

The structure and development of the glandular trichomes of *Teucrium montanum* (Lamiaceae)

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Four distinct types of glandular and nonglandular (clothing) trichomes were studied by light and scanning electron microscopy in different plant parts of *Teucrium montanum* L. (sect. *Polium* (MILL.) SCHREB.). Peltate glandular trichomes, which are composed of one basal cell, one stalk cell and four- to eight-cellular glandular head; short capitate glandular trichomes with unicellular basal and stalk cell and bicellular head; long capitate glandular trichomes with one or two basal cells, one to four stalk cells and one head cell; clothing nonglandular trichomes composed of one to six cells and of uni- or bicellular foot (basal cell). The ontogeny of glandular trichomes is described. Qualitative differentiation of glandular trichomes (presence or absence of distinct types on various plant parts) among three subspecies of *Teucrium montanum* have not been found.

Key words: Lamiaceae, *Teucrium*, *Teucrium montanum* L., trichomes, ontogeny.

Introduction

The glandular trichomes are surface plant structures, which are usually in direct contact with surroundings. By their physical properties and by the production of different chemical products they play a great role in the protection against herbivores and pathogens, in the pollination and in other interactions between plants and environment.

Teucrium montanum L. is an aromatic species of the Lamiaceae growing in dry, calcareous stony or rocky grounds. Its European area extends from Spain, through South and Central Europe, to Crimea in Ukraine (TUTIN & WOOD, 1972). In the complex of *Teucrium montanum* SOJÁK (1983) recognised three morphologically distinct entities of species rank (*T. montanum* L., *T. pan-*

nonicum A. KERN. and *T. parnassicum* (ČELAK.) WETTST.). On the contrary KMEŤOVÁ (1993) and MÁRTONFI (1994) adopt the conception of subspecies: *T. montanum* L. subsp. *montanum*, *T. montanum* subsp. *pannonicum* (A. KERN) DOMIN, *T. montanum* subsp. *jilae* (JUZ.) SOÓ. These taxa differ in the length and shape of the clothing – the nonglandular hairs, especially of outer calyx, stem and leaves. *T. montanum* subsp. *montanum* has short and appressed clothing trichomes, whereas *T. montanum* subsp. *pannonicum* is a taxon with long and patent trichomes. *T. montanum* subsp. *jilae* represents an “intermediate” type. The distribution of subspecies is partially overlapping. The differentiation in chromosome numbers and in pollen grains has not been found (MÁRTONFI, 1994).

Trichome micromorphology in the genus *Teu-*

Table 1. Studied material of *Teucrium montanum*.

Subspecies	no. of collection (or no. of cultivation)	origin
<i>montanum</i>	PM/1990/2	Slovakia, Košecké Rovné, 500 m a.s.l., coll. MÁRTONFI, 1990
<i>jailae</i>	PM/1990/5,6	Slovakia, Slovenský Kras, Dvorníky, coll. MÁRTONFI, 1990
<i>pannonicum</i>	PM/1990/11	Slovakia, Poráč, coll. MÁRTONFI, 1990
<i>montanum</i>	PM/1990/16,18	Slovakia, Muráň, coll. MÁRTONFI, 1990
<i>pannonicum</i>	PM/1991/21,22	Slovakia, Pieniny, Lesnica, coll. MÁRTONFI, 1991
<i>jailae</i>	PM/1994/100	Slovakia, Jaklovce, 420 m a.s.l., coll. J. et R. MRÁZ, 1994
<i>pannonicum</i>	PM/1992/37	Slovakia, Kojšov, 900 m a.s.l., coll. P. MRÁZ, 1992
<i>jailae</i>	PM/1994/101	Slovakia, Veľká Lodina, 700 m a.s.l., coll. P. MRÁZ, 1994
<i>montanum</i>	PM/27	France, Quatzenheim W of Strassbourg, 137 m a.s.l., (Jardin botanique de l'Université de Strassbourg, France)
<i>montanum</i>	PM/44	origin unknown (Botanischer Garten der Universität, Frankfurt Main, Germany)
<i>montanum</i>	PM/45	origin unknown (Institute de botanique de l'Université, Neuchâtel, Switzerland)
<i>montanum</i>	PM/54	origin unknown (Jardin alpin commun, Meyrin, Switzerland)

