

Phyton (Horn, Austria)	Vol. 43	Fasc. 1	109–133	21. 7. 2003
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Trichomes of *Origanum dictamnus* L. (Labiatae)

By

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With 5 figures

Accepted October 1, 2002

Key words: *Origanum dictamnus* L., Labiatae, Lamiaceae, development, trichomes, glandular, non-glandular, morphology, functions.

Summary

VRACHNAKIS Th. 2003. Trichomes of *Origanum dictamnus* L. (Labiatae). – *Phyton* (Horn, Austria) 43 (1): 109–133, with 5 figures. – English with German summary.

The morphology and distribution of the trichomes on the aerial parts of *Origanum dictamnus* were studied by light and scanning electron microscopy. The leafy stem is covered with a thick indumentum as a result of the branched non-glandular hairs unique within the genus. The glands are distinguished to two main types: the big peltate hairs, characteristic within *Labiatae*, as main site of the lipophilic secretions and the diverse forms of capitate hairs as the most numerous type of glandular trichomes. In the early stage of the plant and in the young expanding tissues a distinct type of capitate hair, the trichome-hydathodes are abundant. Their name, according to their function, is due to their unique hydrophilic secretion. On the reproductive organs, the “fragile” floral glandular trichomes, as another type of capitate hairs with alluring function are distinguished. The stalked glandular hairs, are considered as a third type of capitate hairs, are the most common glands, present on all the plant parts. The complex hairiness of the plant is depicted in the floral elements where glandular, non glandular, integrated glandular/eglandular and peculiar hairs are present. The trichome versatility and the variegation of the papillate-cell (transformed ordinary cell) in flowers are attributed to their role as (scent/visual/tactile) attractants and make obscure the division of the epidermal elements in *Origanum dictamnus*.

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Zusammenfassung

VRACHNAKIS Th. 2003. Haartypen von *Origanum dictamnus* L. (Labiatae). – *Phyton* (Horn, Austria) 43 (1): 109–133, 5 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die Morphologie und Verteilung der verschiedenen Trichome auf den oberirdischen Teilen von *Origanum dictamnus* wurden licht- und rasterelektronenmikroskopisch untersucht. Der Stengel und die Laubblätter sind von einem dichten Filz von verzweigten nicht drüsigen Haaren bedeckt, die charakteristisch für die Gattung *Origanum* sind. Zwei Haupt-Typen von Drüsenhaaren sind anzutreffen: die für *Lamiaceen* charakteristischen großen sitzenden Drüschuppen, die am meisten lipophile Substanzen produzieren und verschieden gestaltete Köpfchenhaare als die am häufigsten vorkommenden Drüsenhaare. In frühen Entwicklungsstadien der Pflanze, auf jungen noch wachsenden Geweben, finden sich zahlreiche Trichomhydathoden, die ein wässriges Sekret abgeben. Auf allen Teilen der Blüte finden sich fragile Drüsenhaare mit einem großen einzelligen Drüsenköpfchen, die eventuell im Dienste der Anlockung stehen. Eine dritte Type von gestielten Köpfchenhaaren findet sich häufig an allen Pflanzenteilen. Die meisten Haartypen finden sich auf den Teilen der Blüte, auf denen Drüsenhaare und nicht drüsige Haare anzutreffen sind und eine Reihe von sonderbaren Haarausprägungen, die sich nicht sicher einer Type zuordnen lassen. Diese Vielfalt der Haare im Blütenbereich, zu denen noch einfache Papillen als Auswüchse normaler Epidermen dazukommen, hängt eventuell mit deren Rolle bei der Attraktion von Blütenbesuchern zusammen, wobei teils Geruchsstoffe, teils visuelle Reize, teils Berührung eine Rolle spielen könnten.

Introduction

Origanum dictamnus L. [syn: *O. pseudodictamnus* SIEBER, *O. dictamnifolium* SAINT-LAGER, *O. saxatile* SALISBURY, *Majorana dictamnus* (L.) KOSTELETSKY, *M. tomentosa* STOKES, *Amaracus dictamnus* (L.) BENTH., *A. tomentosus* MOENCH, *Dictamnus creticus* HILL (cit. IETSWAART 1980)] is an aromatic subshrub of *Labiatae* (*Lamiaceae*), endemic of the island of Crete. Recorded in error from East Peloponnese by HALACSY 1902, ZAGANARIAS 1940, and as a casual from Malta (TURLAND & al. 1993), *O. dictamnus* is the only *Origanum* species with branched hairs. Belonging to the section *Amaracus* it is closely related to *O. calcaratum* JUSS. (SE. Aegean, Crete endemic); it resembles other endemics in the area: *O. vetteri* BRIQUET & BARBEY on Karpathos (Cretan area), *O. symes* A. CARLSTRÖM on Symi (SE. Aegean), *O. scabrum*; BOISS. & HELDR. on Euboea and Peloponnese, *O. cordifolium* (MONTBRET ET AUCHER EX BENTHAM) VOGEL on Cyprus and has also similarities with other endemics of the continental East Mediterranean (IETSWAART 1980, CARLSTRÖM 1984, PATON 1994, KOKKINI 1997).

O. dictamnus is mentioned from the Minoan era (FAURE 1987), through the centuries from physicians and philosophers like Asklepios, Euripides, Aristotle, Hippocrates, Theophrastus, Virgil, Galen, Dioscorides, to many in our time, due to the healing properties attributed to it. The ability to heal wounds of arrowed wild-goats (Fig. 1b), to stop bleeding, to stimulate

the nervous system and cure skin diseases, have made it synonymous to a panacea in the folk medicine of Crete, where it is widely used as a tea. It has been known under many names such as: "dictamnus" deriving either from shrub (thamnus) of mount Dicti (locality where it grows) or from the Cretan goddess Dictinna, who helped women during childbirth; "maliarohorto" (woolly herb), referring to its hairy leaves, and "erontas" (Eros), indicating that like true love which is hard to find so is this plant hard to find and collect from the rather inaccessible sites where it thrives (FRAGAKI 1969, PLATAKIS 1975, HAVAKIS 1980).

The plant occurs on several places on Crete (Fig. 1a), in calcareous cliffs, crevices, gorge-beds, alt. 0–2000 m, as an obligate chasmophyte (KYPRIOTAKIS 1998). It is commercially cultivated at the SW. edge of the mount Dicti (Fig. 1a4), and occasionally seen in gardens elsewhere. It can be found, as "Dittany of Crete", in rock gardens, treated as an alpine-house plant in the old and new world where a mediterranean climate prevails (ELLIOTT 1966, INGWERSEN 1981, TUCKER & ROLLINS 1989, LEADLEY 1997). Several artificial hybrids, all of garden origin, are known. The expected natural hybridisation with *O. calcaratum* in the NE. Crete, where the distribution of the two species just overlaps (IETSWAART 1980, PATON 1994), is not confirmed (KYPRIOTAKIS 1998, VRACHNAKIS 2002).

As one of the oldest pharmaceutical plants with commercial interest (OHLOFF 1992, LANGE & SCHIPPMANN 1997, SKOULA & KAMENOPOULOS 1997) it has been widely studied. These studies are focused on the composition of its essential oils (SKRUBIS 1979, KATSIOTIS & OIKONOMOU 1986, HARVALA & al. 1987, ECONOMAKIS & al. 1999, SKOULA & al. 1999) and on the peltate glandular trichomes, characteristic within the *Lamiaceae* genera as the (main) site of the essential oils. BOSABALIDIS & TSEKOS 1982 and BOSABALIDIS 1987, 1990, investigated the glandular scale (peltate glandular trichome) formation on the leaf epidermis of *O. dictamnus*. HUSAIN & al. 1990 studied by SEM its leaf and nutlet surface. VALENTINI & al. 1991, compared it with *O. cordifolium* and MATTERN & VOGEL 1994 compared the glands of the calyx with that of the leaf of *Amaracus dictamnus* (*O. dictamnus*).

