited territory covering an area of about 140000 ha, located in northwest of Iran. Hyrcanian vegetation zone is a green belt stretching over the northern slopes of Alborz mountain ranges and covers the southern coasts of the Caspian Sea. This site has a total area of 1.85 million ha and stretches from Astara in the northwest to Gorgan vicinity in the northeast of Iran [13].

All of the oak species of Iran categorize into one subgenus *Quercus* and two sections: *Quercus* and *Cerris* [14]. Species with lobed leaves, which are the object of this research, belong to the section *Quercus*. So far, only two taxonomic studies have been done on *Quercus* in Iran. The first and the most complete study of genus *Quercus* in Iran, including also the most important herbaria in Europe was done by Djavanchir Khoie [15] in his PhD thesis. He identified 9 taxa of lobed leaved species based on leaf and acorn morphology. Another treatise on genus *Quercus* was published by Menitsky [14] in Flora Iranica and he recognized 4 taxa in this group. Since 1971, there have been many local studies and new collections revealing high diversity among the species of sect. *Quercus*, so a comprehensive study of the genus is necessary.

Numerous observations of the surface features and size variations of pollen grains of *Quercus* with LM, TEM and SEM have often been undertaken for classification or identification of *Quercus* species and have proved to be of some help in this respect [4,8,16-27].

This study presents pollen SEM and LM observations and

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pollen size measurements of all taxa of lobed leaved oaks growing in Iran for the first time. Analyzing these data we tried to reveal the most useful morphological characters for the taxonomy of this section. The previous study on the genus was focused on properties of foliar epidermis of *Quercus* subgen. *Quercus*, sect. *Quercus* and confirmed nine taxa of this section as follows: *Q. cedrorum* Kotschy; *Q. infectoria* Oliv. subsp. *boissieri* (Reut.); *O. Schwarz* var. *boissieri*; *Q. infectoria* Oliv. subsp. *boissieri* (Reut.); *O.Schwarz* var. *tenuicarpa* (Djav.-Khoie) Jamzad and Panahi; *Q. infectoria* Oliv. subsp. *boissieri* (Reut.) *O. Schwarz* var. *pfaeffingeri* (Kotschy ex Tchihatcheff) Jamzad and Panahi; *Q. komarovii* A. Camus; *Q. longipes* Steven; *Q. macranthera* Fisch. and C. A. Mey; *Q. petraea* (Matt.) Liebl. subsp. *iberica* (Steven) Krassiln; *Q. robur* L. subsp. *pedunculiflora* (K. Koch) Menitsky [28].

Material and methods

Pollen grains of 9 taxa of Quercus, section Quercus (4 spp. and 5 subspp.) were collected from living plants throughout their geographic range in Iran. Most of the Iranian Quercus taxa are also distributed in the neighboring countries, mainly in Turkey, Iraq and Caucasian area. The voucher specimens are deposited in the Herbarium of Research Institute of Forests and Rangelands of Iran (TARI). Furthermore, other previously collected specimens of TARI and the Herbarium of Natural Resources Faculty, University of Tehran (NRF) were sampled. At least 10 voucher specimens were studied and two collections were sampled for each taxon in order to ensure constancy of pollen characters among different populations of each particular species. Materials and collecting data of examined taxa in the present study are listed in Tab. 1. Pollen grains were prepared by the standard acetolysis method [29], after which they were mounted in glycerin and sealed with paraffin wax prior to LM observation. Pollen grains were studied by an Olympus LM under a $\times 100$ lens. Measurements were made on 30 grains systematically scanning the slide for each taxon. Grains lacerated or wrinkled were not measured. The mean, range, standard deviation (SD) and coefficient of variation (CV) were calculated for polar axis (P), equatorial diameter (E) and wall thickness (WT). The ratio of polar axis to equatorial diameter (P/E) was provided as an index of pollen shape [30]. Normality of the distribution of variables (P, E and WT) was assessed by test of Kolmogorov-Smirnov (p < 0.001) and ANOVA, with post-hoc Duncan's test, was used to compare the mean values for each variable.

For SEM, after acetolysis, the pollen grains were put in absolute alcohol, a few drops of which were placed on previously numbered aluminum stubs, air dried at room temperature and sputter-coated with gold-palladium for 5 minutes in a Humer II Sputtering Device. The micromorphological features and quantitative characters of pollen grains were studied with use of a Hitachi (S-4160) SEM at an accelerating voltage of 15 KV. The terminology follows mainly that of the following references [22,23,30-33].