crium has been studied mainly in the sections *Chamaedrys* (MILL.) SCHREB. and *Scorodonia* (HILL) SCHREB. (GRZYBEK, 1965, 1967; BINI MALECI & SERVETTAZ 1991, 1992; SERVETTAZ et al., 1992; SERVETTAZ et al., 1994; ANTUNES & SEVINATO-PINTO, 1991; BINI MALECI et al., 1995). The presence or unpresence of trichomes and oil glands on nutlets can be used as additional taxonomical markers in the infrageneric classification of genus *Teucrium* (MARIN et al., 1994). PUECH (1984) et NAVARRO (1995) evaluated the species in sect. *Polium* (MILL.) SCHREB. from Mediterranean area also on the basis of characters of clothing hairs. GRZYBEK (1967) included *Teucrium montanum* in morphological and anatomical comparison (incl. trichomes) of five species of the genus *Teucrium* indigenous in Poland. WERKER et al. (1985a,b,c) described the modes of secretion of glandular trichomes in some species of *Lamiaceae*.

The development of glandular trichomes has been described in few species of *Lamiaceae*: *Calamintha mentifolia* HOST (HANLIDOU et al., 1991), *Origanum* L. spp. (BOSABALIDIS & TSEKOS, 1982, 1984), *Sideritis syriaca* L. subsp. *syriaca* (KAROUSOU et al., 1992). In the genus *Teucrium* such development has not been examined yet.

The aim of the present study was evaluation of the structure and development of the glandular trichomes and search for pattern of the distribution of various types of glandular trichomes among the subspecies: *T. montanum* subsp. *montanum*,

T. montanum subsp. *pannonicum*, *T. montanum* subsp. *jailae*.

Material and methods

The seeds of *Teucrium montanum* were obtained from European botanical gardens and from natural populations in Slovakia. The material has been collected from the plants cultivated in the Botanical Garden of the University of P. J. Šafárik, Košice, Slovakia. Selected voucher specimens are deposited in the herbarium KO. The list of the analysed subspecies and their origin is given in the Table 1.

Different ontogeny stages of the trichomes have been studied on the cotyledons, hypocotyl, epicotyl of the seedlings; on the young and mature stem, leaves and flower organs.

Light microscopy. Hand cut or peeled epidermis of various plant organs was examined. Lipophilic substances were stained with Sudan III. Light microscopic figures were drawn with using the ABBE's apparatus. For microscopic preparation, segments of the plant organs were fixed with FAA, dehydrated in ethanol series, embedded in paraffin and sections 10–15 µm thick were prepared using microtome. The sections were stained with Safranin O, Delafield's hematoxylin, examined with light microscope and photographed (NĚMEC et al., 1962).

Scanning electron microscopy. Small pieces of material (leaves, stems, calyces, corollas, anthers, stamens) were fixed with FAA in cacodylate buffer (0.1 M) at pH 6.6, postfixed with 1 per cent OsO₄, dehydrated in ethanol series and in 2,2-dimethoxypropane, and coated with 20–30 nm gold layer (MRÁZ & POLÓNYI, 1988). The samples were examined in scanning electron microscope Tesla BS-340.

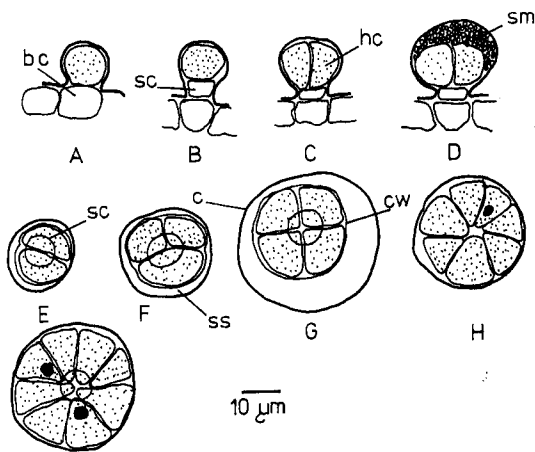


Fig. 1. Development of peltate trichomes (A). A-D, lateral look on ontogeny stages, E-I look from above on the developed glandular head (2,3,4,7,8-cellular stage) (bc - basal cell, c - cuticle, cw - cell wall, hc - head cell, sc - stalk cell, sm - secreted material, ss - subcuticular space).