In the present work a study of the aerial surface of *O. dictamnus* from seed germination until seed formation takes place. The morphology and distribution of all the types of trichomes on the different organs were investigated and compared with those of the related species and especially with *O. calcaratum* studied by VRACHNAKIS 2002.

Materials and Methods

Plant material

Flowering branches of *O. dictamnus* were collected from characteristic sites of its distribution: mount Giouchtas, alt. 750 m; coastal-rock at sea level in SW. Crete; mount Ida, alt. 450 m; SW. edge of the mount Dicti, alt. 400 m; gorge Ha, SE. Crete,

alt. 320 m (Fig. 1a1 & Fig. 1c; Fig. 1a2; Fig. 1a3; Fig. 1a4; Fig. 1a5 & Fig. 1d respectively) and from specific local gardens and local nurseries, during the summer 1998 and 1999. Rooted cuttings from the nursery Maurosotis (Athens) were cultivated in the greenhouse of the Institut für Pflanzenphysiologie, KFUNI Graz, Austria and rooted plants (garden origin) were transplanted to the Botanical Garden of Graz. Seeds (nutlets) from different samples were germinated in containers under 12h light/dark, 20°/15° C, 70% RH, 180 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR in growth chamber (Heraeus Vötsch) and in greenhouse conditions starting on 1 December 1999. The conditions in the growth chamber were shifted to: 17h light/7h dark, 23°/17° C, 55% RH on 30 March 2000. Containers from growth chamber and greenhouse, as well as containers with germinated seeds and growing plants from cuttings, were placed outside of the greenhouse area on 14 April 2000. A potting mix based on sand was used and irrigation was the only agriculture practice to the growing plants. For a comprehensive study, samples were collected from the Botanical Garden of Innsbruck, Austria, the Botanical Garden of Wageningen, Holland and herbarium material was provided by Dr. Kypriotakis Z. (Technological Education Institute of Crete). Voucher specimens are deposited in Institut für Pflanzenphysiologie, Graz and plants can be found in *Hortus Botanicus Graecensis*.

Light microscopy (LM)

Free-hand sections of all plant's parts were observed under a Zeiss Axioplan Photomicroscope. Paraffin-oil was used for hydrophilic secretions (HEINRICH 1973a) and Oil Red for the localisation of lipophilic substances (GREEN 1991).

Scanning electron microscopy (SEM)

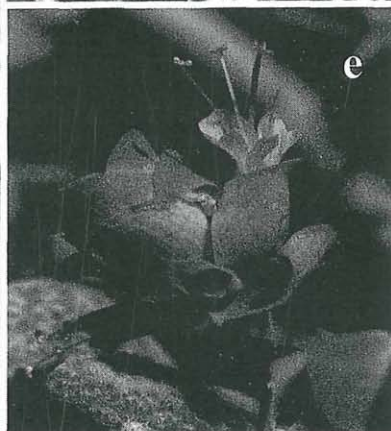
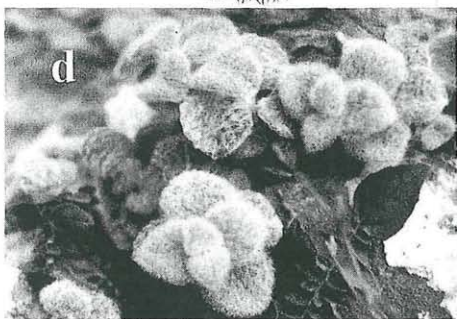
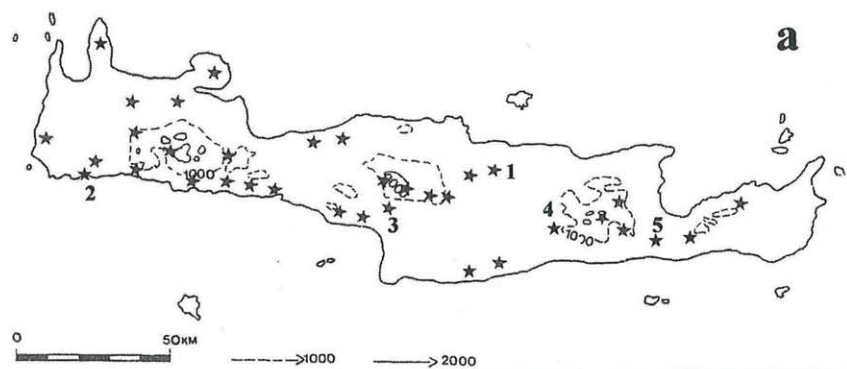
Plant parts were fixed with 2.5% glutaraldehyde in 0.05 M cacodylate buffer at pH 7.2 for 4 h. and dehydrated in a graded acetone series, critical point dried with CO₂ and the specimens sputter-coated with a thin layer of gold (Agar Sputter Coater B7340). Observations were carried out on a Philips XL 30 ESEM, operating at 20 kV.

Measurements

Measurements took place during the life-cycle of the plants. The number of trichomes was counted on SEM images, and directly on LM at 400 $\times$ magnification. The size of cells and trichomes was measured and the number of trichome cells was determined on LM (1000 $\times$ magnification). Micromasurements were confirmed using an image analysing system (Optimas 5.2 for Microsoft Windows, Optimas Corporation). Measurements (per mm² surface area) took place at cotyledons, leaves and bracts.

Fig. 1. *Origanum dictamnus*.

- a. distribution on Crete: after KYPRIOTAKIS Z. 1998 and the author; 1,2,3,4,5: samples capital
- b. arrowed wild-goat eating "dittany" by Cornelius G. Decker (1643–1678)
- c. growing on calcareous rock, mount Giouchtas, alt. 750 m.
- d. growing on calcareous rock, gorge Ha, alt. 320 m.
- e. flowering with exposed flower-organs
- f. axillary flowering in early stage



Data represent mean values of randomly chosen plant material of different origin. Observations took place in vivo and under a Zeiss SV8 Stereomicroscope.

Results

Trichome formation during growth and development

The life cycle of *O. dictamnus* is divided in seedling, vegetative and reproductive stage.

In the early stage when the seedling emerges on germination, the hypocotyl and cotyledons, although looking glabrous, are pubescent (Figs. 2a, b). In hypocotyl capitate hairs (stalked glandular trichomes and trichome-hydathodes); 1-celled non-glandular trichomes and occasionally peltate glandular trichomes at its top can be found. In the abaxial (lower) side of the cotyledon capitate hairs are present, while peltate hairs and non-glandular hairs are absent. In the adaxial (upper) side, all types of glandular hairs are present and 1 or 2-celled non glandular ones (Figs. 2a, c and Table 1). Trichomes are present with developing ordinary cells and developing stomata (of the abaxial cotyledon). At the tip of the cotyledon epithem-hydathodes can be found. Hypocotyl and the cotyledons have a pink-red appearance.

Table 1. Trichomes on a mature cotyledon, a fully-expanded leaf and floral elements of *O. dictamnus* (per mm² area for flat tissues, n = ± 60).