Results

Size variations

The pollen grains observed in this study are categorized in medium class (26-50 μ m). The mean values of polar axis and equatorial diameter differ significantly among studied taxa (ANOVA, p < 0.001). On the average, *Q. infectoria* subsp. *boissieri* var. *boissieri* and *Q. petraea* subsp. *iberica* have the lowest and the highest values of polar axis, respectively. Regarding to equatorial diameter, *Q. macranthera* with the highest value and *Q. infectoria* subsp. *boissieri* var. *pfaeffingeri* with

Tab. 1 List of species and the collection data.

Taxon	Collection data	Habitat
Q. cedrorum	Iran: West Azerbaijan, Mirabad, Molla Allah Cemetery, 1425 m, Panahi and Pourhashemi 95052 (TARI) Iran: West Azerbaijan, Sardasht, Djavanchir, No number (NRF)	Zagros
Q. infectoria subsp.	Iran: Kurdistan, Baneh- Sardasht road, Djavanchir 2046 (NRF)	Zagros
boissieri var. boissieri	Iran: West Azerbaijan, Mirabad, Khedr-abad village, 1290 m, Panahi and Pourhashemi 95050 (TARI)	8
Q. infectoria subsp.	Iran: Kurdistan, Baneh, Belakeh, 1650 m, Djavanchir 25 (NRF)	Zagros
boissieri var. tenuicarpa	Iran: Kurdistan, Baneh, Between Armardeh and Nirvan, 1523 m, Panahi and Pourhashemi 91435 (TARI)	-
Q. infectoria subsp.	Iran: Kurdistan, Baneh, Mirhesam, 14-rigeh Cemetery, 1550 m, Panahi and Pourhashemi 95022 (TARI)	Zagros
boissieri var. pfaeffingeri	Iran: Kurdistan, Baneh, Between Belakeh and Baneh, Djavanchir 2050h (NRF)	
Q. komarovii	Iran: East Azerbaijan, Kallibar, Arasbaran, Djavanchir 2052 (NRF)	Arasbaran
	Iran: East Azerbaijan, 10 km from Kallibar to Khodaafarin, 1850 m, Mozaffarian and Mohammadi 37616 (TARI)	
Q. longipes	Iran: West Azerbaijan, Khoy, Djavanchir 2054 (NRF)	Zagros
	Iran: East Azerbaijan, Oskou, Gunbarf village, 2240 m, Panahi and Pourhashemi 95105 (TARI)	
Q. macranthera	Iran: Mazandaran, Siahbisheh, Djavanchir, 2054c (NRF)	Hyrcanian and
	Iran: East Azerbaijan, Kallibar, Protected region from Makidi to Veinagh, 1700 m, Wendelbo and Assadi 17057 (TARI)	Arasbaran
Q. petraea subsp. iberica	Iran: East Azerbaijan, Kallibar, Protected region from Makidi to Veinagh, Wendelbo and Assadi 17026 (TARI)	Hyrcanian and
	Iran: Mazandaran, Chalous road, 2 km to Siahbisheh, 2450 m, Runemark and Mozaffarian, 28082 (TARI)	Arasbaran
Q. robur subsp.	Iran: Kurdistan, Baneh-Marivan, Shipaneh-jow, Pirsharif Cemetery, 1598 m, Panahi and Pourhashemi 91401	Zagros
pedunculiflora	(TARI)	
	Iran: Kurdistan, Baneh-Marivan, Bayan-darreh village, Sheikh musa Cemetery, 1736 m, Panahi and Pourhashemi 91401 (TARI)	

the lowest value set into different classes. The wall thickness (Fig. 1a,b,e,f,i,j) is equal on mesocolpium and apocolpium in each pollen and ranges from 1.84 µm in *Q. cedrorum* to 2.6 µm in *Q. komarovii*. All of the pollen grains have three colpi running parallel to the polar axis and converging close to the polar ends.

Shape

Light microscopic analyses have revealed that the shape of pollen grains ranges from suboblate (P/E = 0.75-0.88; Fig. 1a-d, Fig. 2d), through oblate-spheroidal (P/E = 0.88-1.00; Fig. 1e-h, Fig. 2l, Fig. 3h,l, Fig. 4d,h,l) to prolate-spheroidal (P/E = 1.00-1.14; Fig. 1i-l, Fig. 2h, Fig. 3d). Descriptive statistics of polar axis, equatorial diameter, P/E and wall thickness of pollen grains are summarized in Tab. 2.

