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STRUCTURE AND MODE OF SECRETION OF GLANDULAR TRICHOMES IN CLARY SAGE (*SALVIA SCLAREA* L.) (**)

Riassunto — *Struttura e modalità di secrezione dei tricomi ghiandolari di* Salvia sclarea *L.* Sono state studiate la morfologia, distribuzione e modalità di secrezione dei tricomi ghiandolari presenti sulle foglie ed infiorescenze di *Salvia sclarea* L., mediante l'uso della microscopia ottica ed elettronica a scansione. Sulla base delle differenze istochimiche e morfologiche sono stati evidenziati un tipo di tricomi a secrezione idrofila e tre tipi a secrezione lipofila. I tricomi idrofili sono piuttosto corti e di tipo capitato; i tricomi lipofili sono di tipo peltato e capitato. Questi ultimi sono stati ulteriormente suddivisi, in base alle caratteristiche morfologiche, in tipo I (caratteristico della plantula e degli stadi giovanili della pianta) e tipo II (caratteristico dell'infiorescenza). La secrezione idrofila è composta di mucillaggini, mentre quella lipofila soprattutto di olii essenziali. Nei peli peltati e nei capitati di II tipo è presente anche una componente idrofila. L'infiorescenza è la parte della pianta più ricca in tricomi di tipo lipofilo e quindi la più ricca in olii essenziali.

Abstract — The morphology, distribution and modes of secretion of glandular trichomes found on the leaves and inflorescence of *Salvia sclarea* L. were studied using Light and Scanning Electron Microscopy.

On the basis of histochemical and morphological differences, one type of trichome with hydrophilic secretion and three types with lipophilic secretion were identified. The hydrophilic trichomes are short and capitate; the lipophilic ones are either peltate or capitate. These latter have been further subdivided into type I (characteristic of seedlings) and type II (characteristic of the inflorescence). The hydrophilic secretion is composed of a mucillage-like substance, while the lipophilic secretion is composed mostly of essential oils.

In peltate hairs and in type II capitate trichomes, a hydrophilic component is also present. The inflorescence is the part of the plant which is the richest in lipophilic glandular trichomes and therefore in essential oils. The leaves and inflorescence show different types of glandular hairs; this is consistent with the different oil composition in the two parts of the plant.

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Key words — Labiatae - Salvia sclarea - glandular trichomes - morphology - secretion.

Introduction

Some species of the *Labiatae* have glandular trichomes which are responsible for the characteristic scent given off by almost all these plants (Metcalfe and Chalk, 1950; Uphof and Hummel, 1962; Fahn, 1980). The secreting structures of some of them have been already studied ultrastructurally (Amelunxen, 1964, 1965; Schnepf, 1972; Bosobalidis and Tsekos, 1982), chemically (Amelunxen *et al.*, 1969; Kulakovskaya, 1975; Werker *et al.*, 1985 a, b, c), anatomically and histochemically (Then and Verzar Petri, 1969; Shevchenko and Denisova, 1971; Picci and Clementi, 1974; Verzar Petri and Then, 1975; Bruni and Modenesi, 1983; Modenesi *et al.*, 1984).

Clary sage (*Salvia sclarea* L.) grows wild in the Mediterranean area, but is also cultivated for its essential oils content. This plant is, in fact, commonly used in folk medicine as an antiseptic, antispasmodic, astringent, balsamic, emmenagogue, stimulant and stomachic, and in the industry chiefly in the production of cosmetics and spirits (Garnier *et al.*, 1961; Paris and Moyse, 1971; Duke, 1985).

This paper was designed to study the morphology and distribution of glandular trichomes on the inflorescence and leaves of Clary sage. The trichomes were observed at different developmental stages, in order to reconstruct the main phases of formation, storage and release of the secretion.

Materials and methods

Light and Scanning Electron Microscopy observations were carried out on seedling leaves and on leaves of two year plants. Moreover, inflorescence was observed before blossom, when the single flowers were no longer than 5 mm. The plants were cultivated at the Botanical Garden of Florence and gathered over a two year period (1984-1986).

Light Microscopy

Small fresh pieces of the above plants were stained with Toluidine Blue O (T. B.) 1% pH 4.4 (O'Brien and McCully, 1981) for poly-

saccarides. Nile Blue sulphate (N. B. S.) was used for lipophilic substances (neutral lipids, essential oils and cutin) (JENSEN, 1962). These lipophilic substances appeared pink under standard conditions and bright yellow under fluorescent blue light (460 nm). Sudan Black B (S. B.) and OsO_4 were also used for lipophilic substances staining.