Plant parts	Peltate glandular	Capitate glandular	Non-glandular	Other types
Abaxial side of cotyledon	—	68–103	—	—
Adaxial side of cotyledon	3.1–3.5	80–110	+	—
Abaxial side of leaf	3.2–3.9	48–95	+	—
Adaxial side of leaf	2.8–3.6	62–106	+	—
Abaxial side of bract	0.1–0.4	155–320	+/-	—
Adaxial side of bract	0.8–1.1	135–295	+/-	—
Outer calyx	+	+	+	—
Inner calyx	—	—	+/-	—
Outer corolla	+	+	+	+
Inner corolla	—	—	—	+

Variation in the values is partly caused by the non homogenous distribution of the epidermal elements on the plant surfaces (see also text).

In the vegetative stage the decussate phyllotaxy is consisting from leaves of increasing size up to the middle of the stem and then decreasing upwards to the top (Figs. 1b, c). When the first leaf primordia appears, glandular and non-glandular hairs with undeveloped ordinary cells consist their epidermis (Fig. 5a). With the leaf expansion, in the abaxial side capitate hairs are concentrated across the raised veins and on the petiole. Peltate hairs are located at the periphery of the lamina and on the sides of

the veins. The non-glandular hairs protrude from the veins, leaf-margin and petiole. Stomata are in abundance on the leaf-blade (Figs. 2d, e and Table 1). On the adaxial leaf side, all types of hairs and few stomata are uniformly distributed (Figs. 2f, g and Table 1). In young leaves the most upper part is devoid of peltate hairs while different stages of these hairs co-exist at the leaf-base (Figs. 2d, f). Epithem-hydathodes can be found as ending of the main vein and anthocyanin is present at the leaf-margin. The non-glandular hairs are branched, resulting in an obscured epidermal surface due to their "woolly" cover (Figs. 1d, f and 3a, b, d). The leaf size depends on its age and position on the stem, reaching its maximum at the middle stem ($\pm 6^{\text{th}}$ node). In these fully-expanded leaves all the epidermal elements are differentiated and their density on both leaf sides is almost equal (Table 1). The indumentum of the internodes is similar to that of the leaves.

The reproductive stage: After six months of cultivation, the main and axillary stems terminate into inflorescence, and flowering branches appeared from the upper stems. The spike like inflorescence comprises successive pairs of bracts subtending two flowers per verticillaster, attached with pedicel (stalk of individual flower) to the peduncle (main axis of the inflorescence). The conversion from the vegetative to the reproductive stage results in intermediate leaves-bracts. Within this stage, the characteristic white woolly of the "leafy" stage is replaced by the rather glabrous and remarkably variegation of the floral elements (Figs. 1b, c, e, f).

The bract although looking "naked", bears glandular and eglandular trichomes. Few peltate hairs are concentrated at the base of the abaxial (outer) side, while at the adaxial (inner) bract blade a greater number of these trichomes is uniformly-distributed (Figs. 1e, f). Occasionally, short non-glandular hairs (branched or unbranched) are present at the bract base or along the bract-margin. The capitate hairs are in abundance on both sides, densely at the base (Figs. 4a, g, h and Table 1). Their characteristic big cuticular-head, within this stage, allows the name: floral glandular trichomes (Fig. 5e). The tip of bracts possesses epithem-hydathodes and stomata as in the leaves, but in reduced number. The whole bract has a membranous appearance with a brilliant red-purple colour in a decreasing gradient from bract-apex to bract-base (Figs. 1e, f and 4a). The leaf/bract indumentum is intermediate to that of a most upper leaf and a bract (Fig. 3h).

In the outer calyx peltate hairs on the sides of the raised veins and many floral trichomes densely downwards to its base and pedicel are present. Small non-glandular trichomes can be found along the calyx margin and towards its base (Figs. 4b, d and Table 1). The inner calyx lacks peltate hairs; but possesses floral hairs and in some ecotypes is characterised by a hairy throat of long 4-8 celled unbranched non-glandular hairs (Figs. 4c, d;

5d, m and Table 1). The tip of calyx lobe possesses epithem-hydathodes. Stomata and colour of the calyx are similar to that of bracts. The peduncle's indumentum is similar to that of the pedicel, dominated by the floral glandular trichomes.

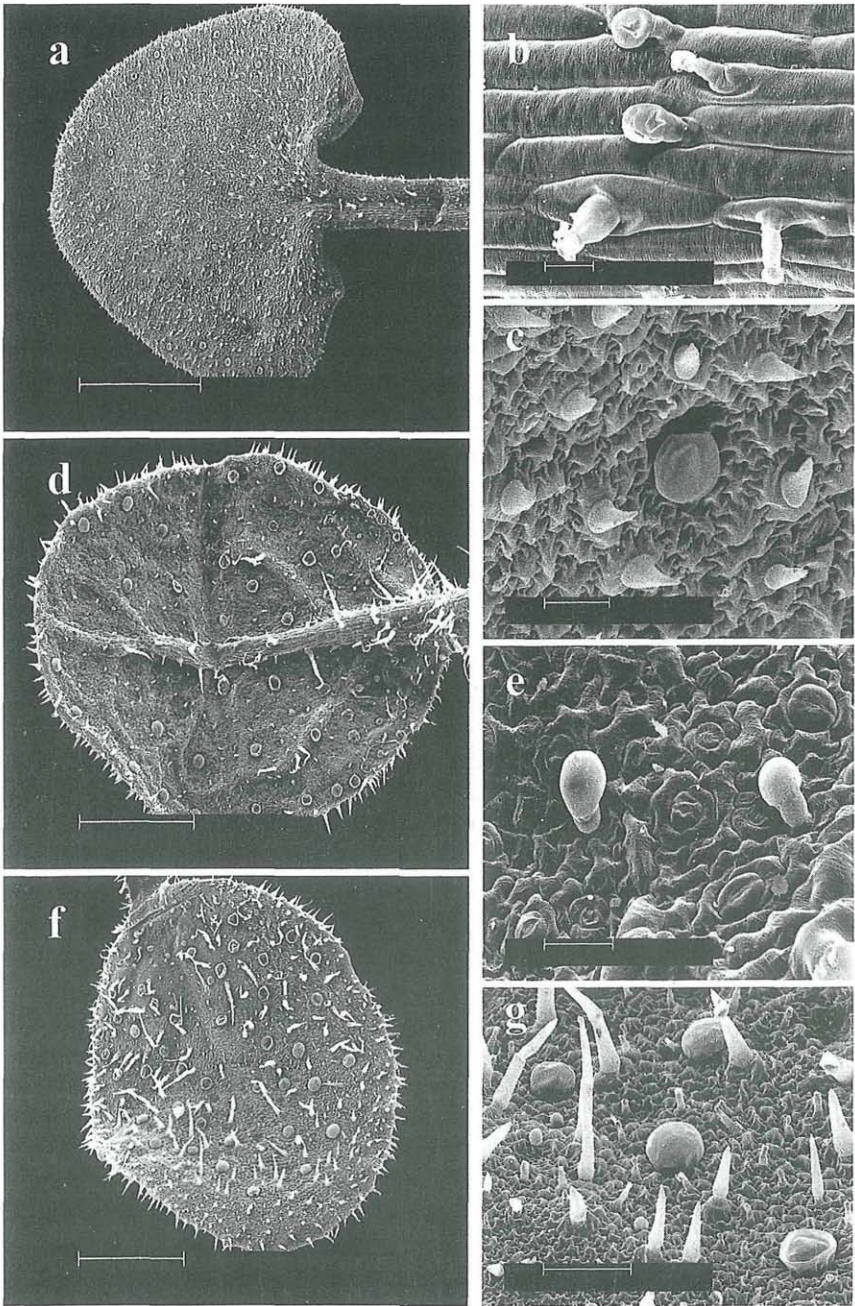
When the corolla comes out of the calyx and opens, it reveals a pubescent epidermis (Fig. 1e). On the outer corolla, (from the tubular part up to the bilabiate mouth) peltate hairs and several types of stalked hairs are present (Figs. 4d, e, i; 5l and Table 1). Their distinction between glandular and non-glandular is not clear since branched and unbranched hairs with acute to variously "headed" terminations can be found (Figs. 4i and 5l, n). The inner corolla lacks peltate hairs while peculiar hairs are present near the insertions of the filaments (Figs. 4n, o; 5o and Table 1). The colour of the opened corolla is pinkish to purple, intense in the inner corolla and the corolla's lobes where the typical puzzle-like ordinary cells are transformed to papillae-cells (Figs. 4j, k, o). The didynamous stamens ascends under the upper lip of the corolla (Fig. 1e). The 2-lobed anther, joined by the expanding connective with the hairless filament presents a variegated papillosous epidermis. Distinct glandular hairs on the underside of the connective and occasionally few trichomes protruding from the pollen sacs are the only trichomes to be found on the anthers. Papillate-cells of different forms and the white colour of the aggregated pollen grains (visible with naked-eye) in contrast with the deep-purple of the anther are the characteristic features of the stamen (Figs. 4f, l, p and 5p). The style lacks trichomes, while in the bifid stigma the conical papillate-cells are transformed to smaller receptive papillae on the inner stigmatic lobes. Like the other floral tissues the papillosous style and stigma exhibit a pinkish to purple coloration. Trichomes on the ovary and on the seeds were not observed.

