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Pollen, nutlet and trichome micro-morphology of *Satureja* from flora of Iran, and their systematic implications

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İran florasından bazı *Satureja* türlerinin polen, nutlet ve trikom mikro-morfolojileri ve sistematik açıdan önemi

Abstract: Pollen, nutlet, and trichome micro-morphology of 12 species of *Satureja* (*Lamiaceae*) from the flora of Iran were examined by light and scanning electron microscopy (SEM). Our investigations indicated that these species have hexacolpate pollen with a prolate, (exceptionally sub-prolate shape) and microreticulate ornamentation. In most species the periclinal walls of the surface cells of the nutlets are wrinkled, and as a secondary sculpturing, the surface exhibits both spherical-ovoid pits and a tuberculate pattern on one seed, or a regular papillae-tuberculate pattern. In a few species, the nutlets display an undulate-reticulate pattern. *S. isophylla* and *S. khuzistanica* differ from the other studied species by the size of nutlets and *S. bachtiarica*, *S. hortensis*, and *S. kermanica* are distinguished by their nutlet sculpturing. *Satureja* species possess non-glandular trichomes together with two types of glandular trichomes, classified as sub-sessile (peltate) and capitate. Notably, the large distinctive capitate trichomes consisting of a multiseriate stalk with an enlarged, rounded multicellular head as well as the extremely long trichomes that are in two subtypes: acicular trichomes and trichomes with ridges and marked internodes are uniquely exhibits in *S. khuzistanica*. The characteristics of trichomes and nutlet were constant among different populations of *Satureja* species. The functions of both glandular and non-glandular trichomes have also been discussed. We indicated that while pollen characteristics among *Satureja* species show consistency, our findings of the micromorphological characteristics of trichomes and nutlets could provide diagnostic characters at species level and may enhance our understanding of the relationships among these species in future phylogenetic studies.

Key words: *Satureja*, Menthinae, nutlet, trichome, pollen

Özet: İran florasından 12 *Satureja* (*Lamiaceae*) türünün polen, nutlet ve trikom mikro-morfolojisi ışık mikroskobu ve taramalı elektron mikroskobu (SEM) ile incelenmiştir. Araştırmalarımız, türlerin hekzakolpat polene ve prolat (nadiren sub-prolat) şekle sahip olduğunu ve mikro-retikulat ornamentasyona sahip olduğunu göstermiştir. Çoğu türde, nutlet yüzey hücrelerinin periklinal duvarları buruşuk olup, ikincil yüzey desenlemeleri olarak hem küresel-oval çukurlar hem de tuberkulat desenler görülür ya da düzenli papillalı-tüberkül desen bulunmaktadır. Az sayıda türde, nutlerde undulat-retikulat desen görülmektedir. *S. isophylla* ve *S. khuzistanica*, nutlet boyutları açısından diğer incelenen türlerden farklıdır. *S. bachtiarica*, *S. hortensis* ve *S. kermanica* ise nutlet yüzey desenlemeleri bakımından diğerlerinden ayrılmaktadır. *Satureja* türleri, non-glandular trikomların yanı sıra sub-sessil (peltat) ve kapitat olmak üzere iki tür glandular trikom taşımaktadır. Ancak, çok hücreli yuvarlak bir başa sahip ve çok hücreli bir sap içeren büyük kapitat trikomlar ile iki alt tipi bulunan; asikular trikom ve çıkıntılar ve belirgin internodlar içeren uzun trikomlar yalnızca *S. khuzistanica*'da bulunmaktadır. Trikom ve nutlet özellikleri, bu türün farklı popülasyonları arasında sabit kaldığı görülmüştür. Aynı zamanda glandular ve non-glandular trikomların işlevleri de tartışılmıştır. Bu çalışma, *Satureja* türleri arasında polen özelliklerinin tutarlılık gösterdiğini, ancak trikom ve nutlet mikromorfolojik özelliklerinin tür düzeyinde ayırt edici karakterler sağlayabileceğini ve gelecekteki filogenetik çalışmalarda türler arasındaki ilişkilerin daha iyi anlaşılmasına katkı sağlayabileceğini göstermektedir.

Anahtar Kelimeler: *Satureja*, Menthinae, nutlet, trikom, polen

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1. Introduction

Satureja L. is a genus belonging to *Lamiaceae*, subfamily *Nepetoideae*, tribe *Mentheae*, subtribe *Menthinae* (Harley et al., 2004). It is indicated that the genus contains 38 species that are either annual herbs or perennial shrubs and subshrubs, widely occurring in the Mediterranean region, N Africa (Morocco and Libya), the Caucasus and W Asia (including Saudi Arabia, Iraq, and Iran) (Harley et al. 2004). According to the most recent revision (Bordbar and Mirtadzadini, 2024), *Satureja* has 12 species in Iran distributed in the northern, northwestern, western, southwestern, and southeastern regions of the country. Most of the species are endemic to the flora of Iran and distributed mainly in dry rocky limestone slopes of Irano-Turanian region (Bordbar and Mirtadzadini, 2024). This region is characterized by very dry summers and a temperate continental climate, extending from Syria and Anatolia to Turkestan and the Pamirs (Djamali et al., 2012).

The species are well-known aromatic plants rich in terpenoids, such as carvacrol, γ-terpinene, thymol, p-cymene, β-caryophyllene, linalool, and have widely used as flavoring in foods, herbal teas, and traditional medicine

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(Amanlou et al., 2005; Sadeghi-Nejad et al., 2011; Alizadeh, 2015; Mazandarani and Monfaredi, 2017).

