



STRUCTURE OF TRICHOMES FROM THE SURFACE OF LEAVES OF SOME SPECIES OF *KALANCHOË* ADANS.

ELŻBIETA WERYSZKO-CHMIELEWSKA* AND MYKHAYLO CHERNETSKYY**

Department of Botany, Agricultural University, ul. Akademicka 15, 20–950 Lublin, Poland

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The paper presents the results of studies on the structure of non-glandular and glandular trichomes occurring on the surface of leaves of eight species of the genus *Kalanchoë* Adans. (Crassulaceae DC.). Stereoscopic, light and scanning electron microscopy were used to observe the length and number of trichomes on a 1 mm² area of both surfaces of the leaf blade, the shape and number of their cells, the content of anthocyanins or tannins in the cells, cuticle sculpture, the presence of surface waxes, and protuberances of the cell walls of the mentioned structures. Considerable differentiation of trichome structure was observed. Trichomes were divided into eight types. Four were for non-glandular trichomes: bushy three-branched type (*K. beharensis* Drake et Castillo, *K. millotii* Hamet et H. Perr., *K. tomentosa* Bak), peltate stellate type (*K. hildebrandtii* Baill.), peltate sagittal-hastate type (*K. hildebrandtii*, *K. orgyalis* Bak.), and peltate rhomboid type (*K. rhombopilosa* Mann. et Boit.). The remaining four were for glandular trichomes: clavate type (*K. gastonis-bonnierii* R. Hamet et H. Perr.), capitate type (*K. beharensis*, *K. manginii* R. Hamet et H. Perr., *K. millotii*), peltate type (*K. millotii*) and truncate type (*K. orgyalis*). The presence of different types of dead non-glandular and glandular trichomes on the surface of the leaves, the morphology of which was studied in the present work, may be considered an important adaptation to the conditions of the natural environment.

Key words: *Kalanchoë* species, leaf, trichomes, structure, adaptation.

INTRODUCTION

Trichomes occur in plants in a great variety of forms, and are sometimes very complex structurally. As creations of the epidermis, they can be found on different parts of plants, fulfilling different essential functions (Esau, 1965). They are constant and typical features of taxa of different ranks, used for diagnosing plant material in different fields of science, for example in botany and pharmacognosy (Aneli, 1975).

During observations of leaf epidermis structure in over twenty species of the genus *Kalanchoë* Adans. (Crassulaceae DC.) from Madagascar, we noticed trichomes on plants of eight taxa. It is difficult to find reports on the structure of trichomal elements of the epidermis in this genus of plants. In papers on *Kalanchoë*, only the presence or absence of trichomes on the surface of shoots has been considered, with the type of structure seldom given (Hamet, 1907, 1908; Solereder 1908; Berger, 1930; Boiteau and Mannoni, 1948, 1949; Uphof, 1962; Metcalfe and Chalk, 1965; Jacobsen, 1981; Boiteau and Allorge-Boiteau, 1995; Rauh, 1995; Descoings, 2003). The descriptions do not clarify the forms of trichome structure. We undertook detailed

studies of the structure of trichomes on the leaf surface in selected species of *Kalanchoë*, to expand the list of characters for identification species of the genus. The results of these observations offer a better picture of the specific adaptations of plants to environmental conditions, and can be applied in taxonomy.

MATERIALS AND METHODS

Leaves of eight species of plants from the genus *Kalanchoë* were obtained from the glasshouse of the Botanical Garden of Marie Curie-Skłodowska University in Lublin: *Kalanchoë beharensis* Drake et Castillo, *K. gastonis-bonnierii* R. Hamet et H. Perr., *K. hildebrandtii* Baill., *K. manginii* R. Hamet et H. Perr., *K. millotii* R. Hamet et H. Perr., *K. orgyalis* Bak., *K. rhombopilosa* Mann. et Boit., and *K. tomentosa* Bak.

The surface of freshly gathered, typical, fully developed leaves of individual species of *Kalanchoë* was examined with an Olympus SZX 12 stereoscopic microscope. Attention was paid to the density, size, shape and color of the trichomes. The structural features of the trichome were examined in semi-permanent

e-mail: *elzbieta.weryszko@ar.lublin.pl **mczerneckyj@yahoo.com

glycerin preparations from fresh material, observed with a light microscope. In observations of the peridermal preparations, the number of non-glandular and glandular trichomes was counted in 1 mm² areas on both surfaces of the leaf blade, and the span of peltate hair plates was measured. The results are average values calculated from 30 measurements of two leaves from five plants of each species. The number of cells in uniseriate stalks of the trichomes of individual taxa was determined, and number of cells in the secretory structure of trichome glands.