Types of Trichomes

The aerial parts of *O. dictamnus* possess non-glandular (eglandular) and glandular trichomes. The glandular trichomes are of two kinds, peltate and capitate ones.

Fig. 2. The early vegetative stage.(SEM micrographs)

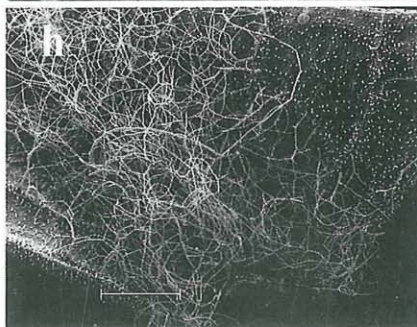
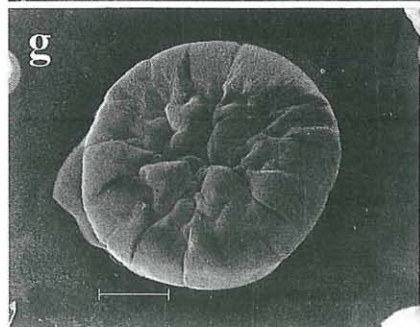
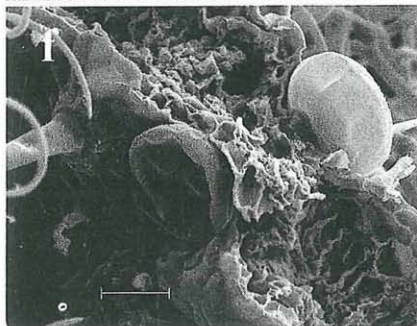
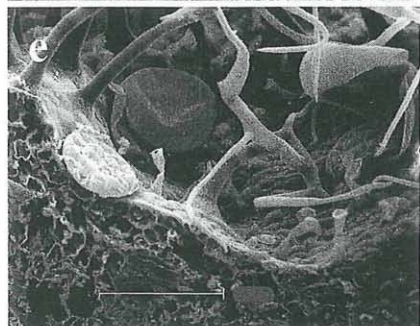
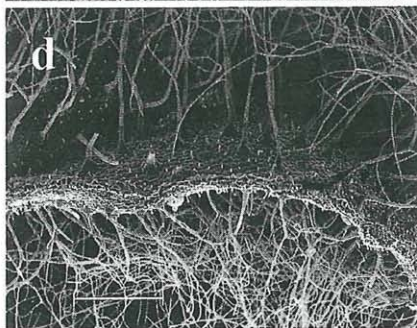
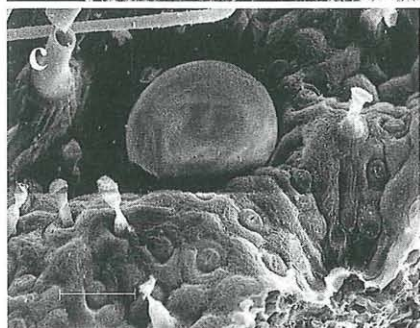
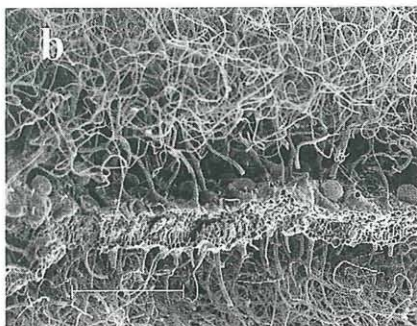
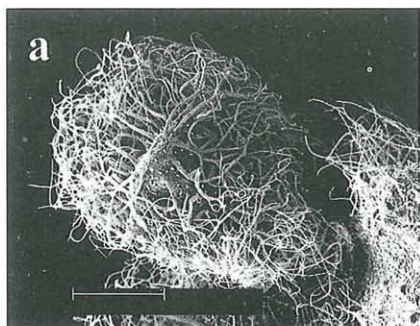
- a. adaxial side of a cotyledon, bar: 1 mm
- b. capitate hairs on hypocotyl, trichome-hydathodes in bending position, bar: 20 μ m
- c. adaxial side of a cotyledon, peltate hair surrounded by 1-celled eglandular hairs, bar: 100 μ m
- d. abaxial side of a first leaf, bar: 500 μ m
- e. trichome-hydathodes and stomata on abaxial side of a first leaf, bar: 20 μ m
- f. adaxial side of a first leaf, bar: 500 μ m
- g. peltate and non-glandular hairs on adaxial side of a first leaf, bar: 100 μ m



A peltate glandular trichome consists of a basal cell, a very short stalk cell and a large round head of up to 16 secretory cells arranged in two concentric circles. The diameter of a 12–16 celled head is: 75 μm –95 μm (± 10) (Figs. 3g and 5h, i, j, k). In SEM micrographs, the heads show a smooth or wrinkled surface, revealing the presence of a large subcuticular space or emphasises the head-cells outlines, due to close attachment of the cuticle to the upper cell walls (Figs. 2c, g; 3c, e, f and 4g, h). Under LM, the cuticular head is opaque to hyaline, the subcuticular space is either homogeneously filled with material, or emulsified by numerous coloured droplets (Figs. 5g, h, i). With Oil Red, reddish droplets can be seen in long time immersed material (Figs. 5k, l). When using paraffin oil, hydrophilic material was secreted out of the head (Fig. 5j). Under the stereoscope or with unaided-eye (Fig. 1f), the colour varies from opalescent/pale yellow to orange/red-brown (the latter common to old material). The peltate hairs are often sunken to various degrees into epidermis, forming a ring of peribasal cells (Figs. 2c and 3c, e, f). On the leaf blade, peltate hairs are sunken, “forming” more peribasal cells than on non-flattened tissues (vein sides, internodes, calyx, corolla), where the peltate hairs are not sunken (Figs. 4d, h, i and 5l). Nevertheless, on a flat tissue a 12–16 celled-head peltate hair can be surrounded by equal in number or more peribasal cells. Peltate hairs can be found at sheltered locations: grooves formed by infolds of the abaxial leaf margins, sides of raised veins, inner bract. They are rare on protruding or hairless tissues: veins; leaf, bract, calyx top; abaxial cotyledon; inner corolla; stamen and pistil (Table 1). Generally they are present under the protective “canopy” of the eglandular hairs (Figs. 3a, b, d, h). The long life span of the peltate hair is evident, since, even in old (herbarium) samples the spherical head, due to accumulated material, is similar to that of a young tissue. Evidence of secretion of lipophilic material out of the cuticle or pores on it was not observed. The occasionally rupture of the cuticular layer was caused by artificial damage. Undamaged peltate hairs can be found after a heavy rain or snow.