Apertures

Pollen grains of examined taxa are single, isopolar, radially symmetrical. Their pores are sometimes indistinct and their apertures are tricolpate, tricolporoidate or tricolporate with colpi of medium length (Fig. 2b, Fig. 3g). The geniculus is sometimes present (Fig. 3d).

Exine ornamentations

The exine ornamentations in mesocolpium (Fig. 4f) and

apocolpium (Fig. 4g) are mostly similar. The main surface features of the investigated pollen grains are subdivided into structural patterns (assumed expressions of exine structure, exposed at the tectum surface), sculptural patterns (projections superimposed upon the tectum surface) and suprasculptural patterns (superimposed upon sculptural features) as stated below:

STRUCTURAL PATTERNS. Regarding to these patterns of exine, five types of patterns can be distinguished. Tectum surface between sculptural features may be psilate-verrucate (Fig. 4b,c), verrucate (Fig. 2b,c, Fig. 3b,c,f,g, Fig. 4f,g), scabrate (Fig. 2j,k), scabrate-verrucate (Fig. 2f,g, Fig. 4j,k) and psilate-scabrate (Fig. 3j,k). Furthermore, structural patterns include perforations of varying density (dense, Fig. 2g,k, Fig. 3f,j, Fig. 4g; sparse, Fig. 2b, Fig. 3b, Fig. 4c,k) and varying distribution (regular, Fig. 2c,g, Fig. 3b,j, Fig. 4f,k; irregular, Fig. 4b,c; lineate, Fig. 2k, Fig. 3g).

SCULPTURAL PATTERNS. The sculptural protuberances, which occur on the tectum may be gemmate (e.g. Fig. 3b,c, Fig. 4f,g) or gemmate-verrucate (Fig. 2f,g) in appearance. These projections may have uniform size and shape and their distribution may be regular (Fig. 3f,g), irregular (Fig. 3j, Fig. 4b,k) or interlocking in their form with diameter more than 1 μ m (Fig. 2k, Fig. 4f,g).

SUPRASCULPTURAL PATTERNS. The sculptural

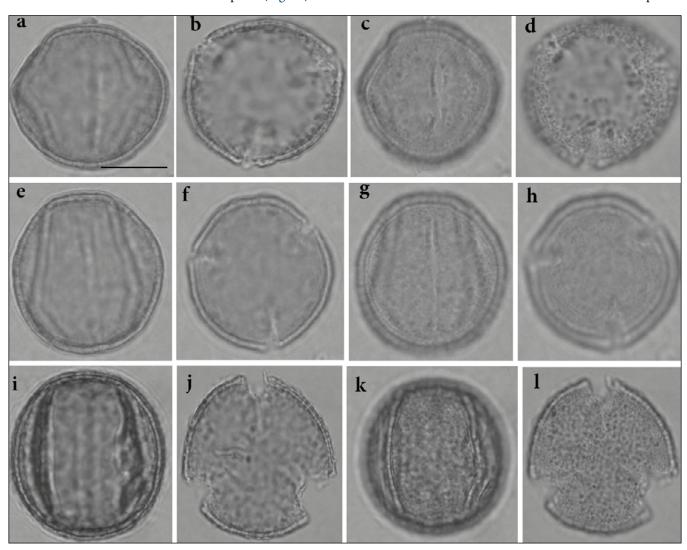


Fig. 1 LM micrographs of pollen grains in *Quercus* sect. *Quercus*. **a-d** *Q. macranthera*. **e-h** *Q. longipes*. **i-l** *Q. petraea* subsp. *iberica*. **a,c,e,g,i,k** Equatorial view. **b,d,f,h,j,l** Polar view. Scale bar: 10 μm.