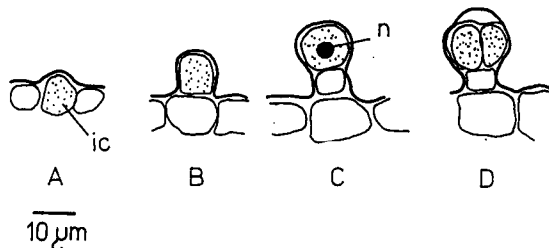


Fig. 2. Development of short capitulate trichome (B). A-D lateral look on the ontogeny stages. (ic - initial cell, n - nucleus).

Results

Types of the trichomes

The organs of *Teucrium montanum* bear numerous glandular and nonglandular trichomes on their surfaces. They can be classified according to BINI MALECI & SERVETTAZ (1991):

A: peltate trichomes with one basal cell, one stalk cell, and glandular head composed of four to eight cells; the subcuticular space is remarkably great (Fig. 1A-I; Plate 1/4-5, 2/1; 2/2).

B: short capitulate trichomes composed of one basal cell, one stalk cell, and two head cells, with smaller subcuticular space in comparison with the type A (Fig. 2A-D; Plate 1/3, 3/2).

C: long capitulate trichomes, which have usually one (sometimes two) basal cell, the stalk com-

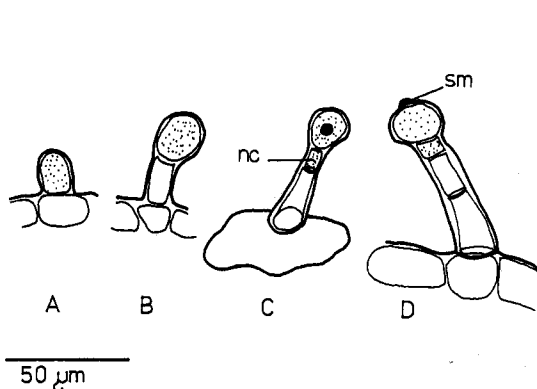


Fig. 3. Development of the long capitulate trichomes of type C. (nc - neck cell, sm - secreted material).

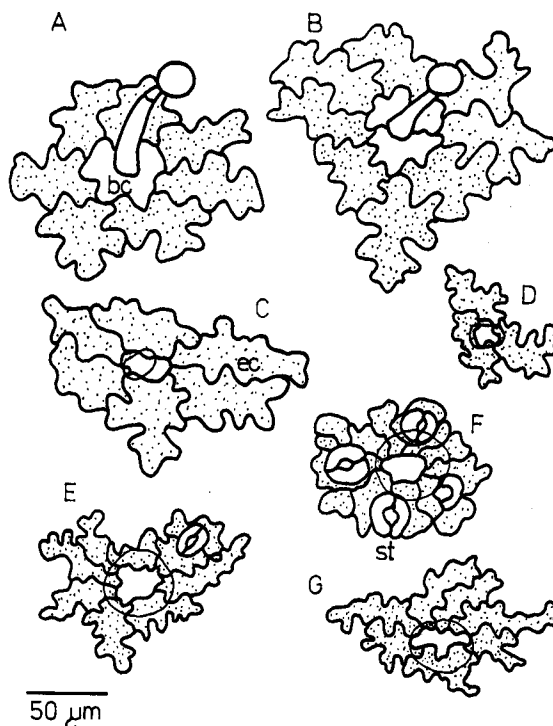


Fig. 4. Arrangement of the epidermal cells (dotted) around the basal cells (undotted) of glandular trichomes on the leaves. A-B basal cells of C trichomes; C-D basal cells of B trichomes; E-G basal cells of A trichomes (F - young leaf). (bc - basal cell, st - stomata, ec - epidermal cell).

posed of one to four cells (the upper one is often shorter and marked as neck cell, and one cell head; sometimes with small subcuticular space (Fig. 3A-D; Plate 1/2).