Fig. 3. The leafy stage. (SEM micrographs)

- a. small leaf covered by non-glandular hairs, bar: 500 μm
- b. cross section of mature leaf (sample: SW. Crete), bar: 500 μm
- c. abaxial side of leaf, epidermal elements and hollow scars of the peltate hairs, bar: 50 μm
- d. cross section of mature leaf (sample: Botanical Garden Innsbruck, Austria) bar: 500 μm
- e. trichomes on abaxial epidermal surface, bar: 100 μm
- f. sunken, swollen and collapsed peltate hairs in opposed leaf surfaces, bar: 50 μm
- g. peltate hair with detached cuticle and secreted cells in turgor, bar: 20 μm
- h. trichomes on the base of a leaf/bract, bar: 500 μm



The capitate glandular trichomes are trichome-hydathodes, stalked glandular trichomes and floral glandular trichomes.

Trichome-hydathodes consist of an almost invisible basal cell and a short stalk bearing a pear-like head cell of $15\text{ }\mu\text{m}$ (± 5), characterised by their early presence on growing parts of vegetative tissues. They do not protrude from the plant surface, are almost in a bending position, and do not form a subcuticular space (Figs. 2b, e). Under LM, the head is opaque to hyaline. Using Oil Red, colouration of the head was not observed. Its character is shown using paraffin oil, with distinct droplets of aqueous/hydrophilic material secreted out of the globose head, obviously in fresh material of well watered plants (Fig. 5b). The life span of the trichome-hydathodes is short and their detection in dry or old material is not easy.

Under the name stalked glandular trichomes, several forms of glandular trichomes with distinct stalk are included (Figs. 2b; 3c and 5c, l). The form and size of the basal cell varies, as well as the number and size of the stalk cell(s). The variation in shape and size of the head-cell did not allow to predict the maturity of a stalked hair. A developing stalked hair does not differ from a developing trichome-hydathode, and the difference of a capitate stalked hair from a "floral" one is just the head size. At the same location of the plant tissue different forms of stalked hairs can be found. In the reproductive organs, their variation is even greater and branched stalked glandular trichomes are observed in the outer corolla (Fig. 5n). The stalked hairs are the most common trichomes (not always the most numerous), and protrude from all plant surfaces. Under LM, no specific colouration was detected within the "head", which was either opaque to hyaline, or filled with an emulsion of droplets. The reaction with Oil Red and paraffin oil is similar to that of the peltate hairs (Figs. 5c, l). The short life span is evident due to occasionally collapsed stalked hairs in dry material.

"Floral" glandular trichomes are characterised by the big "cuticular" sphere of the head-cell, which can reach $35\text{ }\mu\text{m}$ in diameter and their abundance on to reproductive organs (Figs. 4d, g, h and 5m). In surface view, a floral hair resembles a small peltate one, due to a short, narrow stalk cell and a short basal cell (Fig. 5f). In many cases due to the optical "emptiness" of the stalk cell, floral hairs look suspended from the tissue (Fig. 5e). SEM micrographs of successive stages reveal their "pump-like" nature. The material secreted in the subcuticular space, seems to be sucked and transported to the head cell via the stalk cell, at the expense of the basal cell. Floral trichomes can often be seen collapsed or with the cuticle unstuck, revealing the temporariness of the accumulated secretion. Cuticle detachment occurs only at the upper region of the glandular head, while towards the base the cuticle adheres closely to the cell wall (Fig. 4m). Under LM, the head is filled with a homogenous opalescence to pale-yel-

low secretion. Observations were not always clear due to their "fragile" character and the interference of the secretion with solutes of other origin (nectar). The use of Oil Red intensified the peripheral "cuticular" line and various coloured (in the red tone) droplets can be seen (Fig. 5f). Using paraffin oil, solutes in the size of the head-sphere were secreted and interfered with it (Fig. 5e, m). Their short life span is evident, whilst the sphere is "shining" in carefully dried material (visible even with unaided eye).

The non-glandular trichomes (eglandular hairs), at least in the vegetative stage, are considered to be of one type. In cotyledons 1-celled hairs appear as conical papillae, due to their form and warty cuticle (Fig. 2c). Branching of the hairs occurs generally at the 2-leaves stage of the plant. The non-glandular trichomes of *O. dictamnus* are unbranched or branched uniseriate, unicellular to multicellular, pointed, distinctly articulated between cells, with acute to obtuse apex, erect or leaning from the plant organs and can reach 3mm length (Figs. 2d, f, g; 3e, h; 4g and 5c, g). Their surfaces are cuticular ornamented or smooth. The hair base is embedded in the epidermis, surrounded by a collar of upwardly inclined epidermal cells (pedestal cells), (Figs. 2g and 3c, e, f). The number and the degree of elevation of pedestal cells follows the rules of the peribasal cells of the peltate hair. In the reproductive stage the hairs (only in some ecotypes) of the calyx-throat are unbranched and uniform (Fig. 5d), but those at the corolla are out of rules. Non-glandular hairs are in abundance on the leafy stem, covering entirely the leaves; they are present in specific places on reproductive organs and their presence is related with that of the glandular hairs (Figs. 1d; 3a, b, d, h and Table1). In young tissues, the vacuole of their basal-cell is often coloured by anthocyanins. As the eglandular hairs do not terminate in a gland, predictions of their maturation are relative. Their unclear life span seems to be not important for the plant itself, since even dead (air filled), they can be functional as a protection.

Unusual hairs of the reproductive stage: in the outer corolla branched glandular hairs (Fig. 5n) and integrated (glandular/eglandular) hairs can be found (Figs. 4i and 5l). In the inner corolla unicellular, narrow hairs, with blunt end and warty cuticle, 25 μm length (Fig. 4n), can be found and unicellular, club forming hairs, with several knobs, 15–35 μm length (Figs. 4o and 5o), are occasionally present. The use of Oil Red shows a pink colouration. The glandular hairs on the underside of the anther's connective (Figs. 4l, p and 5p) look like peltate hairs, but consist of a 1-celled head (30–50 μm length) instead of the multicellular head of the peltate hair.

Although papillae can be classified as trichomes, they are treated as papillate-cells, a differentiation of ordinary cells (pavement cells). The ordinary cell is the most frequently occurring cell type in the epidermis of *O. dictamnus*. In surface view a developed pavement cell is either puzzle-like for flatly surfaces, or rectangular elongated for elongated tissues

(Figs. 2b, e; 3c and 5b). This is the rule in the vegetative stage, while in the floral organs, pavement cells with protruding walls and cuticular striations (papillate-cells) are apparent (Figs. 4f, k, o and 5o). This change in the cell shape is to be seen also as change in colouration and was observed to be massive (as a group of cells). Papillate-cells are uncommon on the outer tubular part of corolla, while in the region of the bilabiate mouth and in the entire inner corolla, papillate-cells are the rule. The uniformity of the "papillose" pollen sacs can be "interrupted" from the distinct glands under the connective. Papillate-cells are able to secrete, as the receptive papillae of the stigmatic lobes and the papillate cells of the *tape-tum*.