Along with morphological features, the micro-morphology of pollens, properties of nutlets, and types of trichomes have been pointed out to be useful in Lamiaceae at various taxonomic levels (Wagstaff, 1992; Navarro and Oualidi, 2000; Moon et al., 2008a,b, 2009; Salmaki et al., 2008, 2009; Krawczyk and Głowacka, 2015). The investigation of such characters can provide valuable information for the delimitation of the taxa and also is suggested to be beneficial for phylogenetic interpretations in this family (Abu-Asab and Cantino, 1987; Cantino, 1990). Until now, several studies have focused on the micro-morphology of pollens (Moon et al., 2008c), nutlets (Husain et al., 1990; Kaya et al., 2009; Semerdjieva et al., 2023), and trichomes (Malmir et al., 2014) of *Satureja* species, however, they include only a few species belonging to the flora of Iran. Therefore, a comprehensive study encompassing all Iranian species of *Satureja* is lacking. This study aims to provide detailed descriptions of the pollen, nutlet, and trichome micro-morphology of the Iranian species of *Satureja* to evaluate the systematic significance of the observed characteristics in light of the variations among the taxa of the genus.

2. Materials and Method

2.1. Plant material

The examinations were performed on the herbarium samples belonging to 12 species of *Satureja* from flora of Iran deposited in MIR herbarium (Table 1). The delimitation of the taxa follows Bordbar and Mirtadzadini (2024).

Table 1. Taxa studied and their locality information

Taxon	Locality information
S. avromanica Maroofi	W, Kordestan Prov., Auraman valley, SW of Bölbar village, 35°14'08.5"N, 46°17'36.9"E, 1012 m, 05.X.2017, *Mirtadzadini 3029* (MIR)
S. bachtiarica Bunge	W, Bakhtiari, N of Ardal, Darkash canyon, 32°03'08.7"N, 50°39'43.3"E, 2721 m, 27.X.2016, *Mirtadzadini 1991* (MIR). Kordestan Prov., Dezli to Auraman, Kalam defile, 35°20'15.52"N, 46°13'9.54"E, 1690 m, 05.X.2017, *Faruqinia 3024* (MIR). Kermanshah Prov., Kerend, near Asiab-Tanureh village, 34°29'40.14"N, 46°08'39.07"E, 1874 m, 03.XI.2016, *Bordbar 1995* (MIR). C, Yazd Prov., 13 km from Mehriz to Tang-e Tshenar, 31°30'38.0"N, 54°21'30.3"E, 1946 m, *Mirtadzadini 1987* (MIR). Esfahan Prov., Semirom, 6 km from Semirom toward Vanak, 31°26'48.34"N, 51°30'07.62"E, 26.IX.2014, *Mirtadzadini 1993* SW, Fars Prov., South west of Estahban, Kuhbehesht, 29°06'43.16"N, 54°02'03.55"E, 1829 m, 14.X.2016, *Bordbar 1952* (MIR).
S. hortensis L.	NW, West Azarbaijan Prov., Khoy to Maku, 28.VIII.2008, *Mirtadzadini 3808* (MIR). Ardabil Prov., Givi, 15.X.2007, *Mirtadzadini 1958* (MIR)
S. intermedia C.A.Mey.	NW, Ardabil Prov., Talesh area, east of Khalkhal, after Kalestan village, Soltan-e Khuni, 37°42'52.74"N, 48°36'13.28"E, 2695 m, 08.VIII.2012. *Mirtadzadini 1980* (MIR).
S. isophylla Rech.f.	N, Mazandaran Prov., between Tshalus and Karaj, 14 km to Siabishe from Tshalus, 14.VIII.2013, *Mirtadzadini 1978* (MIR). SW of Nur, 5 km from Poul to Largan village, 36°23'07.76"N, 51°32'29.4"E, 1420 m, 27.X.2011, *Mirtadzadini 1979* (MIR).
S. kermanica Payandeh, Bordbar & Mirtadz.	SE, Kerman Prov., S of Kerman, N of Mt. Jupar, 29°59'11.3"N, 57°12'10.8"E, 2289 m, 21.X.2016, *Mirtadzadini 1943* (MIR). Kerman to Jiroft, Dehbakri, Marghak, 29°07'18.39"N, 57°52'43.06"E, 05.IX.2015, *Bordbar 1962* (MIR).
S. khuzistanica Jamzad	W, Ilam Prov., 16 km to Mehran from Ilam, S of Banroshan, 33°33'17.79"N, 46°13'12.98"E, 900 m, 13.XII.2019, *Mirtadzadini, Bordbar & Doostmohammadi 3803* (MIR) (type locality of *Satureja rechingeri*). Lorestan Prov., Pol-e Dokhtar to Andimeshk, road of Emamzada Shah Ahmad, 32°48'30.0"N, 47°59'47.5"E, 830 m, 17.IX.2019, *Mirtadzadini 3805* (MIR). Pol-e Dokhtar to Andimeshk, near Emamzada Shah Ahmad, 32°48'03.4"N, 48°00'04.0"E, 1150 m, 17.IX.2019, *Mirtadzadini 3804* (MIR).
S. edmondii Briq.	W, Kermanshah Prov., 5 km from Bisotun toward Sonqor, Mt. Parow, Nojubaran defile, 34°26'20.4"N, 47°24'14"E, 1376 m, 04.XI.2016, Bordbar 2032 (MIR). Kordestan Auroman region, Speriz village, North slopes of Mt. Shahu, 1300 m, 30 Oct 2021, 04 Nov 2021, *Advay 4155* (MIR).
S. macrantha C.A.Mey.	NW, East Azarbaijan Province, NE of Tabriz, Ahar road, 28.VIII.2007, *Mirtadzadini 1981* (MIR). Aras valley, E of Siahrud, SW of Nurduz, 38°50'05.5"N, 46°11'10.4"E, 996 m, 10.VII.2016, *Mirtadzadini and student team 1971* (MIR).
S. macrosiphonia Bornm.	W, Lorestan Province, 75 km from Khoramabad to Andimeshk, 33°04'56.1"N, 48°13'57.3"E, 1230 m, 18.IX.2019, *Mirtadzadini 3811* (MIR). 20 km SW of Aleshtar, Bastam dam, 33°41'9.40"N, 48° 9'0.61"E, 1540 m, 21.IX.2022, *Mirtadzadini & Bordbar 5156* (MIR).
S. mutica Fisch. & Mey.	NE, SW of Ashkhana, S of Jauzak, 37°25'16.7"N, 56°40'49.3"E, 1333 m, 30.X.2019, *Mirtadzadini 3829* (MIR). 17 km from Tangrah to Bojnurd, 37°22'07.5"N, 55°57'38.5"E, 753 m, 29.X.2019, *Mirtadzadini 3831* (MIR). N, Gilan Prov., South of Rasht, Ganja toward Rudbar, 36°51'53.0"N, 49°29'04.2"E, 180 m, 13.IX.2019, *Mirtadzadini 3821* (MIR).
S. sahendica Bornm.	NW, East Azarbaijan, south of Qaraghaj, south west of Pir-e Saqqa village, 365140.5°N, 465613.8°E, 2459 m, 08.VII.2016. *Mirtadzadini 1984* (MIR).