Furthermore small pieces of material were fixed by glutaraldehyde in phosphate buffer (pH 7.4), embedded in glycomethacrylate and cut into 1-2 μm thick sections. These were then stained as follows: Periodic Acid Shiff's (PAS) reaction for the general location of polysaccarides (JENSEN, 1962); Calcofluor for cell wall and extracellular mucillages (O'BRIEN and MCCULLY, 1981); Ruthenium Red (R.R.) for pectic-like substances (JENSEN, 1962); Coomassie Brilliant Blue (C. B. B.) for protein (FISHER, 1968) and fluorescamine for glycoproteins (BRUNI, 1979).

Scanning Electron Microscopy (S. E. M.) (Jeol $JSMU_3$)

Small pieces, fixed as above, were first dehydrated with acetone, followed by critical point drying and finally coated with gold.

OBSERVATIONS

Preliminary tests (BINI MALECI, 1984) showed that glandular trichomes of *S. sclarea* were different as regards their morphology, distribution and secretion. Concerning the last one, the histochemical staining allowed to identify two different types of glandular trichomes:

1) trichomes with hydrophilic secretion, which stained with T. B., PAS, etc.;

2) trichomes with lipophilic secretion, which stained with N.B.S., S.N. and OsO_4.

For each group the morphology, distribution and secretion mode were studied.

1) *Hydrophilic substance secreting trichomes*

Morphology and distribution - Short capitate hairs no longer than 45 μm (Figg. 1 a, b, c, d). They consist of one basal epidermal cell, a stalk cell and a neck cell, all widely vacuolized, and a distal rounded secretory cell.

A great many hydrophilic trichomes are found on the whole ex-

posed plant. Therefore they are present on the cotyledons, stems and leaves, where they are generally arranged in rows along the veins. On the adaxial surface of the leaf, they are the only type of glandular trichomes. Such trichomes are also distributed on the whole inflorescence, particularly on the bracts.

Hydrophilic trichomes are characteristic of the first stage of the ontogenesis. For instance, buds 1-2 mm long, show completely formed and functioning trichomes. Young leaves, 1-2 cm long, present numerous functioning trichomes; mature ones often have a wrinkled and inactive apical cell. The older part of the plant, e.g. the leaves at the end of summer, have no trichomes at all.

Principal phases of the secretion process - At an early stage the secretory cell presents a dense cytoplasm with few, small vacuoles and an evident nucleous. During the initial secretion phase, the number and size of the vacuoles grow. Granules intensely stained by PAS, Calcofluor and R.R. are found along the external wall.

In the next stage the granules disappear and the cytoplasm is removed from the cell wall, forming an extracytoplasmic space. This one is filled with material having the same stain sensivity as the granules (Fig. 1 b).

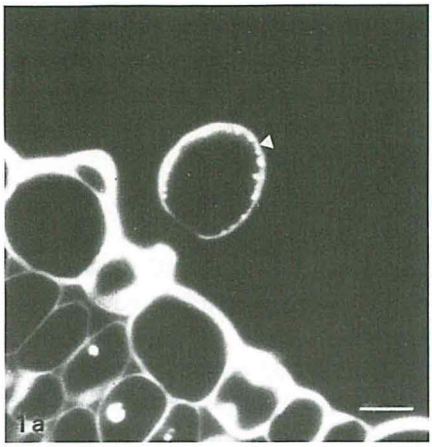
In an advanced stage of the secretion, small infraparietal spaces are formed (arrow in fig. 1 b). These stain in the same way as the extracytoplasmic substances. The accumulated material escapes through the cell wall as evidentiated by S.E.M. (Fig. 1 c). When the cell is completely emptied, it looks wrinkled (Fig. 1 d).

2) *Lipophilic substance secreting trichomes*

These trichomes can be morphologically divided into two types: peltate and capitate hairs. The latter can be further subdivided into

Fig. 1 - Hydrophilic substance secreting trichomes. 1a) Early stage of secretion. Many fluorescent granules (arrow) along the external wall of the secreting cell. Calcofluor ×830. Bar = 10 μm. 1b) Advanced stage of secretion. Wide extracytoplasmic space (big arrow) filled with PAS positive material. On the right, infraparietal space (small arrow) filled as above. a) secreting cell; b) neck cell; c) part of the stalk cell; basal epidermal cell not visible in this section. PAS ×1330. Bar = 10 μm. 1c) Advanced stage of secretion. Small amounts of material on the surface of the secreting cell, interpreted as secretion. S.E.M. ×1500. Bar = 10 μm. 1d) End of secretion. Wrinkled secreting cell. S.E.M. ×1500. Bar = 10 μm.