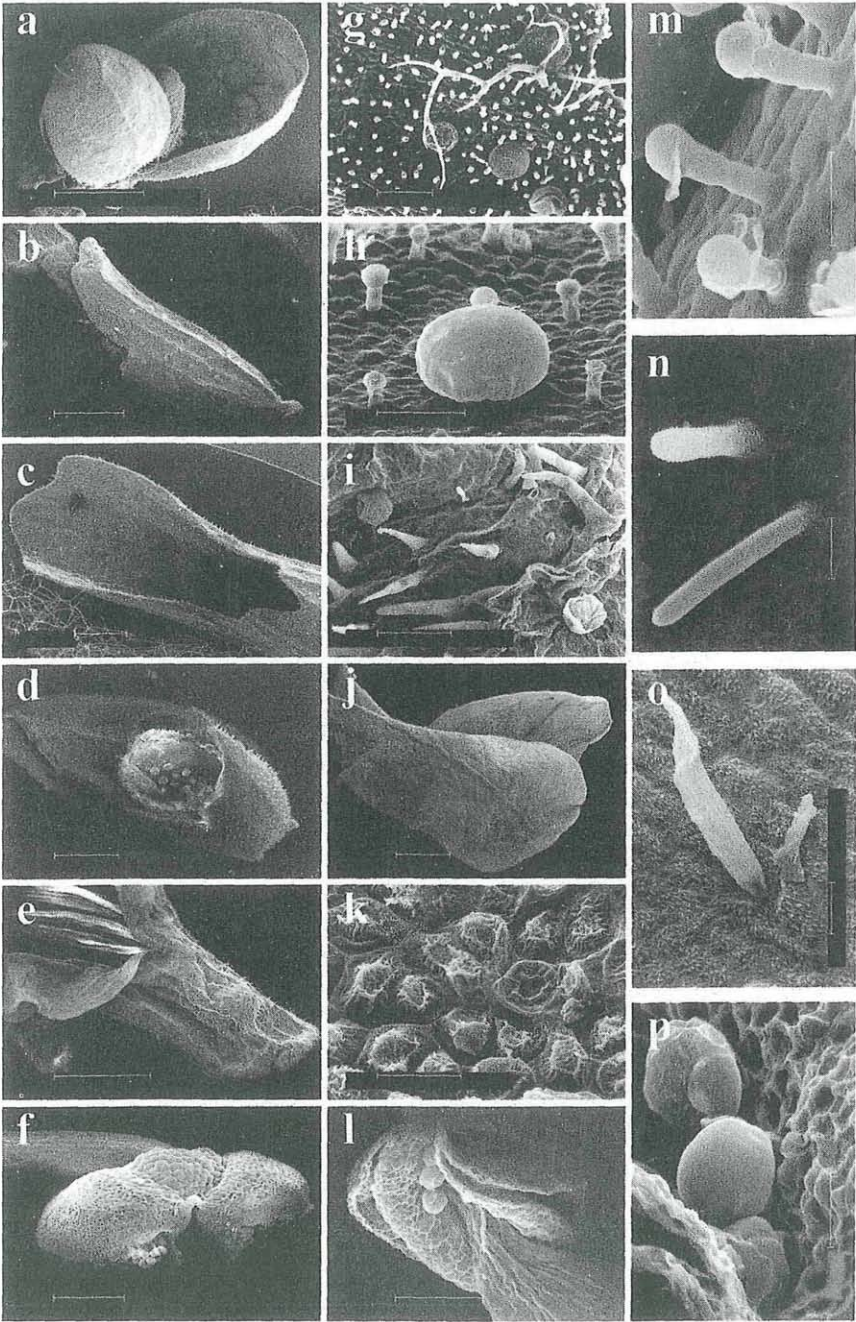
Epithem-hydathodes (passive-hydathodes) were observed in most of the plant's organs as vein terminations. Under LM, 3–5 big open stomata obviously on young tissues can be seen. When using paraffin oil guttation or any secretion was not observed. The use of Oil Red coloured the openings with intense red.

Discussion

All the examined ecotypes of *O. dictamnus* showed a stability in their gross and trichome phenology, at least in the vegetative stage, with the branched non-glandular hairs, as a taxonomic marker, unique within *Origanum* (IETSWAART 1980). The early presence of trichomes on leaf primordia is the rule in *Lamiaceae* (BRUN & al. 1991, WERKER 1993, ASCENSAO & al. 1995, 1999) and in other families as early pointed out by HOFMEISTER 1868, PFITZER 1872. The glandular hair types of the leaf epidermis in

Fig. 4. The reproductive stage. (SEM micrographs)

- a. successive bracts and enclosed calyx, bar: 1mm
- b. outer calyx with enclosed part of the corolla's tube, bar: 1mm
- c. inner calyx, bar: 500 μ m
- d. closed corolla covered by trichomes inside partly destroyed calyx, bar: 500 μ m
- e. corolla's tube and part of bilabiate mouth, bar: 1 mm
- f. protruded connective connects the papillose pollen sacs, bar: 200 μ m
- g. "hairy" base of the outer bract, bar: 100 μ m
- h. peltate hair surrounding by floral hairs on outer bract, bar: 50 μ m
- i. glandular and non-glandular hairs on the outer tubular part of the corolla, bar: 100 μ m
- j. lobes of the bilabiate corolla's mouth, bar: 500 μ m
- k. papillate-cells on inner corolla, bar: 20 μ m
- l. glands on the underside of the anther's connective, bar: 100 μ m
- m. cuticle's detachment of floral glandular trichomes, bar: 20 μ m
- n. unicellular, cuticular ornamented hairs on inner corolla, bar: 20 μ m
- o. "tuberculate" hair on inner corolla, bar: 20 μ m
- p. glands and papillate-cells on the underside of the anther's connective, bar: 20 μ m