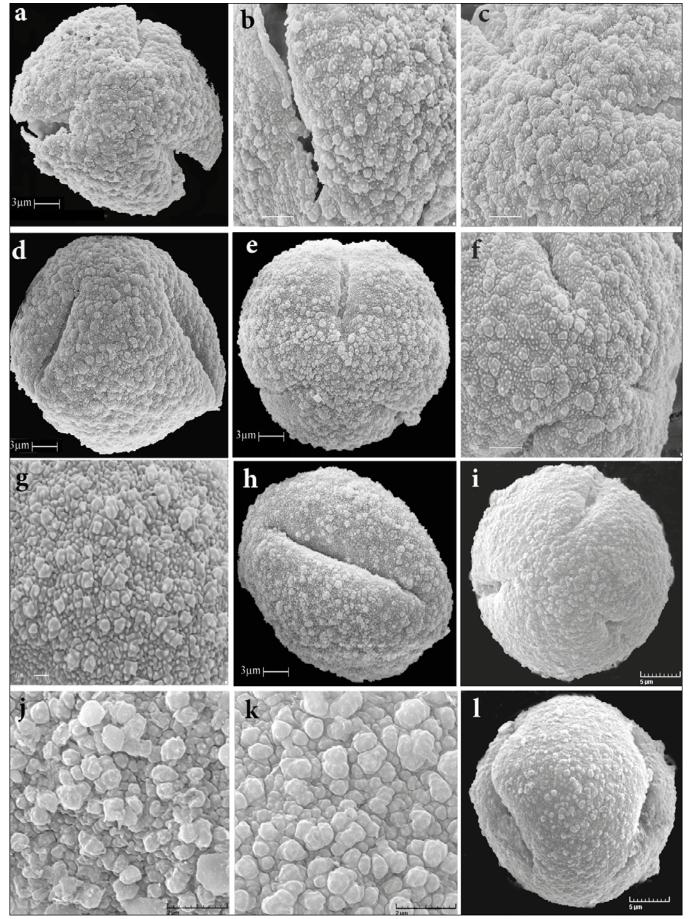


Fig. 2 SEM micrographs of pollen grains in *Quercus* sect. *Quercus*. **a-d** *Q. macranthera*. **e-h** *Q. petraea* subsp. *iberica*. **i-l** *Q. robur* subsp. *pedunculiflora*. **a,e,i** Polar view. **d,h,l** Equatorial view. **b,c,f,g,j,k** Mesocolpium and apocolpium.

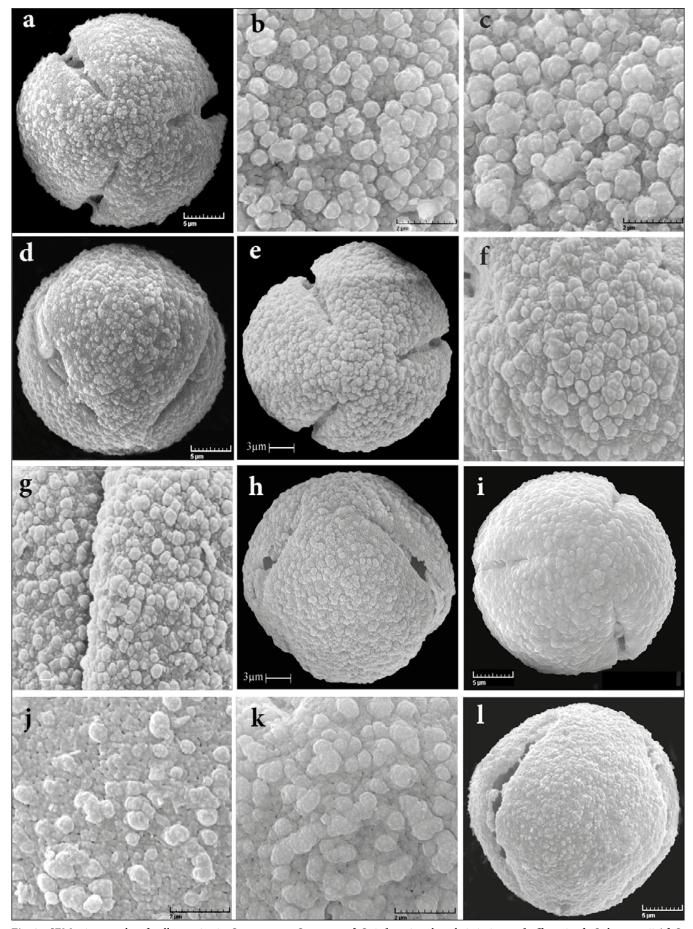


Fig. 3 SEM micrographs of pollen grains in *Quercus* sect. *Quercus*: **a-d** *Q. infectoria* subsp. *boissieri* var. *pfaeffingeri*. **e-h** *Q. komarovii*. **i-l** *Q. longipes*. **a,e,i** Polar view. **d,h,l** Equatorial view. **a,b,f,g,j,k** Mesocolpium and apocolpium.

