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Dedicated to Prof. dr. sc. ZVONIMIR DEVIDÉ on the occasion of his 80th birthday

Xeromorphism of trichomes in *Lamiaceae* species

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The xeromorphic adaptation of epidermal cells of *Lamiaceae* plant leaves, the consequence of their adaptation to an arid habitat, was investigated. These xerophytic species inhibit transpiration in different ways, depending on the number, the form and the position of trichomes, whether they are dead hairs or live glandular structures. The *Salvia* genus is characterized on one hand by multicellular, uniseriate and scaled dead hairs and on the other hand there are several types of glandular structures, generally with voluminous heads. Lavender and rosemary (*Lavandula angustifolia* Mill. and *Rosmarinus officinalis* L.) have well-developed ramified forms of dead hairs with different ends and different levels of flexibility. The representatives of the *Satureja* genus have cone-shaped trichomes, showing predominant glandular structures (with unicellular base, unicellular stalk and twelve-cell head) and a slight structural variation. While glandular trichomes are frequent in this genus, non-glandular trichomes are rare and few. In *Salvia*, although no glandular trichomes are developed, it has numerous simple, uniseriate, multicellular hairs. This is how the leaf epidermis, by xeromorphic changes, ensures the preservation of the entire plant.

Key words: *Lamiaceae*, xeromorphic, glandular trichomes, hairs

Introduction

The trichomes are mostly developed out of one young epidermal cell, whether it grows only unicellular hairs or also dividing, multicellular hairs. Regarding the shape, there are seven main non-glandular and glandular trichomes: papillae, simple or unbranched (short and long); two to five-armed stellate, scales, branched and some specialized types of trichomes (METCALFE and CHALK 1985).

Apart from the shape, trichomes also differ in their functions. Non-glandular trichomes are always composed of dead cells; they are normally filled with air and are white because of the total reflection of light. These hairy layers prevent sunrays from falling directly on the epidermis, which, as a consequence, heats less, and transpiration slows down. Glandular trichomes are usually called only glands. If secretions remain within the plant tissue,

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they are called internal glands (METCALFE and CHALK 1985), while on the other hand; external glands squeeze the secretion out to the surface. They consist of: one basal cell, a single stalk composed of one or several cells and a head, consisting of one or more glandular cells (RUDALL 1994). Almost all glandular trichomes have endodermic cells under excretory cells. They prevent the penetration of secreted matters back into the plant through apoplasts (FAHN 1990). Numerous glandular trichomes are found for example in many olfactory plants, especially of the *Lamiaceae* species (ANTUNES et al. 1997). The walls of these glandular cells are differentiated into the cuticle, cuticular layer, pectin, and cellulose layers (FAHN and CUTLER 1992). Golgi's bodies and cisternae of ER are enlarged during secretion phase. Glandular cells contain numerous mitochondria, while the number of other organelles varies according to the type of secretion. Secretion takes the shape of a drop, first within the protoplasm, and then, as the drop grows, it is squeezed out through the cell wall. In this process, the secretion is collected between the cellular layer and cuticle, in the so-called subcuticular space. In some cases this space stays small, indicating the existence of pores in the cuticle. In other cases the process of secretion ends by the death of the cell, as, due to the large quantity of oil, the cuticle first grows in height and at the end is torn apart (FAHN 1990). Different types of glandular trichomes found with the species of *Lamiaceae* family include unicellular and multicellular stalks with up to five cells in *Salvia sp.* and unicellular or rarely multicellular heads, as in *Melissa officinallis* and *Salvia sp.* (WERKER et al. 1985).

The importance of the morphology and anatomy, as well as the oil content, of the glandular cells, has been proposed over the last years as the basic element for the taxonomic classification of a separate *Satureja* group species, which would change the existing position of genera within families (HANILDOU et al. 1990).

Material and methods

Plant material was collected from several different locations. *Salvia officinalis* L.was picked in Split, on the southern slopes of Marjan, while *Lavandula angustifolia* Mill. and *Rosmarinus officinalis* L. were also collected in the Split district – Spinut. *Salvia bertolonii* Vis., *Satureja montana* L., *Satureja cuneifolia* Ten. and *Satureja subspicata* Bartl. ex Vis. come from Kozjak.