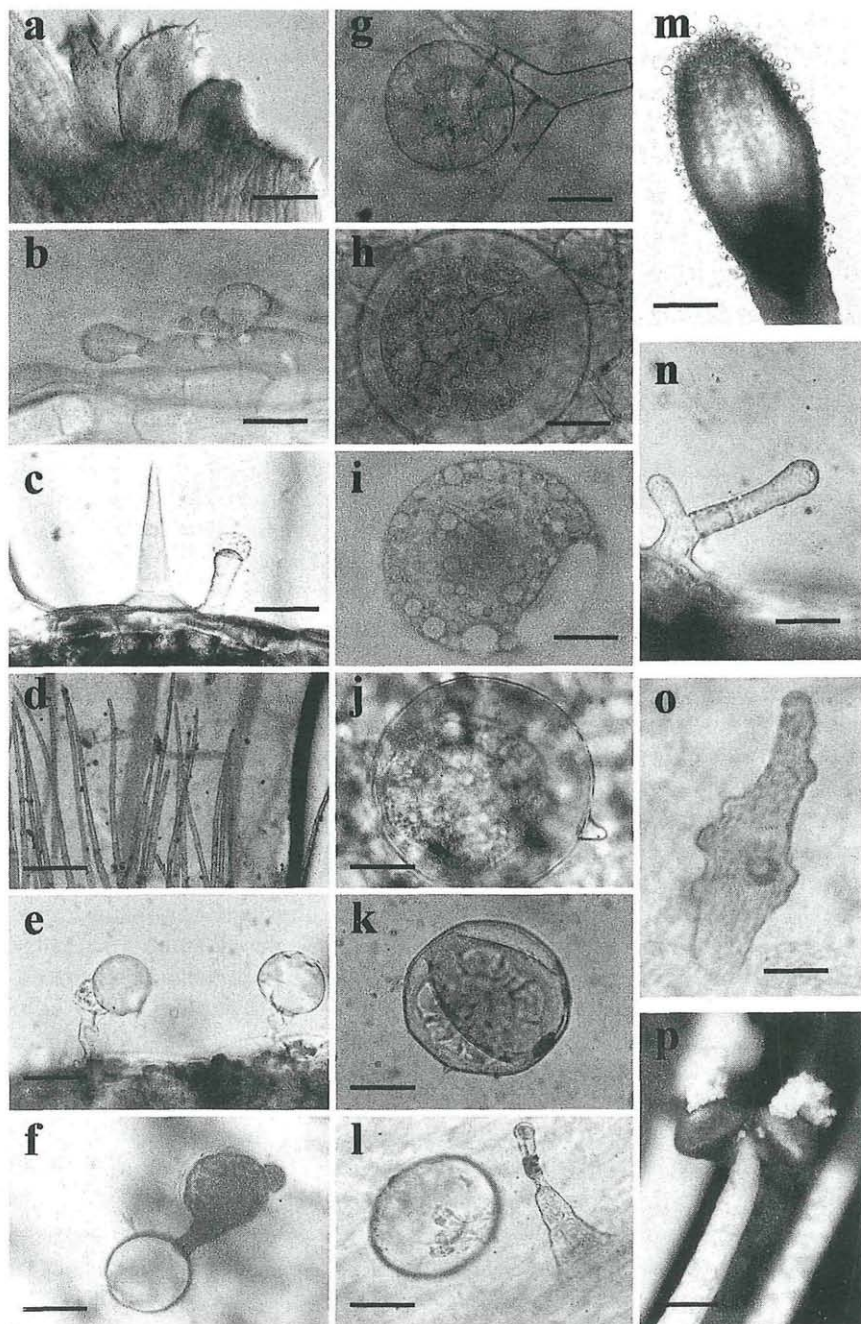
O. dictamnus are identical to those reported for *Monarda fistulosa* (HEINRICH 1973), *O. syriacum* (DUDAI & al. 1988), *O. vulgare* (WERKER & al. 1985a) and *O. calcaratum* (VRACHNAKIS 2002).

The head of the peltate hairs (characteristic for *Labiatae*: "Labiatae-Drüsen" KLUG 1926) in *O. dictamnus* was found to consist of up to 16 cells, while BOSABALIDIS & TSEKOS 1982 reported a 12-celled head. The density of the peltate hairs on developed leaves agrees with the findings of IETSWAART 1980, BOSABALIDIS 1990. The appearance of the head content as emulsion correlated with the reaction of paraffin oil and Oil Red indicates the different nature of the secretion (hydrophilic and lipophilic). HUSAIN & al. 1982 report too a hydrophilic nature, whilst BOSABALIDIS 1990 consider that the subcuticular space is filled entirely with essential oil. Both natures for the enclosed material are reported for *O. x intercedens* (BOSABALIDIS & al. 1998) and *O. calcaratum* (VRACHNAKIS 2002). The role of the peltate hairs, to be the "first line of defence" against herbivores (KELSEY & al. 1984), seems to be not the case with *O. dictamnus*. Due to their hidden character and the absence of evident secretion of the phytotoxic (BROWN & al. 1987) components out of the cuticle, the peltate hairs are rather protected than providing protection to the plant (WERKER 2000, VRACHNAKIS 2002). For these trichomes DUKE 1994 points out that there is no evidence for a direct function as a physical impedance to insects, and this is confirmed in *O. dictamnus* due to the impermeable "barrier" of the eglandular hairs. The undamaged, reddish, peltate hairs of this plant are also reported from herbarium material by BOSABALIDIS & TSEKOS 1982, HUSAIN & al. 1990.

The appearance of trichome-hydathodes (salt glands: WERKER 2000) in the early stage of *O. dictamnus* correlated with their bending position and

Fig. 5. LM micrographs: a.-o.; Stereomicroscope: p.

- a. trichomes on first leaf primordia, bar: 100 µm
- b. trichome-hydathodes secreting hydrophilic droplets, with paraffin-oil, bar: 30 µm
- c. stalked glandular (right) and 1-celled eglandular hair on a young leaf, bar: 30 µm
- d. hairy calyx-throat from sample 1 (mount Giouchtas), with Oil Red, bar: 100 µm
- e. "fragile" floral glandular trichomes on bract, with paraffin-oil, bar: 30 µm
- f. floral glandular trichomes on bract reacting with Oil Red, bar: 25 µm
- g. branched eglandular and 8-celled peltate hair on a young leaf, bar: 25 µm
- h. peltate hair on bract, bar: 25 µm
- i. peltate hair on leaf emulsified of different osmiophilic droplets, bar: 25 µm
- j. peltate hair on bract, with paraffin-oil, bar: 25 µm
- k. 12-celled peltate hair on flower primordia, with Oil Red, bar: 30 µm
- l. capitate and peltate hair on outer corolla, with Oil Red, bar: 20 µm
- m. floral hairs on calyx primordium, with paraffin-oil, bar: 100 µm
- n. branched glandular hair on the outer corolla's tube, bar: 15 µm
- o. "tuberculate" hair on inner papillose corolla, with Oil Red, bar: 5 µm
- p. glands and pollen-grains contrasting in colour the anther's lobes, bar: 400 µm



their unique hydrophilic secretion confirm their function as active hydathodes. RENNER 1909 relates the basiscopic orientation (bending position) of these trichomes, as opposed to the original acroscopic one of the glandular trichomes, with a special function and NESTLER 1893 points out that the capitula of small trichome-hydathodes may be appressed. The early forming and functioning of the trichome hydathodes in immature organs as well their short-life is reported by MIELKE 1891, UPHOF 1962 and FAHN 1979. ZIEGENSPECK 1949 reported Trichomhydathoden in all the 59 species of *Labiatae* investigated. Their role as active hydathodes is reported for *Monarda fistulosa*, *Mentha piperita* (HEINRICH 1973a, 1977); *Teucrium* (BINI-MALECI & SERVETTAZ 1991); *Scutellaria altissima* (THALER & al. 1992); *Melissa officinalis* (SCHULTZE & al. 1992); *Nepeta racemosa* (BOURETT & al. 1994); *Salvia officinalis* (CORSI & BOTTEGA 1999) and *O. calcaratum* (VRACHNAKIS 2002).

The variability of the other capitate glandular hairs concerning the shape and the nature of secreted material is common for all *Labiatae* so far investigated (KELSEY & al. 1984, WERKER 1993, 2000). In regard their lifespan, UPHOF 1962 stated for *Labiatae* that in old leaves these hairs are usually shed, but the scars remain visible, while in *Hyssopus officinalis* the 1 to 4-cellular capitate hairs persist for a long time (TUNMANN 1906).