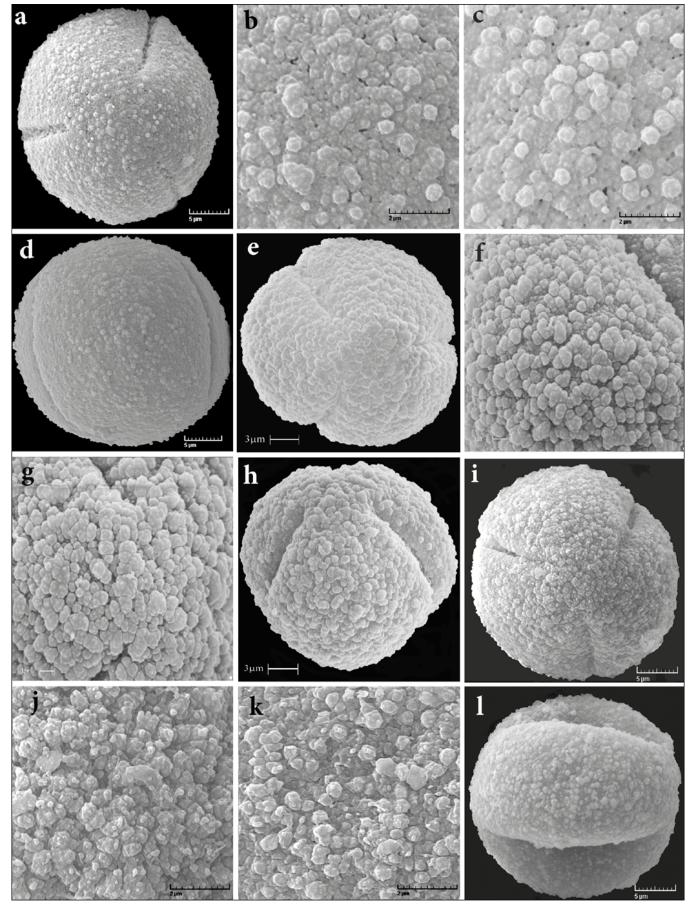


Fig. 4 SEM micrographs of pollen grains in *Quercus* sect. *Quercus*. **a-d** *Q. cedrorum*. **e-h** *Q. infectoria* subsp. *boissieri* var. *boissieri*. **i-l** *Q. infectoria* subsp. *boissieri* var. *tenuicarpa*. **a,e,i** Polar view. **d,h,l** Equatorial view. **b,c,f,g,j,k** Mesocolpium and apocolpium.

Tab. 2 Descriptive statistics of polar axis, equatorial diameter, ratio of polar axis to equatorial diameter and wall thickness of pollen grains.

		P			\boldsymbol{E}			
	Mean (µm)			Mean (µm)				
Taxon	±SD	Range (µm)	CV (%)	±SD	Range (µm)	CV (%)	P/E	WT (µm)
Q. cedrorum	29.8 a* ±2.3	24-33.6	7.7	32.3 a** ±2	29.6-36	6.2	0.93	1.84
Q. infectoria subsp. boissieri var. boissieri	27.9 b ±2.1	24-32	7.5	29.3 b ±1.9	24.8-32.8	6.5	0.96	2.02
Q. infectoria subsp. boissieri var. tenuicarpa	29.7 a ±2.5	24-36	8.4	30.5 c ±2.1	26.4-34.4	6.9	0.98	1.97
Q. infectoria subsp. boissieri var. pfaeffingeri	29.5 a ±1.9	26.4-33.6	6.4	28.8 b ±1.6	26.4-33.6	5.5	1.03	1.95
Q. komarovii	33.5 c ±3.1	27.2-43.2	9.3	34.9 d ±1.6	32-37.6	4.6	0.96	2.6
Q. longipes	29.2 a ±1.3	25.6-32	4.5	29.8 c ±1.4	27.2-32.8	4.7	0.98	1.95
Q. macranthera	35.1 d ±2.6	28.8-43.2	7.4	40.8 e ±2	35.2-45	4.9	0.86	2.51
Q. petraea subsp. iberica	38.3 e ±2.8	32.8-44.8	7.3	33.5 a ±2.4	28-38.4	7.2	1.14	2.1
Q. robur subsp. pedunculiflora	29.1 a ±1.7	25.6-34.4	5.8	29.7 c ±1.4	27.2-32.8	4.7	0.98	1.89