Fig. 2 - 2a) Adaxial surface of the leaf: many large non glandular trichomes and small hydrophilic substance secreting trichomes (arrow). S.E.M. ×75. Bar = 100 μm. 2b) Abaxial surface of the leaf: some hydrophilic substance secreting trichomes (small arrows) and a large peltate hair (big arrow). Non glandular hairs cover most of the leaf surface. S.E.M. ×75. Bar = 100 μm.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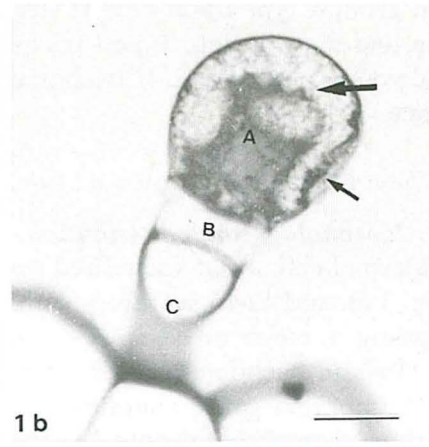

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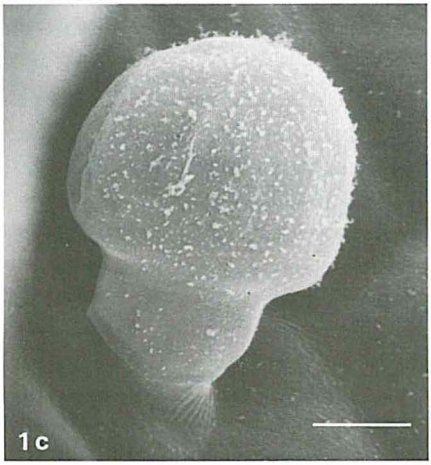
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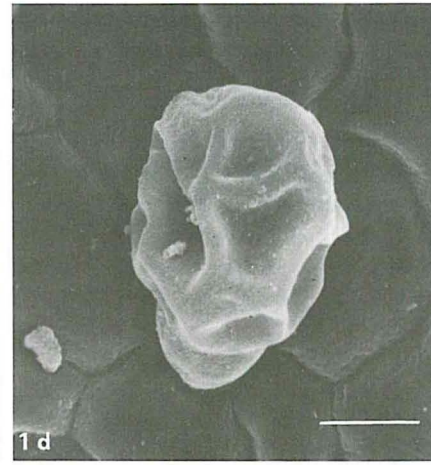
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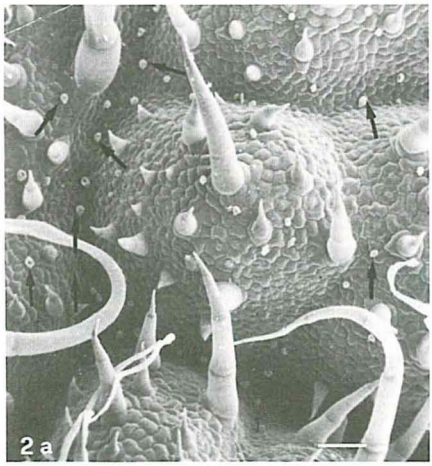
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two groups, type I and type II, according to their morphology, secretion and distribution. Type I trichomes are present only on seedlings and young plants; type II trichomes are present only on the inflorescence.

Peltate trichomes

Morphology and distribution - They are composed of a basal epidermal cell, a flat vacuolized neck cell, with highly cutinized walls (Fig. 3 a), and 12-16 secretory cells. These are attached to each other forming a cover on the neck cell (Fig. 3 a).

Peltate trichomes are present on the abaxial surface of the leaf: each intervein space contains one or two trichomes (Fig. 2 b). Few of them, composed of only 4 secretory cells, are found on the abaxial surface of the cotyledon. Moreover, they are present on the inflorescence, especially on the corolla.

The differentiation of these glands follows the one of hydrophilic trichomes and does not occur at the same time in all the peltate trichomes. In fact young leaves present mature trichomes as well as trichomes at earlier stages of development (Fig. 4).