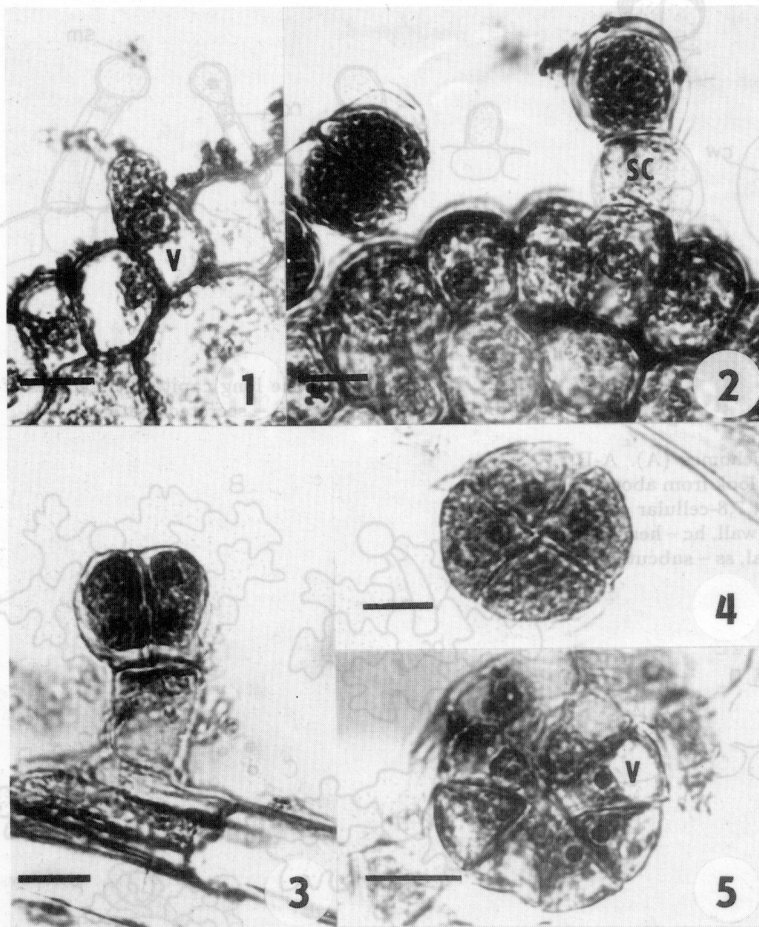


Plate 1. Structure of glandular trichomes on *Teucrium montanum* (bar - 10 μ m).

1. Cotyledon: one cell stage (initial cell) of developed trichome (v - vacuole).
2. Cotyledon: C trichome with one stalk cell (sc).
3. Stem: B type of glandular trichome with 2 head cells.
4. Leaf primordium: four cell of glandular head of A trichome.
5. Leaf primordium: glandular head of mature A trichome with seven secretory cell (v - vacuole).

D: nonglandular clothing trichomes, unbranched, uniseriate, multicellular composed of one to two basal epidermal cells and of one to six cells arranged in one row. Their surface is covered by cuticular micropapillae lacking on basal parts of the trichomes (Plate 3/2).

Ontogeny and structure of glandular trichomes

The trichomes of A type originates from an initial protodermal cell, which enlarges in the apical part. The centrally located nucleus of initial cell migrates to the cell apex. Basal region is vacuolated, apical one has dense cytoplasm. After periclinal division two daughter cells arise. The proximal cell, called basal cell, has a large vacuole with peripheral cytoplasm (Fig. 1A). The distal cell, containing dense cytoplasm, continues in the asymmetrical periclinal division. The result of this is a lower, smaller stalk cell and the upper, larger cell (mother head cell) (Fig. 1B). Mother head

cell divides anticlinally. Mature and fully formed head is composed of four to eight cells (Figs 1G-I; Plate 1/4-5). They are separated by radial cell walls. The nuclei of the mature head cells are centripetally, however, the large vacuoles centrifugally arranged (Fig. 1I; Plate 1/4-5). The cuticle layer becomes detached from the apical parts of the cell walls and the subcuticular space is formed (Figs 1D,1G). It contains a great amount of small droplets of yellowish-brownish colour which move terminally (Fig. 1G). The secreted compounds are released into the surroundings by following cuticle rupture of mature or mechanically damaged trichome. The secreted material gives positive staining with SUDAN III, indicating the presence of the lipophilic substances. The six or seven (rarely 5, 8, 9) epidermal cells of leaves surround the basal cell of the mature peltate gland, which is usually smaller than the epidermal cells (Figs 4E-G).