Means followed by the same letter in the same column are not significantly different at p < 0.001 according to Duncan test. CV – coefficient of variation; E – equatorial diameter; P – polar axis; SD – standard deviation; WT – wall thickness. * p < 0.001; F = 65.4. ** p < 0.001; F = 112.5.

projections themselves may possess suprasculptural features that may be microgemmate (Fig. 4b,c), microscabrate (Fig. 2f,g, Fig. 3b,c,j,k), microscabrate-microverrucate (Fig. 4f,g), microverrucate (Fig. 2j,k, Fig. 3f,g, Fig. 4j,k) or microverrucate-microechinate (Fig. 2b,c). These ornamentations show variation among the studied taxa, but are constant within one taxon. Detailed characteristic of pollen grains of studied taxa is presented in Tab. 3.

Discussion

In this research we studied pollen of nine taxa of *Quercus*, utilizing LM and SEM, which provided valuable data that could be inferred and used for identification of species. The ornamentations of the exine in *Quercus*, although generally a conservative character within the genus, give some additional support to the most recent infrageneric classification of *Quercus*. In fact, the pollen grains of taxa cited above, are easily distinguished one from another by their features.

The main characteristic features of pollen in the *Quercus* species studied here are similar to those reported earlier for this genus (e.g. [4,8,22-24]). Conforming to the results of previous studies all species studied here have pollen grains, which are single, isopolar, radially symmetrical, tricolpate, tricolporoidate or tricolporate. The basic shape of the pollen grains in most taxa studied is oblate-spheroidal, but suboblate and prolate-spheroidal shapes can also be found in few taxa. Based on the species studied here the congruence of some important pollen characters of the genus is discussed below.

With regard to morphological characters, three taxa of *Q. komarovii*, *Q. petraea* subsp. *iberica* and *Q. macranthera* are close together. *Quercus komarovii* distributes in a form of shrub only in Arasbaran Forests, in populations mixed with *Q. macranthera* in upland regions of this forest. *Quercus petraea* subsp. *iberica* grows throughout Hyrcanian and Arasbaran Forests. In Hyrcanian Forests it comes with *Q. macranthera* and *Q. castaneifolia* subsp. *castaneifolia*. *Quercus komarovii* and *Q. petraea* subsp. *iberica* exhibit some morphological similarities, but differences in a tree form, color of branches, color and shape of trunk bark, leaf shape, presence of lobule, shape of cup's scales and number of cup's spirals are noticeable.

In our studies we recognized some diagnostic characters on pollen grains to differentiate these species. The shape of pollen grains in *Q. komarovii* is oblate-spheroidal (P/E = 0.96), exine structure has dense microperforations that connect together and its distribution looks lineate in some sections. Sculptural pattern is gemmate with microverrucate suprasculpture which have smaller than 1 µm size, distributed regularly on the tectum surface. On the other hand, Q. petraea subsp. iberica is characterized by prolate-spheroidal shape of pollen, with P/E ratio of 1.14. In this taxon, polar axis is longer than equatorial diameter and dense perforations are usually distinct, not hidden by gemmate-verrucate sculpture. This ornamentation is mostly sharp-pointed and angular. Secondary ornamentation of microscabrate is seen easily under SEM, too. Quercus macranthera completely differs from the other species because of dense and long hairs on branches, buds, petioles, cupules and adaxial surfaces of leaves. Furthermore, this taxon is characterized by color and shape of trunk bark and presence of permanent stipules. Micromorphological feature of this taxon is suboblate shape (P/E = 0.86) of pollen and microverrucatemicroechinate type of its suprasculpture with spinous protuberances. The very clear differences exist then in the shape of pollen and exine ornamentations between these taxa.