Research was carried out on the representatives of *Lamiaceae* family, the chosen leaves being preserved in 50% ethanol. Freehand cross sections and/or epidermal peels and scrapes were taken and put in a drop of glycerol. Some of the preparations were dyed with Safranine to provide evidence of the existence of cuticle. Analysis and photographing of the preparations were carried out on the Opton Axioscop MC 63 A microscope.

Results and discussion

The species investigated belong to the *Lamiaceae* family, which encompasses genera whose species are often season plants or simples. The whole family is also characterized by aromatic scent because all the plants have glands containing essential oils. Arid habitat

plants are generally backward in growth, have emphasized veins and hypodermis supporting elements, thickened cuticle and dense indumentum (FAHN 1990).

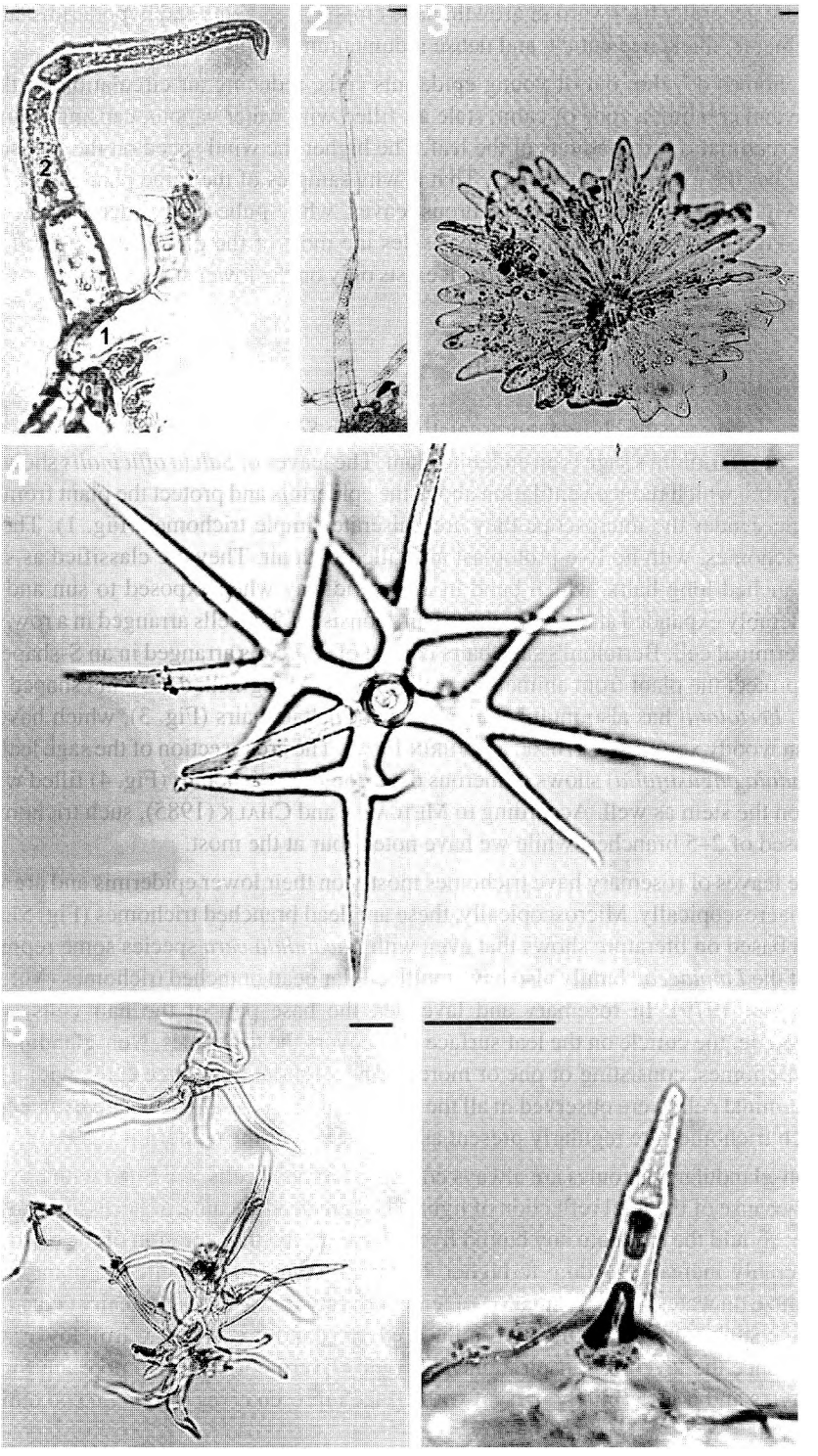
Trichomes develop out of young epidermis cells, reducing air circulation on the leaf surface and creating a zone of calm, stale air filled with water vapour, causing changes in the microclimatic surroundings of the leaf. The higher the wind speed on the leaf surface, the quicker the evaporation of water. That is why samples of the same plant species in regions with higher humidity have glabrous leaves, while pubescence increases as aridity grows. Pubescence is noted on both leaf sides ine most of the plants investigated, while with rosemary (*Rosmarinus officinalis*) it exists only on the lower surface of the leaf (FAHN and CUTLER 1992).

