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MICROMORPHOLOGY AND ULTRASTRUCTURE OF TRICHOMES OF LIBYAN *SALVIA FRUTICOSA* MILL.

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Abstract - Micromorphological and ultrastructural analyses of the leaf trichomes of *Salvia fruticosa* Mill. were performed by light and electron microscopy. The leaves bear numerous non-glandular unbranched trichomes, and peltate, capitate and digitiform glandular trichomes. Very elongated flagelliform non-glandular trichomes densely covered the leaf surfaces, with especially abundance on the leaf margins. Peltate trichomes consist of a basal epidermal cell, a very short stalk cell and a large round head of eight secretory cells arranged in a circle. Capitate trichomes can be divided into two main types, short-stalked and long-stalked, and further into five subtypes according to the number of stalk cells, morphology and number of glandular head cells. Digitiform trichomes consist of one basal cell, one or two stalk cells and one apical secretory cell, which are of similar diameter and approximately equal length.

Key words: *Salvia fruticosa*, Lamiaceae, trichome types, micromorphology, ultrastructure

INTRODUCTION

Salvia L. (sage), the largest genus of the Lamiaceae family, encompasses about 900 species distributed worldwide (Standley and Williams, 1973). *Salvia* species have been used in traditional medicine all around the world since the ancient times. Their essential oils and extracts have shown antimicrobial, antioxidant, antidiabetic, antitumor, antiplasmodial and anti-inflammatory activities (Sivropolou et al., 1997; Dorman and Deans, 2000; Ulubelen, 2003; Tepe et al., 2004; Kamatou et al., 2008; Şenol et al., 2010; Chan et al., 2011). Many *Salvia* species are used as herbal tea and in food, cosmetics, perfumery and the pharmaceutical industry, and some species are grown in gardens as ornamental plants (Kahraman et al., 2010).

In the *Lamiaceae* family, the morphology, distribution and frequency of glandular hairs are used as discriminative characters at various intrafamilial levels. There are a number of studies on the foliar micromorphology of the genus (Serrato-Valenti et al., 1997; Corsi and Bottega, 1999; Kaya et al., 2003; Kamatou et al., 2007; Özkan, 2008; Kahraman et al., 2009; Baran et al., 2010; Celep et al., 2011). The leaves of numerous plants, including *Salvia* species, are densely covered with glandular and non-glandular trichomes, which originate from epidermal cells (Werker, 2000). Developmental and structural studies of trichomes can shed light on the nature of the secreted material and their functional significance. Plant species bearing glandular trichomes generally produce relatively large amounts of bioactive compounds, which include highly concentrated phyto-

chemicals possessing biological activity and potential applications in the pharmaceutical or food industries (Duke, 1994; Burt, 2004; Giuliani and Maleci Bini, 2008, Miguel, 2010). The essential oil produced by glandular trichomes is one of the characteristic features for the Lamiaceae family (Werker et al., 1985).

Salvia fruticosa Mill. (Greek sage) is an aromatic perennial herb or sub-shrub. This species is native in the eastern Mediterranean basin, distributed from Italy, Sicily and Cyrenaica, through the southern Balkan Peninsula to western Syria (Hedge, 1982, Greuter et al., 1986). It is one of the most economically important *Salvia* species, valued for its beauty, medicinal properties, culinary usage, along with its sweet nectar and pollen, and has had an especially long tradition in application in Greece. *S. fruticosa* originating from Greece, Turkey, Lebanon and Jordan, was studied from different aspects, such as the chemical composition or genetic variation of essential oils, antimicrobial, cytotoxic, antiviral, antifungal, antioxidant effects of essential oils and extracts (Bayrak et Augul, 1987; Müller-Riebau et al., 1997; Sivropolou et al., 1997; Karousou et al., 1998; Skoula 1999; Abou-Jawdah et al., 2002; Pitarokili et al., 2003; Arikat, 2004; Savelev et al., 2004; Tawaha et al., 2007; Papageorgiou et al., 2008; Şenol et al., 2010).