Principal phases of the secretion process - At the beginning of secretion the apical cells, all at the same developmental stage, present dense cytoplasm and numerous small vacuoles (Figg. 3 a, c). The secretion accumulates in a subcuticular space formed from the detachment and rising of the outer part of the secretory cells walls (Fig. 3 a). According to the staining reactions S.B. and PAS the detached part of the wall includes the cuticle and a thin pectic inner layer.

In fresh samples, trichomes stain brightly with S.B., OsO_4 and N.B.S. (Fig. 3 b). In the embedded sectioned material they do not stain with such dyes, probably because the lipophilic part of the secretion dissolves during the embedding process. However in the subcuticular space a network, which stains with C.B.B. (Fig. 3 c), Fluorescamine and PAS is visible. It is particularly thick and evident in the young peltate hairs (Figg. 3 a, c), while in older ones, with large subcuticular space, is thinner, with wider meshes. Possibly it bounds, in vivo, the lipophilic part of the secretion. The presence of such a network in the subcuticular space is also confirmed by S.E.M. (Fig. 3 d).

At the end of the secretion process, the subcuticular space looks like a large vesicle; the secretory cells, with their atrophied

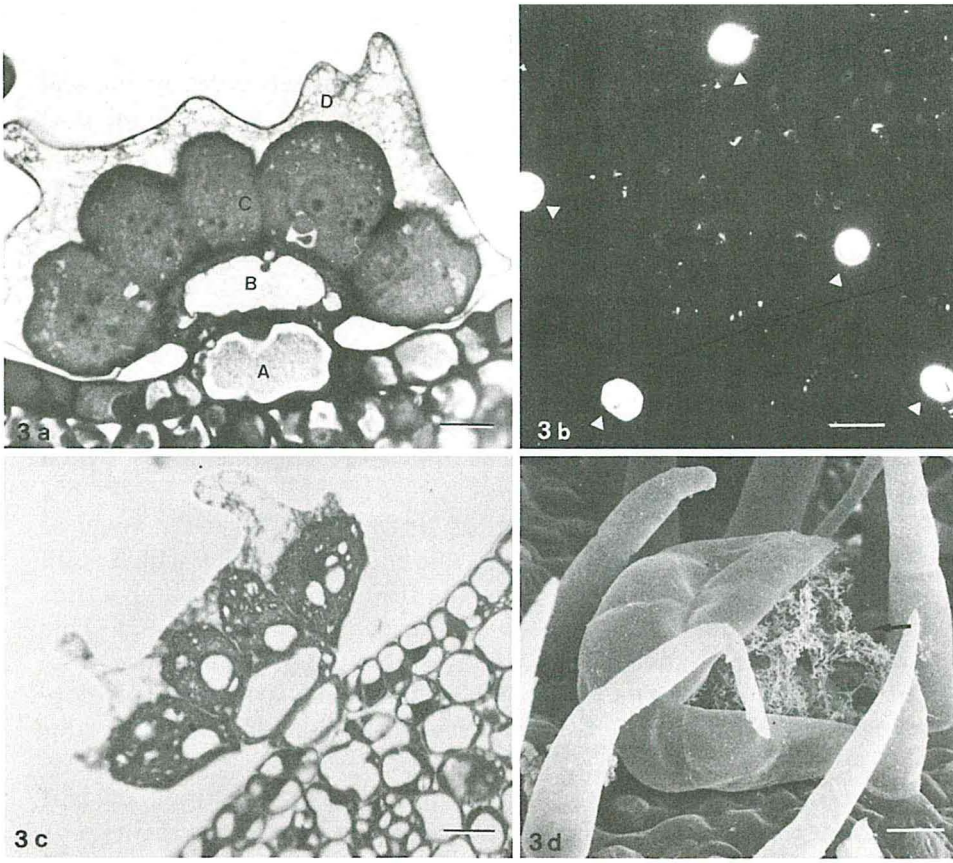


Fig. 3 - Peltate trichomes. 3a) Large hair at the beginning of secretion. a) basal epidermal cell; b) neck cell; c) secreting cells; d) subcuticular space. Note the network stained with T.B. ×830. Bar = 10 μm. 3b) Part of the abaxial surface of young leaf. Some peltate hairs N.B.S. stained in highly fluorescent way (arrowed) ×85. Bar = 100 μm. 3c) Young trichome; network of hydrophilic material stained C.B.B. specific. ×830. Bar = 10 μm. 3d) Hydrophilic network (arrow) within young peltate hair: cuticle slip open along a prearranged line. S.E.M. ×450. Bar = 20 μm.

cytoplasm, adhere to the neck cell and occupy the basal part of the vesicle. The secretion remains in the subcuticular space for a not determined time. In many cases, anyway, an aperture, parallel to the epidermal surface, is visible on the basal part of each gland (Fig. 3 d).