Non-glandular trichomes

Two species are the chosen representatives of the *Salvia* genus; sage grows over a wide area, while Bertoloni's sage is an endemic plant. The leaves of *Salvia officinalis* show dense pilous hairs, which reduce ventilation above the epidermis and protect the plant from direct sunshine. Under the microscope they are uniserate simple trichomes (Fig. 1). These are dead trichomes, with no live protoplast and filled with air. They are classified as simple, non-branched long hairs, which bend in a specific way when exposed to sun and wind. Considerably expanded at the base, these hairs consist of 2–5 cells arranged in a row, with a sharp terminal cell. Bertoloni's sage hairs consist of 3–7 cells arranged in an S-shape at the top to protect the plant from animals as well (Fig. 2). Along with dead hairs shaped in this way, *S. bertolonii* has also multicellular scales or peltate hairs (Fig. 3), which have been noted in woody xerophytes (BEZIĆ and JURIN 1999). The cross section of the sage leaf blade (*Lavandula angustifolia*) shows numerous dead complex trichomes (Fig. 4) filled with air, noted on the stem as well. According to METCALFE and CHALK (1985), such trichomes are composed of 2–5 branches, while we have noted four at the most.

The leaves of rosemary have trichomes mostly on their lower epidermis and are visible even macroscopically. Microscopically, these are dead branched trichomes (Fig. 5). Information based on literature shows that even with *Lavandula vera* species some representatives of the *Lamiaceae* family also have multicellular dead branched trichomes (METCALFE and CHALK 1979). In rosemary and lavender, the base part of the hair cells is more cutinized, ie. the cuticle on the leaf surface also covers the trichomes. Non-glandular elongated trichomes, consisting of one or more but never more than three cells, with a sharpened terminal cell, were observed in all the species of the *Satureja* genus investigated (Fig. 6). Such trichomes are regularly present as a convexity of the epidermis.

Non-glandular trichomes are always composed of dead cells, are filled with air and are white because of the total reflection of light. They are dead because of necessity and not by chance: should they contain any humid live substance, the transpiration of the plant would considerably increase, leading to higher degree of evaporation, while the plant needs to economize on water by the regulation of temperature. Moreover, these »hairy coats« do not allow the sun's rays to fall directly on the epidermis and it gets less warm, lowering as a consequence the level of transpiration. This type of xeromorphism is important for many xerophytes and it is definitely present with all the represenatives of *Lamiaceae* family investigated.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Glandular trichomes

Freehand sections of both sage species show glandular trichomes as well. *Salvia officinalis* has four types of glandular trichomes: short-stalked with a unicellular head, long-stalked with a unicellular head, short-stalked with a multicellular head (Fig. 7) and two-stalked with a unicellular head. Glandular scales with a voluminous head have also been noted (Fig. 8). Such glandular scales were observed by LÄNGER (1997) in other representatives of the *Salvia* genus. Being placed between uniseriate, multicellular trichomes and in the recess between two epidermal cells, they are well protected. After the knobbed part of the gland has cracked, the remaining glandular structure takes the shape of a little basket.

The glandular trichomes of lavender are knob-shaped, are placed on the surface of epidermis and covered with higher and more numerous non-glandular trichomes. Glandular trichomes of rosemary are knob-shaped, short-stalked with a unicellular head.