Considering the importance of *Salvia fruticosa* L. as a medicinal plant, due to the essential oils produced in the glandular trichomes, and lack of data about the leaf ultrastructure and micromorphology, a comprehensive study of the trichomes distributed on adult leaves was done.

MATERIALS AND METHODS

Plant material

Aerial parts of the plants were collected during the flowering period from natural populations in Biadda, which is located on the Green Mountain. in eastern Libya, in March 2010. Voucher samples are stored in the Herbarium of the Institute of Botany and Botanical Garden "Jevremovac", Faculty of Biology, University of Belgrade.

Microscopical investigation

For light microscopy (LM), leaf sections of *S. fruticosa* were fixed with 3% glutaraldehyde in 0.1 M sodium phosphate buffer, pH 7.2, for 24 h at 4˚C. Subsequently, the material was washed in sodium phosphate buffer 3 times over 2 h, post-fixed in 1% osmium tetroxide in same buffer, for 24 h at 4˚C. The fixed material was washed with distilled water, dehydrated in a graded ethanol series and embedded in Araldite resin CY 212 (Agar Scientific Ltd. England). Semi-thin cross sections (1-1.5 μm thick) were cut on a LKB III ultramicrotome and stained with 0.1% methylene blue in 1% borax. Sections were photographed under a Zeiss Axiovert microscope (Carl Zeiss GmbH, Göttingen, Germany).

For transmission electron microscopy (TEM), ultra-thin sections were stained with uranyl acetate and lead citrate and examined with a MORGAGNI 268 (FEI Company, Eindhoven, The Netherlands) transmission electron microscope operated at 100 kV.

For scanning electron microscopy (SEM), adult leaf segments were coated with a thin layer of gold and palladium in a BAL-TEC SCD 005 sputter coater. Both adaxial and abaxial surfaces were examined with a JEOL JSM-6390 LV at an acceleration voltage of 13 kV.

RESULTS

The densely-pubescent leaves bear numerous non-glandular and glandular trichomes on both surfaces. Non-glandular trichomes densely covered the whole leaf surface, but were more abundant on the abaxial leaf side (Fig. 1). Particular abundance was noticed on the margins. They are single, uniseriate, multicellular, pointed, and erect. Numerous trichomes are very elongated, flagelliform, variable in length, consist of five or more cells and are supported by epidermal cells. During the development of the leaf, the density of non-glandular trichomes decreases, although they remain abundant on both surfaces of mature leaves, predominating on the margin and veins of the abaxial surface.

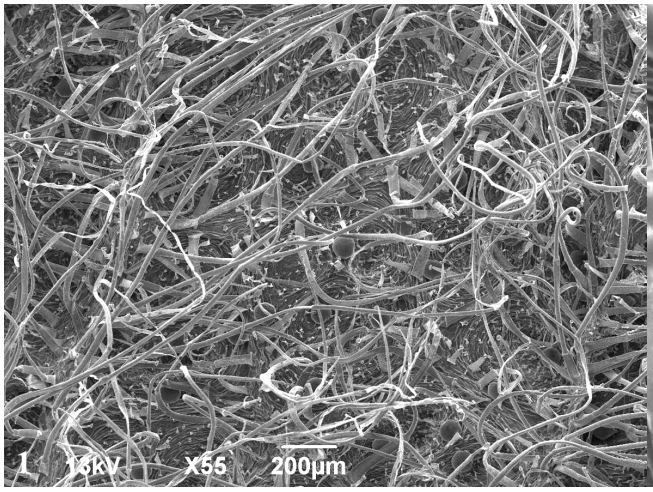


Fig. 1. SEM micrograph showing the morphology of non-glandular and glandular trichomes on the leaf surface of *S. fruticosa*.