Capitate trichomes of the seedlings (Type I)

Morphology and distribution - Capitate trichomes ± 140 μm long (Fig. 5 a), composed of one basal epidermal cell, 2-3 large and elon-

gated stalk cells, a neck cell, with highly cutinized outer walls, and a secreting apical cell. This one is rather round at its distal part and cylindrical at the proximal part (Fig. 5 a).

These trichomes are typical of the early developmental stages of the plant and some still remain on the leaves of 1-year old plants. They completely disappear in the adults. Usually, they are distributed on the abaxial surface of the leaf as well as on the abaxial surface of the cotyledon. The numerous trichomes found on the hypocotyl are characterized by a very long stalk composed at least of 5-6 cells.

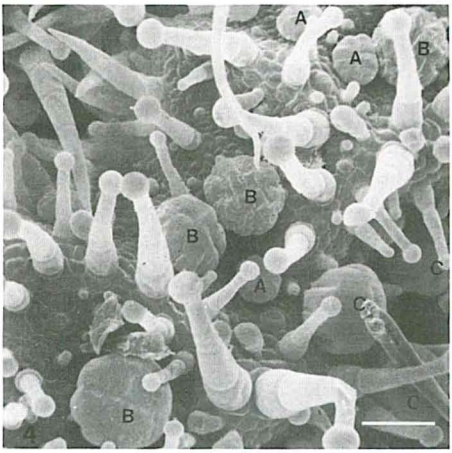
On the buds the differentiation process of these trichomes takes place at the same time as that of the short capitate hairs which secrete hydrophilic substances.

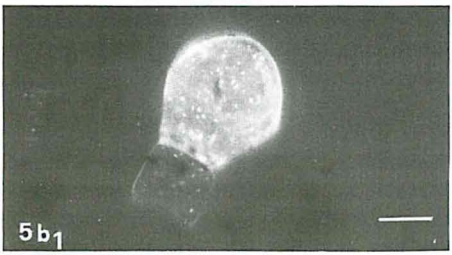
Principal phases of the secretion process - At an early stage of development, the secretory cell presents minute granules which stain with N.B.S. (Fig. 5 b1). Afterwards, the first drop of secretion settles into a small subcuticular space at the cell apex (Fig. 5 b2). This drop increases as the secretion process continues and a large subcuticular space is formed (Fig. 5 b3). Trichomes with this developmental stage have been treated with glacial acetic acid, in order to solubilize the essential oils (JOHANSEN, 1940). Most of the secretion solubilized immediatly, but an apical drop remained evident and required at least 15 minutes of treatment before solvability was reached. The secretion is possibly discharged through the cuticle as no aperture was found. At the end of the secretion process, the whole distal wall of the apical cell collapses and the latter assumes a bowl-like shape with a small bulge at its center (Fig. 5 c).

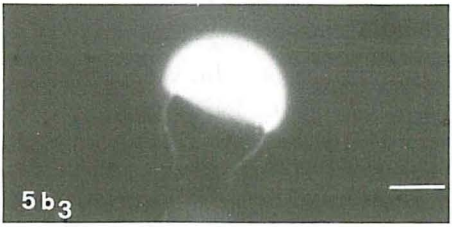
Capitate trichomes of the inflorescence (Type II)

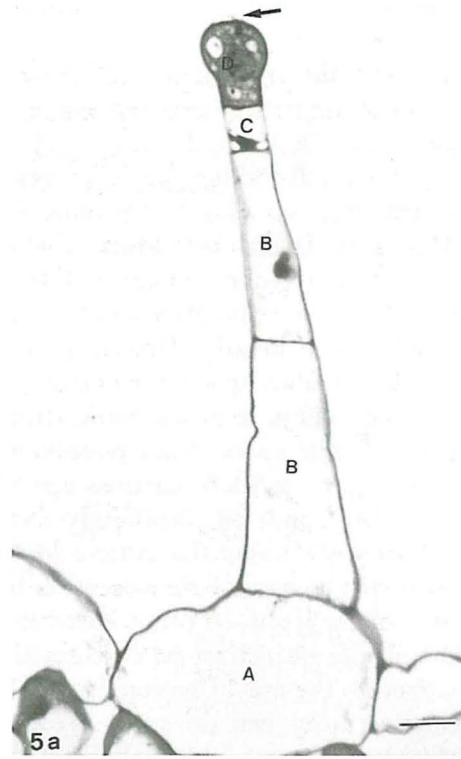
Morphology and distribution - Capitate hairs, ranging from 50 μm to 150 μm height, consist of one basal epidermal cell, rarely two, a large stalk cell, a neck cell with highly cutinized walls and a rather large, round secretory cell (Fig. 6 a). This one presents often, in the small trichomes, a narrow basal part so that the whole cell resembles a lightbulb (Figg. 6 b, c).