2.2 Pollen morphology

Pollen grains were removed from mature anthers of the herbarium specimens (Table 1). Most of the species (10 out of 12 taxa) were represented by two or more specimens from different collections to ensure about the constancy of pollen characters among different populations of the same species. For light microscopy (LM), the pollen grains were mounted in glycerine jelly after acetolysis according to the method described by Erdtman (1960). The diameter of pollen in polar and equatorial views, P/E ratio and length of colpus were measured using 15–30 separate grains by an Olympus BH-2 light microscope equipped with camera photomicrograph system. For SEM, pollen grains were mounted on clean metallic stubs using double-sided adhesive tape and coated with gold. The whole pollen grain and the detailed surface ornamentations were photographed with TESCAN VEGA3 microscope. The terminology follows that of Erdtman (1952) for determination of the shapes and Halbritter et al. (2018) for determination of the ornamentations.

2.3. Nutlet morphology

Nutlets were collected from herbarium specimens (Table 1). When available, two or more specimens from different collections of the same species were sampled. Measurements and optical observations of color and appearance features of the nutlets were carried out with 10–15 nutlets using an Olympus BH-2 light microscope equipped with camera photomicrograph system. For SEM observations, nutlets were mounted on clean metallic stubs using double-sided adhesive tape and coated with gold and examined by means of a TESCAN VEGA3 scanning electron microscopy. The terminology for describing nutlet surface sculpturing mainly follows Stearn (1992) and Kaya et al. (2009).

2.4. Trichome morphology

For each taxon studied, one to three populations were sampled. A list of specimens examined is provided in Table 1. Trichomes were obtained from the stems, leaves, and calyces and investigated with stereo-, light and scanning electron microscopy (SEM). The epidermal surfaces were first observed by light microscopy utilizing hand cut sections. For the scanning electron microscopy, small pieces of stems, leaves and calyces were fixed on metallic stubs using double-sided adhesive tape, and then were coated with gold. The SEM micrographs were taken with a TESCAN VEGA3 scanning electron microscope. The type of indumentum was described and classified following Abu-Asab and Cantino (1987), Satil and Kaya (2007), and Atalay et al. (2016).

Results

3.1. Pollen morphology

Pollen grains of the taxa studied are isopolar and radially symmetric (Fig. 1). The mean of polar axis varies from 40.03 µm to 48.69 µm, and the equatorial axis ranges from 26.99 µm to 34.86µm. The shape of the pollen grains is prolate (P/E = 1.33 – 1.48) with the exception for *S. khuzistanica* Jamzad. In *S. khuzistanica* two types of pollen were observed: prolate (P/E = 1.42) and sub-prolate (P/E = 1.29) pollen grains (Fig. 1b). In all of the species, the pollen grains are hexacolpate, the ambs are circular, and the surface is microreticulate. Simple colpi are distributed symmetrically (Fig. 1) (Table 2). We were unable to detect the octacolpate pollen grain mentioned by Jamzad (2012) for *S. avromanica* Maroofi.

3.2. Nutlets

SEM and LM micrograph of nutlets and their surfaces of the studied taxa are presented in Figures 2 and 3. The size of the nutlets ranged from 1 mm (in *S. isophylla* Rech.f.) to 2 mm in length (in *S. khuzistanica* and *S. avromanica*) and from 0.3 mm (in *S. isophylla*) to 1.5 mm in width (in *S. khuzistanica*). Therefore, the largest nutlets are found in *S. khuzistanica* (Fig. 2g) while the smallest are those of *S. isophylla*. The basic shape of nutlets in most taxa studied is elliptic, but it is widely elliptic in *S. hortensis* L., obovate in *S. isophylla* and widely obovate in *S. khuzistanica*. Elongated elliptic nutlets are also found in *S. avromanica* and *S. macrantha* C.A.Mey. along with elliptic nutlets. In the majority of species nutlets are trigonous, with *S. khuzistanica* displaying slightly trigonous nutlets in transversal section. The areoles are bi-lobed and basal. The nutlet surfaces are glabrous and light to dark brown in color. An irregular pattern of simple or branched dark nerves can be observed under a stereomicroscope. The nerves are more evident in *S. khuzistanica*.