The branched eglandular hairs, that envelop the leaves of *O. dictamnus* with a mat, thicker than the leaf itself, are unique in *Origanum* but not rare within *Labiatae* (MEFCALFE & CHALK 1950, EL-GAZZAR & WATSON 1970). A thick indumentum is a common feature of plants from mediterranean climate and steppes, deserts, and alpine habitats (HABERLANDT 1884, WARMING 1909, EHRLINGER 1984). The first appearance of the eglandular hairs as conical papillae is also reported for *Lamium album* (RAUTER 1871), *Satureja thymbra* (WERKER 2000), *O. calcaratum* (VRACHNAKIS 2002), while in the case of *Coridothymus capitatus* they are considered as another type of non-glandular trichomes (ECONOMOU-AMILI & al. 1982). The occasionally presence of long unbranched eglandular hairs in the calyx throat, without taxonomic value, is not rare within other "hairy" *Origanum* (IETSWAART 1980, CARLSTRÖM 1984). Besides the variability of the eglandular hairs in *O. dictamnus* their defence against various external factors is evident (LEVIN 1973, JOHNSON 1975, HOLMES & KEILLER 2002). Their potential function to protect the glandular hairs and their utility even when dead is reported for many plant species (UPHOF 1962, WERKER 2000).

The reduced pubescence (as compared to leaves) and the remarkable colouration of the bracts is also reported for *O. vulgare* occurring in Greece (KOKKINI & al. 1994) and for *O. calcaratum* (VRACHNAKIS 2002). The outer calyx of *O. dictamnus*, densely covered by glands in contrast to the glabrous inner one, is common within *Labiatae* and is associated with the

leaf hairiness (EL-GAZZAR & WATSON 1970, CANTINO & SANDERS 1986, MATTERN & VOGEL 1994). The role of the "hairy" outer calyx is rather the production of floral fragrances (MEEUSE 1992, MATTERN & VOGEL 1994) than the protection of the enclosed parts of the corolla (WERKER 2000), due to the "fragileness" of the numerous floral hairs which are "ready" to release the secretion even with a light wind. The proposed alluring function of the floral hairs is in agreement with the interference of their secretion with the nectar and with their "pump-like" character, suggested for *O. calcaratum* (VRACHNAKIS 2002). The "pump-like" character of similar anatomical floral attractants is reported by FAHN 1979; while MATILE & ALTENBURGER 1998 point out the rhythmicity of fragrance emission in flowers. Peltate hairs on the outer corolla of *O. dictamnus*, in agreement with finding of MATTERN & VOGEL 1994, are also reported for *O. syriacum*, *O. vulgare*, *Salvia* sp. and *Leonotis leonorus* (WERKER & al. 1985a,b, DUDAI & al. 1988, ASCENSAO & al. 1995). The branched glandular hairs are also reported (but with one glandular branch) for *Meriandra* (BOKHARI & HEDGE 1971), *Phlomis* (AZIZIAN & CUTLER 1982), *Hyptis* (RUDALL 1980), *Rosmarinus officinalis* (WERKER & al. 1985c). Integrated glandular/eglandular hairs are reported on both corolla's sides of *O. calcaratum* (VRACHNAKIS 2002), while UPHOF 1962 points out that in *Labiatae* a confusion between the two kinds of hairs cannot be excluded. The highly differentiated hairs inside the corolla are common in *Lamiaceae* (WERKER 2000) and according to UPHOF 1962, abnormal hairs are not rare in strongly pubescent plants. Trichomes with blunt ends and warty cuticle were also reported for the inner corolla of *Melissa officinalis* (SCHULTZE & al. 1992) and in the inner flower spur of *Tropaeolum majus* (RACHMILEVITZ & FAHN 1975). The unicellular club forming hairs with several knobs, called "tuberculate" by SOLEREDER & MEYER 1928, are reported on petals in *Viola tricolor* and on flower parts of *Vinga minor*, *Capparis*, *Digitalis*, *Mentha*, *Veronica* and *Verbascum* (KURER 1917). Similar trichomes reported on the inside of the corolla tube of *Lavandula officinalis* (WERKER 1993). Glandular hairs on the underside of the connective and trichomes protruding from the anthers were reported in *O. calcaratum* (VRACHNAKIS 2002). Peltate hairs were observed on the underside of the anther lobes in *O. syriacum* (DUDAI & al. 1988), *Leonotis leonorus* (ASCENSAO & al. 1995) and in *Cannabis sativa* (MAHLBERG & al. 1984). The peculiarities of the reproductive organs and in particular of the trichomes can be related with the pollination ecology of *O. dictamnus*, as in the *Lamiaceae* generally (HUCK 1992, PETANIDOU & VOKOU 1993). Hairs inside the corolla can act as osmophores (FAHN 1979), or serve as a guiding arrangement for nectar-searching insects (SCHULTZE & al. 1992). LUNAU 2000 suggests a signalling function "by an expansion of connectives", in species other than of *Labiatae*.

The remarkable floral colouration (red to violet-purple) of *O. dictamnus*, like most *Labiatae*, is caused by anthocyanins (HARBORNE 1992). Although bees (main pollinators for phryganic *Labiatae*: PETANIDOU 1996) are insensitive to red colours, they can receive a visual signal by contrasting colours (HARBORNE 1993). The distinct white pollen-grains and the glands contrasting with the deep purple anther, as well as the distinct venation of the membranous bracts of *O. dictamnus*, which can also be found in *O. calcaratum* (VRACHNAKIS 2002), can act as visual signal and honey guides for the pollinators (HARBORNE 1993, LUNAU 2000). The association of the colouration (anthocyanins) with papillate-cells and "hairless" epidermis is identical for *O. calcaratum* (VRACHNAKIS 2002). Ordinary epidermal cells that undergo an increase in surface extension with cuticular striations (papillate-cells) are the rule in reproductive organs (GLOVER & MARTIN 2000) and the ability of their cuticular striations to enhance light absorption and focusing/reflecting the light into pigment-containing areas is pointed out by GORTON & VOGELMANN 1996. Presence of anthocyanins in young non-floral tissues is reported for other "hairy" plants (NTEFIDOU & MANETAS 1996, NEIL & GOULD 1999). The defensive role of anthocyanins against herbivory and pathogen attack in the glabrous early stage (contrary to their alluring function on flowers) is suggested for *O. calcaratum* (VRACHNAKIS 2002), in agreement with LAMBERS & al. 1998, NEILL & al. 2002. The ability of the papillate-cells for secretion (as those on stigma and *tapetum*), and the confusion of glandular/eglandular hairs, which start their development as papillae, makes the division between trichomes in *O. dictamnus* a difficult task, or according to UPHOF 1962, "the decision to which group the hairs are to be referred, will always remain more or less subjective".

Concluding Remarks

As a plant which thrives in arid environments from sea level up to the alpine zone *O. dictamnus* needs a plasticity in the behaviour, necessary for adaptation in diverse abiotic and biotic factors. To cope with the adverse conditions the epidermis is equipped with specific structures which may act also as receptor for beneficial signals. The results of these needs are the multiforming trichomes. The trichome types are genetically linked, but their development and distribution is forced by environmental demands. In the reproductive stage the ephemerum makes the more easy (in term of time) changes or peculiarities of hairs. Besides the proposals of the ecological significance of plant trichomes, comparative studies from different disciplines will allow us to understand better such hairy aromatic plants which are confined in isolation (endemic) but thrive in a wide range of environments.

Acknowledgements

Prof. Dr. G. HEINRICH for corrections and comments on the manuscript, Ass.-Prof. Dr. E. STABENTHEINER for guidance on SEM, Dr A. PERKTOLD for technical support on figures and Mr. V. MAUROSOTIS for providing material of *O. dictamnus*.

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Jahr/Year: 2003

Band/Volume: [43_1](#)

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Artikel/Article: [Trichomes of Origanum dictamnus L. \(Labiatae\) . 109-133](#)