This type of trichomes is distributed over the whole inflorescence, including the axis. On the basal part of the external surface of the calix, they have a very large size and are most densely grouped (Fig. 7). They are less numerous on the corolla.









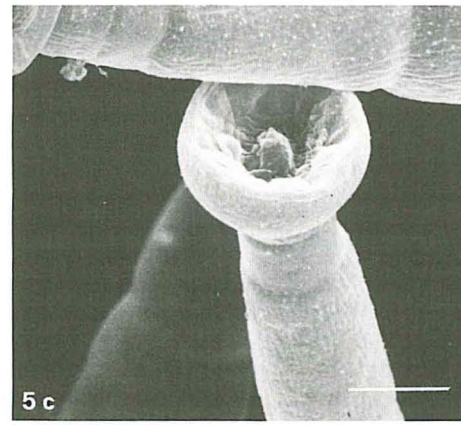


Fig. 4 - Bud: abaxial surface of the leaf. Peltate hairs at various developmental stages: a) very young trichomes with only 4-8 apical cells; b) apical cells begin to secrete and form subcuticular space; c) secretory cells with a large subcuticular space filled with secretion; d) some unicellular protuberances: the birth of the peltate trichome. Secreting hydrophilic and type I capitate trichomes are also present. S.E.M. ×225. Bar = 50 μm.

Fig. 5 - Type I capitate trichomes. 5a) Young trichome; a) basal epidermal cell; b) stalk cells; c) neck cell; d) secreting cell with small subcuticular space (arrow). T.B. ×830. Bar = 10 μm. 5b) Subsequent stages of development: 5b1) small granules in apical cell cytoplasm; 5b2) initial small subcuticular space; 5b3) maximum secretion storage area in subcuticular space. N.B.S. ×830. Bar = 10 μm. 5c) End of secretion; distal wall has collapsed: small central bulge remains. S.E.M. ×1500. Bar = 10 μm.

The differentiation of these trichomes follows the one of hydrophilic hairs; nevertheless on 2-3 mm long buds, they have completely developed and show a subcuticular space filled with secretion.

Principal phases of the secretion process - A lipophilic secretion, which stained with N.B.S. and S.B. is present in these trichomes (Fig. 6 d). At an early stage, the secretory cell has cytoplasm with a great many small vacuoles. A small thickening, stained with C.B.B., Fluorescamine and PAS appears at the apex of this cell before secretion storage begins. This stage is followed by the development of a subcuticular space formed by the outer layers of the secreting cell wall (Figg. 6 b, c). Some filaments and the basal area in the subcuticular space react positively to both C.B.B. (Figg. 6 a, b) and PAS (Fig. 6 c). Such features are hardly recognizable when the subcuticular space is completely expanded.

In some cases the cuticle looks slightly deflated (Fig. 6 e), suggesting that part of the secretion left the subcuticular space through the cuticle itself. In other cases the cuticle looks broken, suggesting the whole secretion was released. The broken cuticle remains attached to the apical secretory cell (Figg. 6 f, 7). After secretion release, the secretory cell does not present any cell degeneration (Fig. 6 f). However, in very old trichomes, this cell is affected by a degenerating process, and there occurs the simultaneous appearance of large lipidic drops.

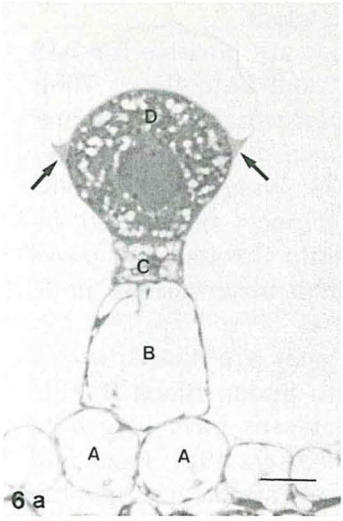
Discussion

The morphology of glandular trichomes — peltate and capitate — found in *S. sclarea* agrees with the records about the whole Labiatae family in the literature (Metcalfe and Chalk, 1950; Uphof and Hummel, 1962; Fahn, 1980).