The nutlet surface exihibits an undulate-reticulate pattern in *S. bachtiarica* Bunge and *S. kermanica* Payandeh, Bordbar & Mirtadz. (Fig. 3b and f respectively). In other species, the cell shape (primary sculpturing) is often not discernible externally. The periclinal walls of the surface cells are wrinkled, and as a secondary sculpturing, the surface has both spherical-ovoid pits and a tuberculate pattern on one seed. However, in *S. hortensis* the pattern is regular papillae-tuberculate (Table 1, Fig. 3).

3.3. Trichome

Two basic types of trichomes are observed on different organs of the plants (Figs. 4 and 5): glandular and eglandular. Based on our observation glandular trichomes are subdivided into two main subtypes: (1) subsessile glands (Fig. 4a and b), also known as peltate hairs (Satil and Kaya, 2007), and (2) capitate trichomes (Fig. 4 d-k).

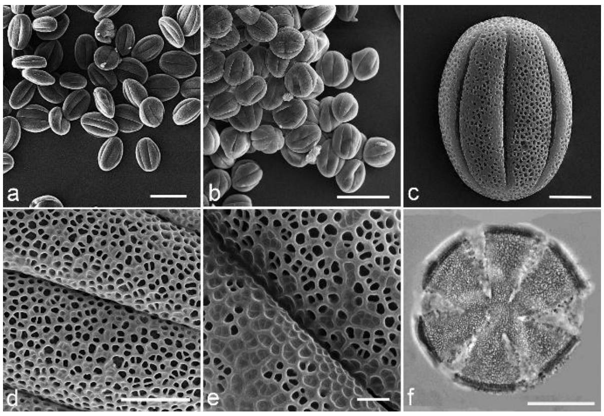

Figure 1. SEM and LM micrograph of pollens of some *Satureja* species from flora of Iran: (a) *S. avromanica.* (b) *S. khuzistanica.* (c) *S. macrantha* (equatorial view). (d) *S. kermanica* (enlarged view). (e) *S. sahendica* (enlarged view). (f) LM micrograph of *S. avromanica* (polar view). (a, b) scale bar = 50 µm, (c, d, f) scale bar =10 µm, (e) scale bar = 2 µm

subsessile glands are multicellular, yellow or red in color regularly distributed in epidermal depressions on the adaxial and abaxial leaf surfaces, on the outer surface of the calyx, and less on the stems. Their size is ranged from 55 µm in *S. isophylla* and *S. avromanica* and up to 100 µm in *S. mutica* Fisch. & Mey. and *S. macrosiphonia* Bornm. Capitate trichomes are of two different forms: small (up to 50 µm) and large (up to 180 µm). Small capitate trichomes have a short uni- or bi-, rarely tricellular stalk (in *S. khuzistanica*, Fig. 4h) with an unicellular clavate (Fig. 4d) or globular head (Fig. 4e and f). Large capitate trichomes consist of a multiseriate stalk (75-90 µm in size) with an enlarged rounded multicellular head (75-90 µm in size) (Fig. 4i-k).

Eglandular trichomes are simple, uniseriate, micro-papillate, and subdivided into three main subtypes: (1) short with one to three cells and conical (Fig. 4l) or elongated conical in shape (up to 250 µm, Fig. 5a-c), (2) long with up to six elongated cells (up to 600 µm, Fig. 5d, up to 1 mm) and (3) extremely long with up to eight elongated cells (up to 1.2 mm, in *S. khuzistanica*, Fig. 5e-f). We found some variation in morphology of extremely long trichomes and sub-divided them into two different types similar to the findings of Malmir et al. (2014): (1) acicular trichomes (Fig. 5f) and (2) trichomes with ridges and marked internodes (Fig. 5f).

Figure 2. LM micrographs of nutlets of *Satureja* species from flora of Iran: (a) *S. avromanica*. (b) *S. bachtiarica*. (c) *S. hortensis*. (d) *S. intermedia*. (e) *S. isophylla*. (f) *S. kermanica*. (g) *S. khuzistanica*. (h) *S. edmondii*. (i) *S. macrantha*. (j) *S. macrosiphonia*. (k) *S. mutica*. (l) *S. sahendica*. scale bar = 1 mm.

The distribution of the various trichome types on the stems, leaves, and calyces of the studied taxa is presented in Table 2. Trichomes of several types can be found on the same organ. According to the results of this study, subsessile glands, small capitate trichomes and both short and long eglandular trichomes are found on the leaves, stems, and calyces of the majority of *Satureja* species, with the exception of *S. khuzistanica*. In contrast, large capitate glandular trichomes and extremely long trichomes with ridges and marked internodes are exclusive to *S. khuzistanica*. Additionally, large eglandular trichomes are only located between the teeth of the calyces of *Satureja* species. Trichomes of several types can present on the same aerial organ. However, *S. avromanica* has only subsessile glands on its leaves and lacks trichomes on stems. In addition, small glandular capitate trichomes are only visible in *S. avromanica*, *S. intermedia* C.A.Mey., *S. hortensis*, and *S. macrantha* (calyx), *S. macrosiphonia* (stem and calyx), and *S. bachtiarica*, *S. edmondii* Briq. & Hausskn. and *S. khuzistanica* (leaf, stem, calyx).