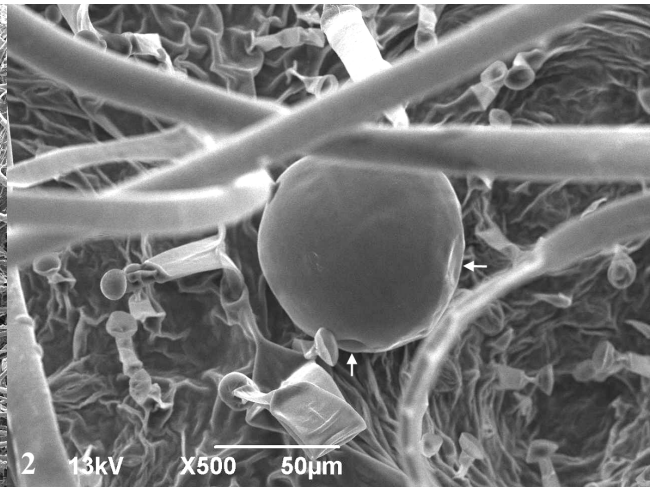
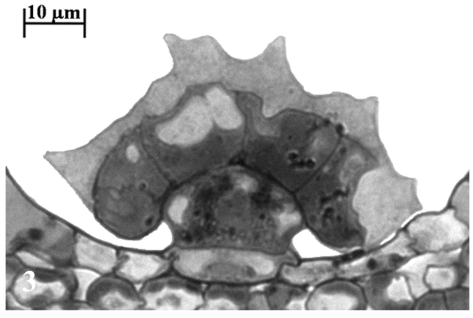


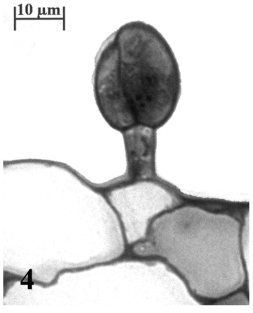
Fig. 2. SEM micrograph of peltate trichome. Note equatorial line (↑).

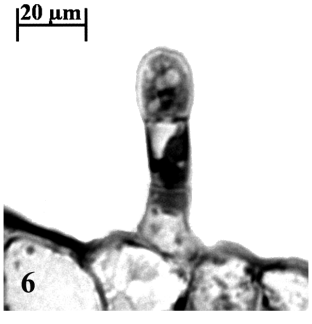
The glandular trichomes are of three main types – peltate, capitate and digitiform. Peltate trichomes have, *in vivo*, a green to brownish color and balloon shape (Fig. 2). They consist of the basal epidermal cell, a very short stalk cell and a large round head of eight secretory cells arranged in a circle (Fig. 3). The peltate glandular hairs have a smooth surface indicating the close attachment of the cuticle to the secretory upper cell walls (Fig. 2). The large space in which the secreted material accumulated developed at the time of secretion by the elevation of the cuticle together with the outermost layer of the secretory cell walls (Fig. 3). An equatorial line of weakness became a visible round head (Fig. 2); the rupture of the cuticle along this line and subsequent rise of the cuticular cap led to release of exudate.

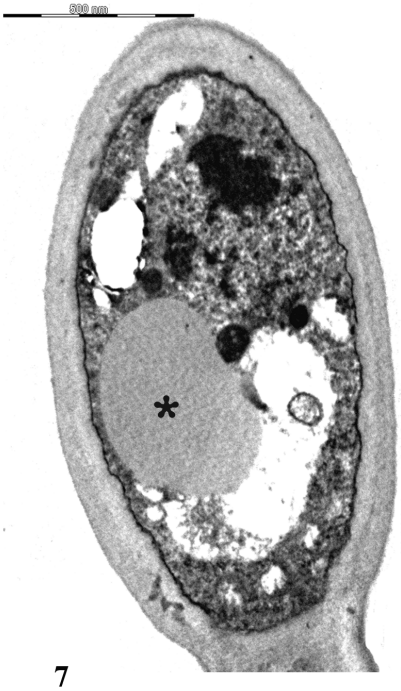
Capitate trichomes can be divided into two main types, short-stalked and long-stalked, and further into five subtypes according to the number of stalk cells, the morphology and the number of glandular head cells, and the secretion process. Short-stalked capitate trichomes subtype I possess one basal cell, one stalk cell with thick cutinized lateral walls and a bicellular ovoid glandular head (Fig. 4). Subtype II have one basal cell, two stalk cells and a globoid secretory head of two cells (Fig. 5), while subtype III capitate trichomes have one basal cell, one stalk cell and one head cell (Fig. 6). The secretory product accumulates inside the apical cells (Fig. 7). Long-stalked capitate trichomes subtype IV possess one basal cell, a long two-celled stalk and a unicellular spherical head (Fig. 8); subtype V have one basal cell, a three-celled stalk and also one cell in the spherical glandular head (Fig. 9).