The leaf blade of the species *Satureja montana, Satureja cuneifolia* and *Satureja subspicata* has multicellular glandular trichomes with a unicellular base, unicellular body and twelve-cellular apex. Based on the investigation of the structure and ontogeny of *Calamintha mentifolia* species glandular structures (HANILDOU et al. 1990), three types of glandular trichomes have been described. The first type is described as glandular scales with a multicellular head, found in h all the hitherto investigated species of the *Lamiaceae* family, although with different numbers of head cells. The type found with *Calamintha mentifolia* has a twelve-cell head and has been described in relation to the leaves of the *Origanum* genus, and *Majorana syriaca* L. (Raf.), *Melissa officinalis* L., *Salvia officinalis* L., *Salvia fruticosa* Mill., *Satureja thymbra* L. species. An eight-cell head appears with *Mentha piperita* L. species and an eighteen-cell head with *Micromeria fruticosa* L. (WERKER et al. 1985). Glandular scales with a twelve-cell head, of which four are the head base cells and other eight are peripheral, can be found within all the investigated *Satureja* species. The head cells discharge essential oils into the subcuticular space, created by the separation of the cuticle from the terminal walls of the head cells (Fig. 9).

The thick layer of trichomes considerably increases leaf reflection for all the wavelengths of solar radiation and reduces radiation absorption, which then protects the leaf from overheating. In this case, the microclimatic conditions of the leaf are characterized by a lower temperature than the environment, thus reducing transpiration (FAHN and CUTLER 1992).

Glandular trichomes are placed in the recesses between epidermal cells. These epidermal cells are elongated, forming a compact wall around a knob-shaped gland, and are capable of squeezing out their secretions through the cellulose layer of the secretorial cell walls

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Fig. 1. *Salvia officinalis*, non-glandular hair: 1-base, 2-stalk cell, 3-terminal cell (Bar 10 μm)

Fig. 2. *Salvia bertolonii*, non-glandular multicellular hair (Bar 10 μm)

Fig. 3. *Salvia bertolonii*, non-glandular multicellular scale (Bar 10 μm)

Fig. 4. *Lavandula angustifolia*, non-glandular branched hairs (Bar 10 μm)

Fig. 5. *Rosmarinus officinalis*, non-glandular branched trichomes (Bar 10 μm)

Fig. 6. *Satureja montan*, non-glandular elongated trichome (Bar 10 μm)

Fig. 7. *Salvia officinalis*, glandular trichome with multicellular head (Bar 10 μm)

Fig. 8. *Salvia bertolonii*, glandular trichome 1-subcuticular space, 2-subcuticular contents, 3-cuticle, 4-epidermis (Bar 10 μm)

Fig. 9. *Satureja montana*, cross-section of glandular trichome 1-cuticle, 2-epidermis, 3-broken headed gland, 4-palisade parenchyma, 5-oil drops (Bar 10 μm)

(FAHN 1990). When the subcuticular section is filled with secretion or when the subcuticular membrane of the epidermal cells cracks, they no longer make a compact wall but separate themselves from the base part of a gland (Fig. 9). There is a difference between the epidermal cells of a knob-shaped gland in the *Satureja montana* and the *Satureja cuneifolia* species. There are 12–18 epidermal cells around the glands of *Satureja montana*, but only 10–13 around those of *Satureja cuneifolia*. Similar values were obtained by BOSABALIDIS (1990) with the *Satureja thymbra* species, where the number of epidermal cells surrounding a glandular trichome ranges from 13 to 15.

In the course of investigation we have noted a difference in the size of recesses housing glandular trichomes. The position and the relationship between dead and living trichomes are always proportional. The deepest recesses are found in savory, there being only a small number of dead trichomes, somewhat less deep in Bertoloni's sage because the number of dead hairs is bigger, while in garden sage there are almost no recesses, due to the biggest number of dead woolly –feathery hairs which reduce transpiration and also protect glandular trichomes.

In the species investigated all the types of hair cells are the reflection of xerophytic adaptation. Apart from the protective and reproductive role, the xeromorphism of the described epidermal cells and/or growths is, in our opinion, above all related to the physiological function of the prevention of transpiration.

It can be stated that in any future research, knowledge of the anatomy of the hair cells of the *Lamiaceae* family will make possible the explication of their physiological role and of new taxonomic relationships within the genera.

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