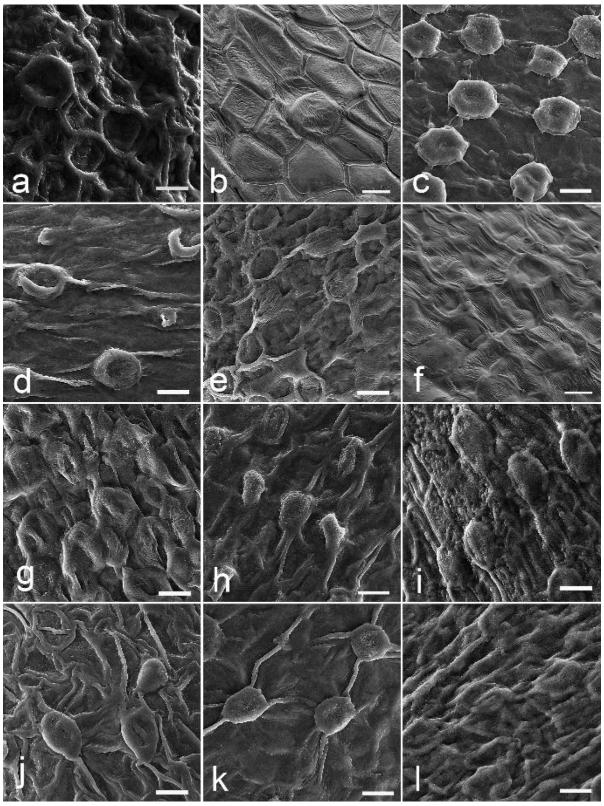

Figure 3. SEM micrographs of nutlet surfaces of *Satureja* species from flora of Iran: (a) *S. avromanica.* (b) *S. bachtiarica.* (c) *S. hortensis*. (d) *S. intermedia.* (e) *S. isophylla.* (f) *S. kermanica.* (g) *S. khuzistanica.* (h) *S. edmondii.* (i) *S. macrantha.* (j) *S. macrosiphonia.* (k) *S. mutica.* (l) *S. sahendica.* scale bar = 20 µm.

The orientation of eglandular trichomes are antrorse, retrorse or spreading. The orientation of the eglandular trichomes (if existed) on the leaves are usually antrose (Fig. 5a-c), and rarely spreading (*S. edmondii* and *S. khuzistanica*). While the orientation of the eglandular trichomes are retrose or spreading on the stems and calyces, rarely antrose on the stem (*S. kermanica*).

Although we did not qualify the density of hairs per unit area, it appears that there is little variation in the density of trichomes among different species. The only *S. avromanica* is an almost glabrous plant with eglandular trichomes absent on the leaves and stems. This type of hair is sporadically scattered on the calyx. Additionally, in *S. khuzistanica* some individuals of the same population are more densely hairy, and *S. macrosiphonia* displays an intra-specific diversity in the density of eglandular trichomes.

4. Discussions

This study provides a comprehensive investigation on the pollen, seed, and trichome micromorphology of 12 Iranian *Satureja* mostly for the first time as discussed below.

4.1. Pollen characters in taxa studied of *Satureja*

According to the results of this study, the pollens are hexacolpate in *Satureja* species. Aperture number has been considered as a useful character to define the subfamily Nepetoideae. This subfamily is characterized by hexacolpate pollen grains (Erdtman, 1945; Cantino, 1992). Prolate shape of pollens were observed in the majority of species, and both prolate and sub-prolate were identified in *S. khuzistanica*. It seems that multiple shapes of pollens within the one taxon are common in Menthinae (Moon et al., 2008c). In general, Menthinae pollens are small to medium in size (13-43 µm), oblate to prolate in shape, mostly hexacolpate (sometimes pentacolpate), and with perforate, microreticulate or bireticulate exine ornamentation types (Moon et al., 2008c). Therefore, the main characteristic features of pollen in the *Satureja* species studied here are consistent with those reported earlier for Menthinae. There are only sporadic reports of pollen characteristics in Satureja, as reports of Fırat (2015) for S. avromanica. In his work, the pollens are prolate- sub-spheroidal and reticulate; however, they appear to be underdeveloped. In another study, the pollen grains of S. montana L. and S. subspicata Bartl. ex Vis. had an oblate-spheroidal shape (Dunkic´ et al., 2007). The external morphology of pollen in Satureja is consistent, and characterized by a microreticulate pattern. Pollen characteristics of the family Lamiaceae have been reported to be of considerable taxonomic importance (Erdtman, 1945; Moon et al., 2008a,b,c); however, the results of this study are indicating that pollen morphology is stable at generic level in *Satureja* and is not useful for comparisons of the species.