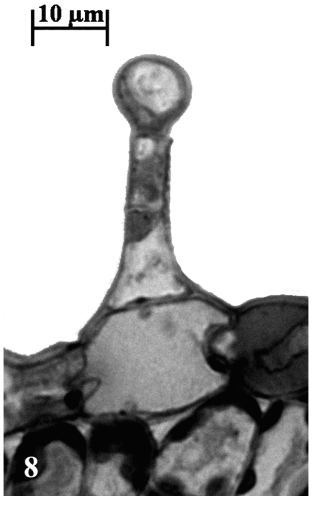
Digitiform trichomes consist of one basal cell, one or two stalk cells and one apical secretory cell. The cells are of similar diameter and approximately equal length (Fig. 10). There is no clear distinction between the head and stalk cells. The glandular apical cells have rounded tips, thin walls and are rich in cytoplasm (Fig. 11). The apical cell of a few digitiform trichomes possesses very small subcuticular spaces, but many of them have not developed a subcuticular space (Fig. 11, 12). In the secretory phase, digitiform trichomes cells contained a dense cytoplasm, numerous dark organelles, osmiophilic drops and translucent vacuoles, and the outer cell wall was covered with a thick cuticle (Fig. 11). During further development, as a result of the accumulation of secretion, the periplasmatic space gradually enlarged, leading to a drastic retraction of the plasma membrane from the cell wall (Fig. 12).











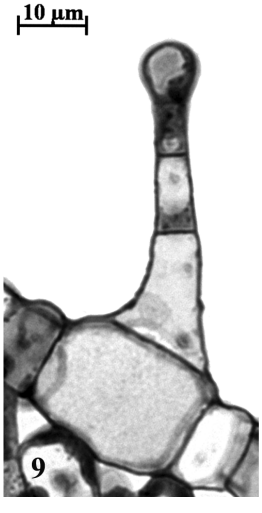


Fig. 3. LM micrograph of peltate trichome of *S. fruticosa* showing basal epidermal cell, very short stalk cell and large head of eight secretory cells.

Fig. 4. LM micrograph of short stalked capitate trichome subtype I.

Fig. 5. LM micrograph of short stalked capitate trichome subtype II.

Fig. 6. LM micrograph of short stalked capitate trichome subtype III.

Fig. 7. TEM micrograph of capitate trichome subtype III showing the secretory product –lipid droplet (*) inside the apical cell.

Fig. 8. LM micrograph of long-stalked capitate trichome subtype IV.

Fig. 9. LM micrograph of long-stalked capitate trichome subtype V.