The ontogeny of B type of trichomes is similar

to ontogeny of the peltate trichomes. The mother head cell divides only once and gives rise to two daughter head cells. B trichomes form a smaller subcuticular space, where secreted material accumulates (Fig. 2D; Plate 1/3). Later it can pass across the cuticle (probably by small pores) on the head surface or it can be released by rupture of the cuticle. The basal cell of B trichomes is associated with 5 or 6 epidermal cells (rarely with 3, 4, 7, 8) and it is always smaller than epidermal cells (Fig. 4D).

The capitate trichomes (C type) initiate from single protodermal cell which undergoes an asymmetrical periclinal division resulting in proximal cell (basal cell), and distal cell (Fig. 3A). The final number of the stalk cells (1 to 4) depends on the number of the distal cell divisions. The head cell is on the top of the stalk. The secreted material is usually extruded through the cuticle on the glandular head, in form of small droplets (Fig. 3D). Sometimes the cuticle can be detached from the cell wall and forms small subcuticular space. After cuticular ruptures secreted material is released and the head acquires the cup-like shape. The basal epidermal cell (sometimes two basal cells) of C trichomes on the leaves does not differ in its size and shape from the surrounding epidermal cells. Their number is usually 6 (sometimes 5 or 7; seldom 4 or 8). In the case of two basal cells, they are surrounded by 8 or 7 epidermal cells (Fig. 4A-B).

Cotyledons and hypocotyles bear only glandular trichomes, whereas the clothing hairs are not present here.

The glandular trichomes originate in early development stages of plant parts. The high number of differentiated glandular trichomes can be seen on the young growing organs (high density of tri-

chomes). Fully developed plant organs bear only mature glands with lower trichome density on the unit of area.

There was no significant difference among three examined subspecies of *T. montanum* in the density and the distribution of the glandular hairs. For this reason all three subspecies of this species are included in the Table 2, describing trichome density and distribution.

Discussion

Structure and distribution of glandular trichomes

Peltate trichomes with four head cells were described in few species of the genus *Teucrium*, mainly in sect. *Chamaedrys* and sect. *Scorodonia* (GRZYBEK, 1965, 1967; BINI MALECI & SERVETTAZ 1991, 1992; SERVETTAZ et al., 1992; SERVETTAZ et al., 1994; ANTUNES & SEVINATO-PINTO, 1991; BINI MALECI et al., 1995). *Teucrium masiliense* L. (sect. *Scorodonia*) has also peltate trichomes with five- to eight-cellular head, but they are present only on the stems (BINI MALECI & SERVETTAZ, 1992). On *Teucrium montanum* GRZYBEK (1967) found peltate trichomes only with four head cells, without the stalk cell, which was not confirmed in the present study.

The results have shown that *T. montanum* have the same types of capitate trichomes (B and C type) as the other species of the genus *Teucrium*.

GÜEMES et al. (1992) provides a key for easier identification of some species related to the *Teucrium buxifolium* Schreber group based on the trichome characters. The authors have described *T. montanum* as a species lacking the capitate trichomes ("sin glándulas pedunculadas"), with only the peltate ones ("glándulas sentadas"). The ex-

Table 2. Trichome distribution on the different plant parts in *Teucrium montanum*.

Symbols indicate progressive increase of trichome number from no trichomes (-) to a number of trichomes which completely cover the surface (+++); ± indicates that few trichomes may be seen occasionally.

Plant parts	Stem	Leaf		Calyx		Corrola tube		Lower corrola lip		Filament
		adaxial side	abaxial side	outer side	inner side	outer side	inner side	upper side	lower side	
A	++	++	+++	++	± ¹	+	±	++ ³	++	-
B	+	+	+	++	± ¹	±	±	+ ³	+	-
C	++	++	++	++	+ ¹	++	+	++ ³	++	+ ⁴
D	+++	++	+++	+++	+ ¹	+	+ ²	+ ³	+	+ ⁵

Notes: ¹mainly in central and basal part; ²usually unicellular; ³in central part of lip, mainly around the veins; ⁴only in the middle part; ⁵in basal and central part, usually unicellular (sometimes bicellular).