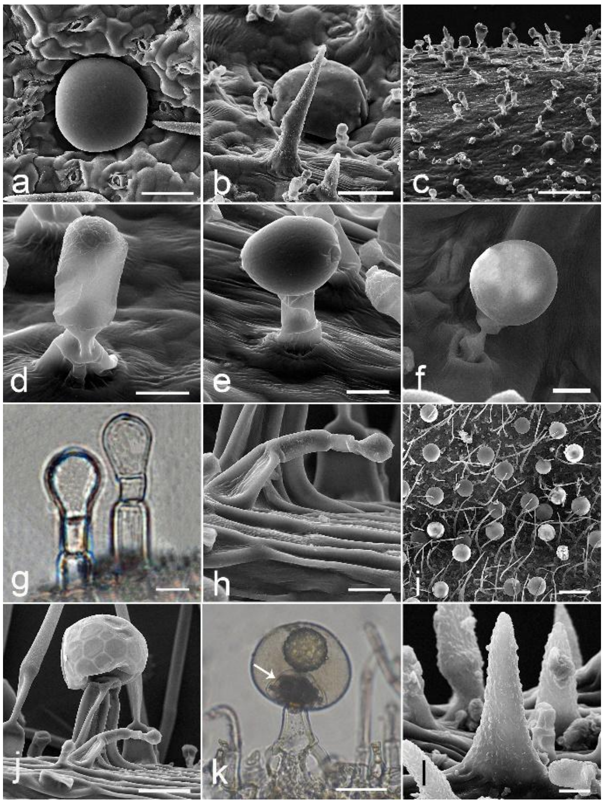

Figure 4. SEM and LM micrographs of trichomes of *Satureja* species from flora of Iran: (a) *S. intermedia*, subsessile gland (leaf). (b) *S. edmondii*, subsessile gland (leaf). (c) *S. edmondii*, small capitate trichomes (calyx). (d) *S. edmondii*, small capitate trichomes with clavate head (calyx). (e) *S. edmondii*, small capitate trichomes with globular head (calyx). (f) *S. khuzistanica*, small capitate trichomes with globular head (leaf). (g) *S. khuzistanica*, small capitate trichomes with bi-cellular stalk (leaf). (h) *S. khuzistanica*, small capitate trichomes with tri-cellular stalk (calyx). (i) *S. khuzistanica*, large capitate trichomes along with extremely long eglandular trichomes (leaf). (j) *S. khuzistanica*, large capitate trichome (calyx). (k) *S. khuzistanica*, large capitate trichome including oil storage (leaf). Secretory cells are shown with arrow. (l) *S. sahendica*, short conical eglandular trichomes (stem). (a, b, j, k) scale bar = 50 µm, (c) scale bar =100 µm, (d-g, l) scale bar = 10 µm, (h) scale bar = 20 µm, (i) scale bar = 200 µm.

4.2. Nutlet morphology in taxa studied of *Satureja*

Features of nutlet micromorphology have been widely used to study and reported to be useful as distinguishing features at different taxonomic levels in the Lamiaceae family (Husain et al., 1990; Moon and Hong, 2006; Kaya and Dirmenci, 2008; Salmaki et al., 2008; Moon et al., 2009; Siadati et al., 2019; Celep et al., 2020).

Moon et al. (2009) indicated that the nutlet characteristics are ratherly consistent at the generic level, although some variation was observed within some genera. *Salvia* L., the largest genus in Mentheae shows a considerable diversity in nutlet characteristics including size, shape, and sculpturing patterns. A similar variation in nutlet morphology is observed in *Monarda* L. and *Nepeta* L. Our results indicate that nutlets vary significantly in size, shape, and sculpturing patterns. These findings are highly consistent with those obtained for *Satureja* species from Turkey (Kaya et al., 2009). They studied 15 *Satureja* taxa from Turkey, of which *S. hortensis*, *S. macrantha* and *S. mutica* (syn. *S. spicigera* (C.Koch) Boiss.) are distributed in Iran as well. Their results identified two main types of nutlets: more or less smooth and sculptured, along with four subtypes: undulate-reticulate, reticulate, reticulate-protuberculate, and papillate-tuberculate. In their study,

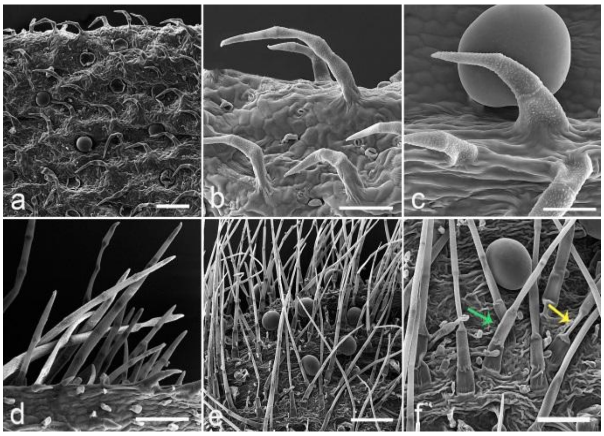

Figure 5. SEM micrographs of trichomes of *Satureja* species from flora of Iran: (a) *S. intermedia*, antrose orientation of eglandular trichomes on leaf surface (leaf). (b) *S. intermedia*, small eglandular trichomes (leaf). (c) *S. mutica*, small eglandular trichomes (calyx). (d) *S. isophylla*, long eglandular trichomes (calyx). (e) *S. khuzistanica*, extremely long eglandular trichomes over large capitate trichomes (calyx). (f) *S. khuzistanica*, acicular trichomes (green arrow) and trichomes with ridges and marked internodes (yellow arrow) (calyx). (a, e) scale bar = 200 µm, (b, d, f) scale bar =100 µm, (c) scale bar = 50 µm

Table 2. Pollen, nutlet and trichome morphological characters of *Satureja* species from flora of Iran