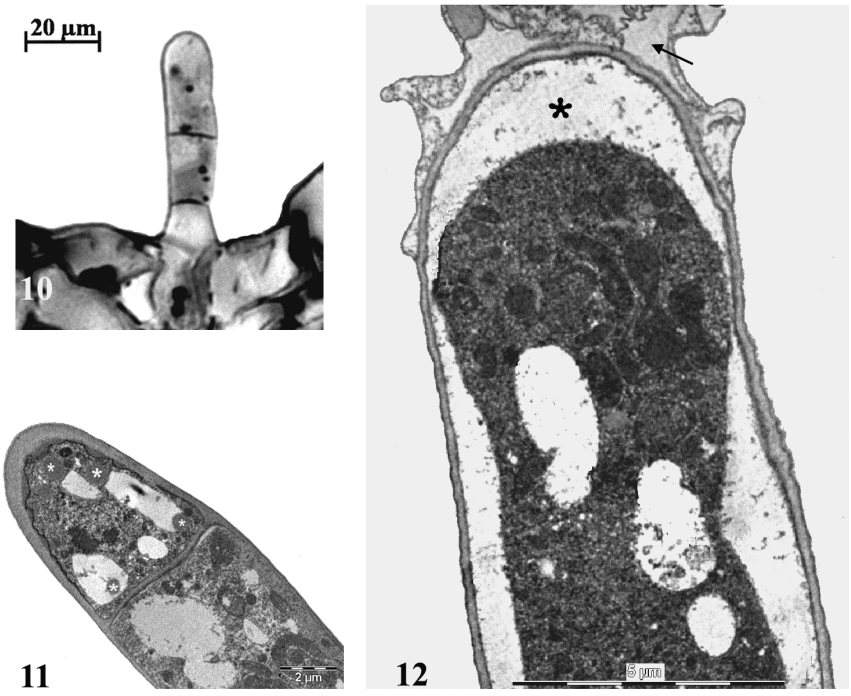


Fig. 10. LM micrograph of digitiform trichome of *S. fruticosa*.
Fig. 11. TEM micrograph of the apical cell of digitiform trichome. Note lipid droplets (*).
Fig. 12. TEM micrograph of the apical cell of digitiform trichome. Note periplasmatic space (*) and subcuticular space (↑) filled with secreted material.

DISCUSSION

The presence of non-glandular and glandular hairs is characteristic for Lamiaceae species (Werker et al., 1985). The distribution of non-glandular trichomes on the epidermis is a natural phenomenon in most angiosperms and could be associated with protection against foraging insects and airborne propagules of fungi (Fahn, 1967).

Glandular trichomes vary in morphology, structure and in number per unit area of the epidermis, among species and organs (Serrato-Valenti et al., 1997; Ascensao et al., 1999). Researchers have mostly found two main types on the leaves and flowers of different Lamiaceae species; peltate with a large secretory head, and capitate trichomes with a stalk and small head. Different variations have been observed in the studied species, in stalk length, head shape and number of cells, release of secretion products, etc.

Several *Salvia* species were studied for their glandular hair characteristics and essential oils composition. Different types of glandular trichomes were found in different species. The results obtained in this research showed that peltate, capitate and digitiform glandular hairs are present on the leaves of *S. fruticosa*.

Peltate trichomes are usually composed of a basal epidermal cell, a short, wide stalk cell and a large round head of several secretory cells, which could vary in number among *Salvia* species from four cells in *S. blepharophylla* (Bisio et al., 1999) and *S. verticillata* (Krstić et al., 2006) to six or eight cells in a single disc in *S. aurea* (Serrato-Valenti et al., 1997) and *S. officinalis* (Werker et al. 1985), or by 12-18 cells arranged in two concentric circles with four central and eight or more peripheral cells (Corsi and Bottega, 1999; Kamatou et al., 2006; Özkan, 2008; Baran et al., 2010; Kahraman et al., 2010). The present

study showed that *S. fruticosa* has peltate glandular trichomes consisting of a basal epidermal cell, a very short stalk cell with cutinized lateral walls and large round head of eight secretory cells arranged in a circle, as was observed in some of the studied *Salvia* species.