The present classification of the *S. sclarea* glandular trichomes was first based on the histochemical type of its secretion. This

Fig. 6 - Type II capitate trichomes. 6a) and 6b) stained with C.B.B.; 6c) PAS reaction. Arrows indicate the non lypophilic part of secretion. a) basal epidermal cell; b) stalk cell; c) neck cell; d) secreting cell. ×830. Bar = 10 μm. 6d) Part of the calix. Highly lypophilic content of secreting cells N.B.S. stained. Note varying sizes of cells. ×200. Bar = 50 μm. 6e) Apical part of secreting cell: cuticle slightly flabby. S.E.M. ×3750. Bar = 2 μm. 6f) End of secretion: broken cuticle attached to secreting cell. T.B. ×830. Bar = 10 μm.

Fig. 7 - Basal part of calix: numerous type II capitate trichomes. Note broken cuticles (arrow). S.E.M. ×75. Bar = 100 μm.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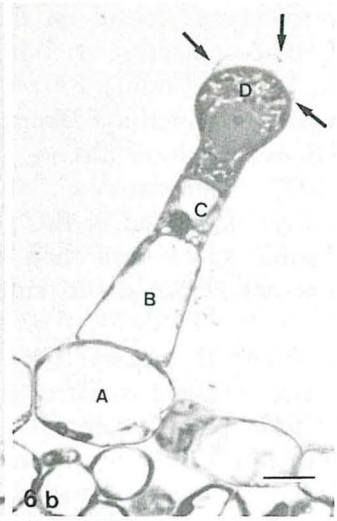
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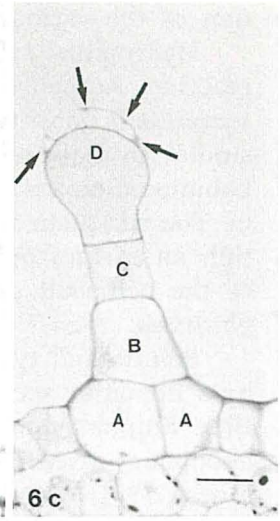
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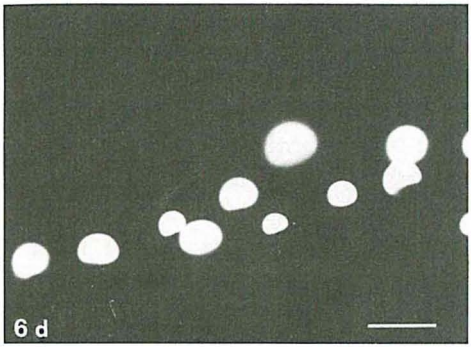
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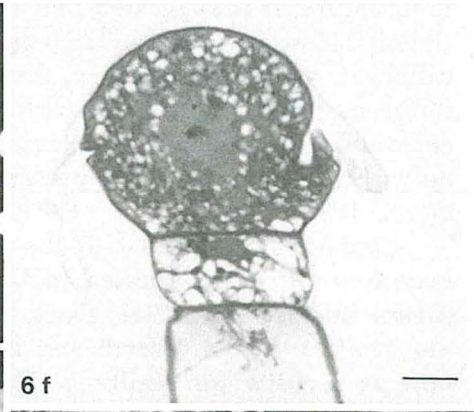
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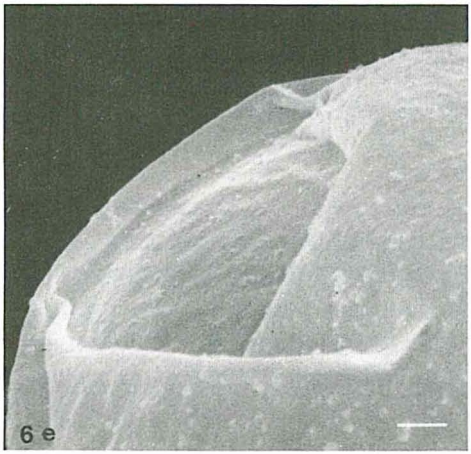
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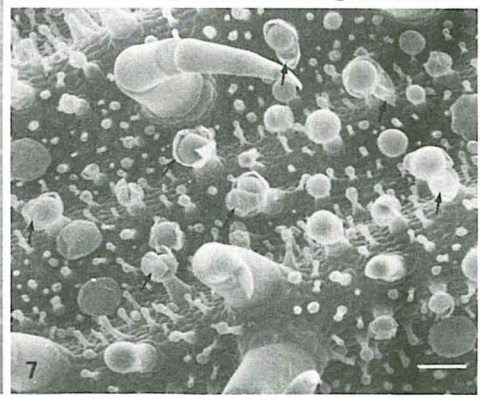
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parameter was then correlated with the morphology and distribution of the various trichomes found on the plant.