	Pollen morphological characters					**Nutlet morphological characters**						**Trichome morphological characters**		
Taxa	**P** (μm)	**E** (μm)	**P/E**	**shape**	**Ornamentation**	**L** (mm)	**W** (mm)	**Color**	**Shape**	**Shape of Transversal section**	**Surface sculpturing**	**Leaf**	**Stem**	**Calyx**
S. avromanica	46.53 ± 1.84	34.86 ± 2.38	1.33	prolate	microreticulate	1.5-2	0.8-1	b-db	elliptic-elongated elliptic	t	p-pt	A	-	B, D
S. bachtiarica	40.16 ± 1.51	26.99 ± 0.53	1.48	prolate	microreticulate	1.2-1.5	0.5-0.7	b-db	elliptic	t	ur	A, B, D^{an}	A, B, $D^{re\ or\ sp}$	A, B, D^{sp}, E
S. edmondii	44.92 ± 0.93	31.64 ± 2.04	1.41	prolate	microreticulate	1.5-1.8	0.6-0.8	b-db	elliptic	t	p-pt	A, B, D^{sp}	A, B, D^{sp}	A, B, D^{sp}
S. hortensis	40.03 ± 1.32	29.96 ± 2.52	1.33	prolate	microreticulate	1.2-1.3	ca. 1	b-db	widely elliptic	t	p	A, D^{an}	A, D^{re}	A, B, D^{an}, E
S. intermedia	48.69 ± 3.12	34.23 ± 2.58	1.42	prolate	microreticulate	1.4-1.6	0.7-0.8	b-db	elliptic	t	p-pt	A, D^{an}	A^{3}, D^{re}	A, B, D^{an}, E
S. isophylla	44.33 ± 1.69	32 ± 1.05	1.38	prolate	microreticulate	1-1.2	0.3-0.5	b-db	obovate	t	p-pt	A, D^{an}	A, D^{sp}	A, D^{sp}, E
S. kermanica	40.25 ± 2.1	28.13 ± 3.39	1.43	prolate	microreticulate	1.2–1.5	0.5–0.7	b-db	elliptic	t	ur	A, D^{an}	A^{3}, D^{an}	A, D, E^{an}
S. khuzistanica	40.28 ± 1.20 45.98 ± 1.0	31.23 ± 2.51 32.25 ± 2.52	1.29 1.42	sub-prolate prolate	microreticulate	1.8-2	1.2-1.5	b	widely obovate	st	p-pt	B, C, $F^{an\ \&\ sp}$	B, F^{sp}	B, F^{sp}, E
S. macrantha	46.48 ± 1.78	33.42 ± 2.24	1.39	prolate	microreticulate	1.2-1.5	0.5-0.7	b-db	elliptic-elongated elliptic	t	p-pt	A, D^{an}	D^{re}	A, B, D^{sp}, E
S. macrosiphonia	45.43 ± 0.89	32.36 ± 1.84	1.40	prolate	microreticulate	1.5-1.8	0.8-1	b-db	elliptic	t	p-pt	A, D^{an}	A, B, D^{re}	A, B, D^{an}, E
S. mutica	42.33 ± 1.05	31.66 ± 1.48	1.33	prolate	microreticulate	1.3-1.5	0.8-1	b-db	elliptic	t	p-pt	A, D^{an}	A^{3}, D^{re}	A, D^{an}, E
S. sahendica	42.71 ± 1.65	29.10 ± 1.59	1.46	prolate	microreticulate	1.2-1.5	0.7-0.8	b-db	elliptic	t	p-pt	A, D^{an}	A^{3}, D^{re}	A, D^{an}, E

Pollen characters: P; polar axis, E; equatorial axis, ± standard deviation, **Nutlet characters:** L: length, W: width. Color; b; brown, db; dark brown, Shape of transversal section; t; trigonous, st; slightly trigonous, Surface sculpturing; r; reticulate, ur; undulate-reticulate, p; pitted, pt; protuberculate, g; granulate, **Trichome characters:** Trichome types: A; subsessile glands, B; small glandular capitate trichome, C; large glandular capitate trichome, D; short eglandular micro-papillate trichome, E; long eglandular micro-papillate multi-cellular trichome, F; extremely long trichome, density: 1; dense, 2; sparse, 3; very sparse, orientation of trichome type D, E and F: an; antrorse, re; retrorse, sp; spreading.

nutlets showed a reticulate-protuberculate pattern in *S. macrantha*, papillate to tuberculate surfaces in *S. hortensis*, and reticulate-small tuberculate surfaces with shallow polygonal pits in *S. spicigera*. The latter species synonymized with *S. mutica* by Bordbar and Mirtadzadini (2024). Similarly, in our studies, most species, including *S. macrantha* and *S. mutica* indicated spherical-ovale pits and a tuberculate pattern, while *S. hortensis* revealed a papillate-tuberculate surface. The undulate-reticulate pattern of sculpturing in *S. bachtiarica* and *S. kermanica* is unique among Iranian *Satureja*. These two species also differ from others in their inflorescence and small flowers (Bordbar and Mirtadzadini, 2024). Our results showed that among the studied taxa, *S. khuzistanica* has relatively larger and wider nutlets, while the individuals of *S. isophylla* have shorter and narrower nutlets. *S. khuzistanica* is morphologically recognized from the other *Satureja* species by its large, broad, obovate or elliptic leaves, and *S. isophylla* differs by its caespitose habit and small leaves (Bordbar and Mirtadzadini, 2024). The nutlets of Turkish species of *Satureja* are typically glabrous, or in some species, apically haired (Kaya et al., 2009). In our investigations, the nutlets were exclusively glabrous. We did not observe any intraspecific variation for the taxa studied in characteristics of the nutlets.

Representative nutlet features also proved to be phylogenetically informative mainly at the generic level in Mentheae (Moon et al., 2009). The variation in surface sculpturing, nutlet shape, and size in *Satureja* is highly in consistent with the morphological diversity among species, and may provide useful diagnostic properties for future phylogenetic studies in this genus.