Capitate trichomes are also widespread in Lamiaceae, but they are more variable in stalk length and head shape. They generally consist of one to two stalk cell(s) and one to two cell(s) forming a rounded to pear-shaped secretory head (Werker et al. 1985). Variations in capitate trichomes were noticed, and Werker et al. (1985) for the first time classified capitate hairs as types I, II and III, according to their morphology and secretion mode. Following Werker et al. (1985), type IV capitate hairs were described in *S. officinalis* by Corsi and Bottega (1999). Several researchers divided capitate trichomes into only two types according to the dimensions of the stalk, the morphology of glandular head and the secretion process (Ascensao et al., 1999; Serrato-Valenti et al., 1997, Bisio et al., 1999). Serrato-Valenti et al. (1997) in *S. aurea* described the capitate trichome type 1 consisting of a short stalk and bicellular head, and capitate trichome type 2 consisting of 1-4 stalk cells, a narrow neck cell and globose unicellular head; similar types were found in *S. blepharophylla* (Bisio et al., 1999), *S. albicaulis, S. dolomitica* (Kamatou et al., 2007), etc. In our research we noticed two main types, short-stalked and long-stalked capitate trichomes, but further divided into five subtypes according to the number of stalk cells, the morphology and the number of the glandular secretory head cells and the secretion process. Short-stalked capitate trichomes subtype I have one stalk cell and a bicellular ovoid head, while subtype II have two stalk cells and a globoid glandular head, consisting of two cells. Subtype III of capitate trichomes have one stalk cell and one head cell. Long-stalked capitate trichomes subtypes IV and V have a unicellular spherical glandular cell, but these types of trichomes have a different number of stalk cells. Some other *Salvia* species also shown variations in the morphology of capitate trichomes, and been divided into more subtypes, such as *S. chrysophylla* with 4 subtypes (Kahraman et al., 2010), *S. officinalis* (Corsi et Bottega, 1999), or 3 types in *S. smyrnea* (Baran et al., 2010), *S. verticillata* (Krstić et al., 2006), and *S. argentea* (Baran et al., 2010). Because of the great variations in structure and size of capitate trichomes, and since they form part of the floral specialized properties for pollination, some authors emphasize their significance as a taxonomic character of the Lamiaceae (Navarro et El Oulalidi, 2000).

In the analyzed leaves of *S. fruticosa*, one specific type of glandular trichome was observed – digitiform trichomes. These trichomes are less abundant than peltate and capitate trichomes. A digitiform type of glandular trichome was reported for some Lamiaceae species, such as *Plectranthus ornatus* (Ascensao et al., 1999). These trichomes consist of three to four cells, in line, of similar diameter and approximately equal length (one basal, one to two stalk cells and one apical, head-like cell which does not develop a subcuticular space). There is no clear distinction between head and stalk cells. Talebi et al. (2012) found four types of digitiform trichomes in *Ziziphora tenuior* (one- to four-celled).

Ultrastructural analyses are important in trichome research because the relations among morphology, cytology and secretion processes can be established. Ultrastructural changes during the secretory phase of glandular trichomes were characterized by proliferation of the endomembrane system. Numerous mitochondria are connected with the high metabolic activity of the cell (Dunkić et al., 2007). Smooth ER, leucoplasts without thylakoids containing osmophilic drops, are characteristic organelles involved in terpene production, while dictyosomes are responsible for polysaccharide production (Cheniclet and Carde, 1985; Dunkić et al., 2007; Huang et al., 2008).

The analysis conducted and presented showed that *S. fruticosa* is very rich from the aspect of glandular trichome diversity and quantity. It is suggested that the secretions of the glandular trichomes may be involved in the chemical defense of the plants, or may guide insects, or act as floral rewards to pollina-

tors, but the specific function of each trichome type is not known (Ascensao et al., 1999). Detailed studies of the morphology, anatomy and ultrastructure may be useful in the interpretation of their functions. The abundant non-glandular hairs are involved in mechanical defense, and protect the plant from excessive transpiration and insolation (Corsi and Bottega, 1999).

Some authors (Baran et al., 2010) assumed that features such as abundance and the diversity of glandular trichomes on plant organs, the presence or absence of neck cells, the thickness of their side walls and the stalk length, could show variation according to the xeromorphic character of the plants. The abundant and diverse glandular trichomes and long stalks of the capitate trichomes of *S. fruticosa* show the xeromorphic character of the investigated plant species which, in its native environment, grows as part of the Maquis shrubland and is very drought-resistant.

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