Quercus longipes and Q. robur subsp. pedunculiflora are considered as similar taxa regarding their morphological characters. Quercus longipes is a high tree that appears in the small size stands in West and East Azerbaijan, located in west of Iran. Furthermore, individual trees of Q. robur subsp. pedunculiflora grow in West Azerbaijan and north of Kurdistan. Quercus longipes is characterized by leathery and tomentose leaves, regular cup's spirals and thick pedunculs, whereas Q. robur subsp. pedunculiflora has thin, glabrous or tomentulose leaves with soft and narrow pedunculs. The ornamentations on the tectum surface in these taxa is similar concerning the gemmate sculpture, but in Q. longipes the diameter of sculptural projections is smaller than 1 µm and their distribution on tectum is irregular. Dense microperforations are seen easily in Q. longipes because of psilate-scabrate structural pattern. Quercus robur subsp. pedunculiflora has interlocking form of gemmate sculptures that usually reach to 1 µm in diameter, and secondary ornamentations of microverrucate type upon sculptural patterns. In addition to morphological differences,

Fab. 3 Detailed of pollen grains of studied taxa.

Тахоп	Shape	Apertures	Structural patterns	Structural patterns Sculptural patterns	Suprasculrtural patterns	Perfora density	Perfora distribution
Q. cedrorum	Oblate-spheroidal	Tricolpate-tricolporoidate	Psilate-verrucate	Gemmate	Microgemmate	Sparse	Irregular
Q. infectoria subsp. boissieri var. boissieri	Oblate-spheroidal	Tricolpate-tricolporoidate	Verrucate	Gemmate	Microscabrate-microverrucate	Dense	Regular
Q. infectoria subsp. boissieri var. tenuicarpa	Oblate-spheroidal	Tricolporoidate-tricolporate	Scabrate-verrucate	Gemmate	Microverrucate	Sparse	Regular
Q. infectoria subsp. boissieri var. pfaeffingeri	Prolate-spheroidal	Tricolporoidate-tricolporate	Verrucate	Gemmate	Microscabrate	Sparse	Regular
Q. komarovii	Oblate-spheroidal	Tricolporate	Verrucate	Gemmate	Microverrucate	Dense	Lineate
Q. longipes	Oblate-spheroidal	Tricolporate	Psilate-scabrate	Gemmate	Microscabrate	Dense	Regular
Q. macranthera	Suboblate	Tricolporate	Verrucate	Gemmate	Microverrucate-microechinate	Sparse	Regular
Q. petraea subsp. iberica	Prolate-spheroidal	Tricolpate-tricolporoidate	Scabrate-verrucate	Gemmate-verrucate	Microscabrate	Dense	Regular
Q. robur subsp. pedunculiflora	Oblate-spheroidal	Tricolporate	Scabrate	Gemmate	Microverrucate	Dense	Lineate

our study on the features of pollen grain surface showed distinct and obvious differences among these taxa.

Four taxa of Q. infectoria subsp. boissieri var. boissieri, Q. infectoria subsp. boissieri var. tenuicarpa, Q. infectoria subsp. boissieri var. pfaeffingeri and Q. cedrorum are distributed in Northern Zagros Forests. Considering the morphological characters, delimitation of Q. infectoria and subsequently the number of its subspecies and varieties vary according to different authors [12,14,15]. Quercus infectoria subsp. boissieri is the main taxon of Zagros Forests and is widely distributed in West Azerbaijan, Kurdistan, Kermanshah and Luristan provinces, but other three taxa in this group are only found in the small size stands in Kurdistan and West Azerbaijan. Quercus cedrorum is distinguished from the rest by having leaves with deep lobes and autumn fall. Quercus infectoria subsp. boissieri var. tenuicarpa is different from the others by having black-brown ring around convex hilum of an acorn. Quercus infectoria subsp. boissieri var. pfaeffingeri is characterized by the leaves with entire margin, which is exceptionally rare in other taxa. Our observations showed that these taxa have clear differences regarding some aspects of pollen exine ornamentations. Quercus cedrorum differs from the others because of having psilate-verrucate type of structural pattern and microgemmate suprasculptural patterns. Density of sculptural protuberances in this taxon is lower than Q. infectoria subsp. boissieri. Furthermore, sparse perforations spread irregularly on the tectum surface. Quercus infectoria subsp. boissieri and two its varieties have similarities in structure and sculpture, but differences in suprasculpture. These secondary ornamentations may consist of microscabrate-microverrucate pattern in Q. infectoria subsp. boissieri var. boissieri while microverruvate and microscabrate in its varieties. Furthermore, in these taxa the sizes of sculptural projections, which occur on the tectum surface, are different.

Summarizing, our studies confirm the taxonomical usefulness of micromorphological features of the pollen grains within the studied taxa.

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