4.3. Trichome morphology in taxa studied of *Satureja* and their function

The significance of trichome features has been demonstrated in taxon delimitation at various levels in Lamiaceae (Giuliani and Bini, 2008; Moon et al., 2009; Atalay et al., 2016; Eiji and Salmaki, 2016). Such characteristics provide valuable criteria for comparison and serve as fundamental taxonomic tools in taxon delimitation. Trichomes of various forms are present in the studied species, and have taxonomic value for *Satureja* species. Trichome micro-morphological analyses of *Satureja* species have been described both here and in several publications (Dunkić et al., 2007; Satil and Kaya, 2007; Marin et al., 2010, 2012). In all cases, *Satureja* species have non-glandular trichomes together with two types of glandular trichomes, classified as sub-sessile (peltate) and capitate. Capitate trichomes are widespread in the Lamiaceae, but they vary significantly in stalk length and head shape (Abu-Asab and Cantino, 1987; Giuliani and Bini, 2008). In *Satureja*, these trichomes are typically small. However, the large capitate trichomes characterized by a multiseriate stalk and an enlarged, rounded multicellular head, appear to be unique and are exclusively found in *S. khuzistanica*. This type of trichome has been described in detail by Malmir et al. (2014). However, they categorized it as a peltate trichome. According to Malmir et al. (2014), this trichomes of *S. khuzistanica* comprised on average, 5 voluminous-lengthy stalk cells and 12 secretory cells. Moreover, several bundles of needle-like structures were observed in the secretory head of the trichomes, conforming to the published characteristics of calcium oxalate raphides. However, these needle-like structures were not observed in the trichomes of the samples we investigated

Subsessile glandular trichomes with multicellular heads are diagnostic for the genus *Satureja*, but they are apsent in *S. khuzistanica*. This type of trichome does not occur in some plant species belonging to Menthinae, such as *Clinopodium vulgaris* L. and *Conradina canescens* A.Gray as well (Moon et al., 2009). Sub-sessile glands on *Satureja thymbra* L. and *S. montana* consist of one basal epidermal cell, one stalk cell and a head composed of twelve secretory cells (Bosabalidis, 1990; Marin et al., 2012, respectively). In a study of leaf anatomy and trichomes of 15 *Satureja* from the flora of Türkiye by Satil and Kaya (2007), the sub-sessile trichomes (referred to as peltate trichomes) were found to be comprise one basal cell, one stalk cell, and a broad head containing 12–16-cells, of which 8–12 were described as large and peripheral, while four were noted to be small and located the central area of the head.

Non-glandular trichomes are widely distributed in Lamiaceae (Moon et al., 2009). Non-glandular trichomes likely collaborate together with the glandular trichomes in the mechanical defense against herbivores, and form a physical protection to plants against abiotic stresses. Besides, they comprise living cells that can synthesize, storage and/or release of biologically active compounds, including various classes of secondary metabolites (Tozin et al., 2016). According to the results of this study and previous reports (Satil et al. 2002, 2003; Redžić et al., 2006; Dunkić et al., 2007; Satil & Kaya, 2007; Marin et al., 2010, 2012), eglandular trichomes in *Satureja* are mainly the same and in two types: short and long. Notably, the extremely long trichomes found in two subtypes acicular trichomes and trichomes with ridges and marked internodes, are exceptionally present in *S. khuzistanica*.

In many *Labiatae*, the glandular trichomes are responsible for the secretion and storage of essential oils (Fahn, 1990; Muravnik, 2021). Different species of *Satureja* have different amount of essential oil content (Omidbaigi et al., 2007; Ghorbanpour et al., 2016) but they usually are rich in terpenoids, such as carvacrol, terpinene, thymol, *p*-cymene, *β*-caryophyllene, linalool, and other terpenoids. The variations in the quantitative composition of carvacrol and thymol compounds in the Lamiaceae family were mainly due to the geographical area, genetic diversity, climatic conditions, the existence of different chemotypes, and/or ecological differences (Salehi-Arjmand et al., 2014). For example, it has been shown that perennial winter savory (*S. montana*) accumulates more carvacrol than annual summer savory (*S. hortensis*). The highest and lowest oil yields in *S. rechingeri* were obtained during the full-flowering stage (October) and the pre-flowering stage (July), respectively (Alizadeh, 2015). Low winter temperatures cause overproduction of essential oils due to antioxidant properties that stimulate oxidative stress (Bosabalidis, 2013). These differences may also result from varying densities of glandular trichomes on the aerial parts of the plants. In *Thymus sibthorpii* Benth., glandular hairs are abundant in winter leaves and secrete a higher amount of essential oil, compared to summer leaves (Bosabalidis, 2013). According to the results of this study, *S. avromanica* and *S. isophylla* have the smallest subsessile glands among the studied taxa. *S. avromanica* is nearly glabrous and non-aromatic. The analysis of essential oils in these two species indicated that the amounts of thymol and carvacrol were very low (Sefidkon and Jamzad, 2006; Abdali et al., 2017). Conversely, *S. khuzistanica* has the largest capitate glands on its aerial parts. Alizadeh (2015) stated that a comparison of the quantities of *Satureja* species shows that *S. rechingeri* has the highest oil yield among all *Satureja* species, whether grown in the wild or cultivated. According to Bordbar and Mirtadzadini (2024) this species is now considered a synonym of *S. khuzistanica*.

We conclude that the pollen characteristics among *Satureja* species exhibit consistency; however, the micromorphological features of trichomes and nutlets are variable and may be systematically significance. *S. khuzistanica* is distinguished from the other species by the types of trichome. Additionally, *S. isophylla* and *S. khuzistanica* differs from the other studied species in the size of nutlets and *S. bachtiarica*, *S. hortensis* and *S. kermanica* are different in their nutlet sculpturing. Nevertheless, the general characteristics of trichome and nutlet were consistent among different populations of a given species. overall, our findings are useful contribution to the taxonomy and enhance the understanding of interspecies relationships in the genus *Satureja*. However, the value of these features in *Satureja* may be more effectively assessed through a molecular phylogenetic approach used in conjunction with morphological characteristics.

Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Authors' Contributions

FB contributed to material preparation, data collection, methodology and measured parameters. The first draft of the manuscript was written by FB. MM and MA contributed to material preparation. MM and FS commented on previous versions of the manuscript and read and approved the final manuscript.

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