Hydrophilic substance secreting trichomes are positive for PAS reaction, Ruthenium Red, Toluidine Blue O and Calcofluor. Their secretion is constituted of a mucillage-like polysaccaride. Trichomes similar to those of *S. sclarea* have already been described in other Labiatae (SCHNEPF, 1972; MODENESI *et al.*, 1984; WERKER *et al.*, 1985 b). The secretion is first deposited at the periphery of the cell within an extracytoplasmic space, and then exits through the pores of the cell wall. SCHNEPF (1972) made similar observations in *S. glutinosa.*

Peltate and type I and II capitate trichomes are characterized by a lipophilic secretion, stained specific with Sudan Black B, Nile Blue Sulphate and OsO_4. Since chemical analyses have identified aboundant essential oils in *S. sclarea* (GARNIER *et al.*, 1961; PARIS and MOYSE, 1971; WERKER *et al.*, 1985 c) and these oils are clearly lipophilic in nature, it is suggested that this secretion is made up of essential oils. However in these trichomes the oil composition is probably different, as the morphology, distribution and storage process are different. This is consistent with the chemical analyses which revealed different components in essential oils of both the leaves (where only peltate trichomes are present) and the inflorescence (WERKER *et al.*, 1985 c).

Capitate trichomes with the same morphology as type I have been found in many species, including those of the Labiatae family (UPHOF and HUMMEL, 1962; FAHN, 1980; RODRIGUEZ *et al.*, 1984; WERKER *et al.*, 1985 d). Nevertheless they have not been described until now as peculiar for seedlings. Their secretion accumulates at two sites (Figg. 5 b2, b3), which are evidentiated treating the secretion with glacial acetic acid. Since the apical part dissolves more slowly than the other, it is suggested that it is made up of less volatile oils than those of the rest of secretion.

The morphology and the storage and release of secretion of peltate trichomes are similar to those already known (AMELUNXEN, 1965; SCHNEPF, 1972; BOSABALIDIS and TSEKOS, 1984; BRUNI and MODENESI, 1983; WERKER *et al.*, 1985 a, b, c, d). Capitate trichomes are typical of the inflorescence; in *S. sclarea* they were described by WERKER *et al.* (1985 c) and present morphology storage and release of secretion quite similar to type I and to the various capitate trichomes found in the literature (see above).

Peltate and type II trichomes present a similar secretion, formed

mostly of essential oils and of a small quantity of a substance which stained specific with PAS reaction, Commassie Brilliant Blue and Fluorescamine. This hydrophilic substance is present in the form of filaments in the capitate hairs and in the form of a network in the peltate ones. The presence of non lipophilic material in peltate hairs of some *Labiatae* is reported by WERKER *et al.* (1985 d) and by SCHNEPF (1972) who concludes that the secretion is an emulsion. In the case of *S. sclarea*, probably this suggestion is not valid, as the stored material varies its hydrophilic and lipophilic composition as a function of the trichome age.

As regards distribution, peltate and hydrophilic capitate hairs are found all over the exposed parts of the plant, while lipophilic type I and type II capitate trichomes are found only at specific sites. Hydrophilic trichomes, which are found on the young organs of *S. sclarea*, have been reported in developing organs in *Thymus vulgaris* (MODENESI *et al.*, 1984), in *Origanum vulgare* (WERKER *et al.*, 1985 a) and in other species of Labiatae, e.g. *Salvia officinalis, S. fruticosa, Rosmarinus officinalis*, etc. (WERKER *et al.*, 1985 b).

The distribution of the various trichomes, specific to the different organs and to the growing phases of the plant, suggests that they may play a role in the various phases of its life cycle. For instance, peltate hairs are present on the whole exposed plant; their oil, according to present interpretation (LOOMIS and CROTEAU, 1980) may act as a form of defense against herbivores. The inflorescence presents numerous type II capitate hairs. The function of their secretion may be to attract insects for pollination.

The oil from the inflorescence is mainly composed of type II capitate hair secretion and, to a lesser extent, of peltate hair secretion. The large number of trichomes present on the inflorescence corresponds to its abundant oil content. This is in accordance with the preference which has been given to the inflorescence in folk medicine and especially in industry.

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