Preparations stained with Lugol (J+KJ) liquid were checked for the presence of live cells in the structure of mechanical trichomes on different kinds of leaves. Sudan III was used for detection of ethereal oils and resins, and after treatment with potassium bichromate (K₂Cr₂O₇) the presence of tannins was determined. Trichome shape, cuticle sculpture and surface waxes were observed with a BS-300 Tesla electron scanning microscope. Leaf fragments were fixed for 12 h at 4°C in 2% glutaraldehyde with 2.5% paraformaldehyde in 0.075 M phosphate buffer, pH 6.8 (Glauert, 1974). Then they were dehydrated in an acetone series, critical-point dried in liquid CO₂, and gold-coated with a CS 100 sputter coater.

RESULTS

Except for *Kalanchoë gastonis-bonnieri*, leaves of the examined species are densely covered with non-glandular (*K. beharensis*, *K. hildebrandtii*, *K. millotii*, *K. orgyalis*, *K. rhombopilosa*, *K. tomentosa*) (Figs. 1a, 2a,b, 3b,d,f) or glandular (*K. manginii*) trichomes on both sides (Fig. 1d), very numerous on the abaxial epidermis. Trichomes seldom appear on the surface of the leaves of *K. gastonis-bonnieri*; they are glandular (Figs. 1h,i, 4e) and imperceptible to the naked eye. The non-glandular trichomes on the surface of *K. rhombopilosa* leaves are visible only under magnification. The epidermis of the leaves of *K. beharensis*, *K. millotii* and *K. orgyalis* also produces sparsely occurring glandular trichomes (Figs. 2j-m, o, p, 4g-j) in addition to non-glandular trichomes.

The trichomes on the leaves of particular species of *Kalanchoë* are multicellular, built of elongated biseri-ate stalks (Figs. 1b, g-i, 2f, g, k, n, o, 3a, g, 4a, d, g, h) which can also be observed in cross section (Fig. 4c, f). They vary in structure (Tab. 1) and consist of different numbers of cells, even within one taxon (Tab. 2), though the number of cells in the stalks of both kinds of trichomes is the same. The trichomes on the leaves of the examined *Kalanchoë* species differ visibly in length (Tab. 2).

NON-GLANDULAR TRICHOMES

The non-glandular trichomes occurring on the surface of mature leaves on the shoots of the examined *Kalanchoë* are dead epidermal structures. Live trichomes with clearly visible protoplasts occur only on the youngest

leaves developed from buds. As noted in Table 1, structurally they are bushy three-branched (*K. beharensis*, *K. millotii*, *K. tomentosa*) (Figs. 2b-d, 3f, g) or peltate (*K. hildebrandtii*, *K. orgyalis*, *K. rhombopilosa*) (Figs. 1a-c, 3a, b, d, e).

The peltate or scaly trichomes consist of 4-cellular oblate plates (Figs. 1a, 3a,b) on short stalks (Figs. 1b, d, 3a, e) 19.1 ± 2.36 µm long in *K. rhombopilosa*, 22.3 ± 3.28 µm long in *K. hildebrandtii*, and 42.1 ± 3.49 µm long in *K. orgyalis*. One seriate trichome stalk is built of 2-5 cells (Tab. 2). The peltate part of a *K. rhombopilosa* trichome is rhombus-shaped with concave external walls (Figs. 1a, 3a). The average diagonal length of these parts ranges from 255.3 ± 20.35 to 285.6 ± 19.79 µm (1:1.12 ratio). The cells of some trichomes of this taxon probably contain anthocyanins (Fig. 1a) which make a purple-colored stain on the leaves. The plate of *K. hildebrandtii* and *K. orgyalis* trichomes is sagittahastate in shape (Figs. 1c, 3b,d). This type of trichome and also more peltate trichomes of stellate shape with six arms are observed on *K. hildebrandtii* leaves (Fig. 3d). The trichomes of the two species differ in the span of the oblate parts, averaging 266.3 ± 25.09 µm in *K. hildebrandtii* and 685.1 ± 48.03 µm in *K. orgyalis*.

Microscopic observation of bushy three-branched trichomes (*K. beharensis*, *K. millotii*, *K. tomentosa*) revealed that their three radial bifurcations consisted of four mucronate prosenchyma cells, visible after separating the trichome cells (Fig. 2e,f). In dead trichomes, fragments of two cells twisting around the axis were also seen (Fig. 2i). One seriate trichome stalk can be built of 3-12 cells, and in *K. millotii* can reach even 20 cells (Tab. 2). Some trichome stalk cells of *K. beharensis*, *K. millotii* and *K. tomentosa* accumulate tannin (Fig. 2h), and we observed pigmentation the approximate color of anthocyan in trichome cells at the end of the leaf teeth in *K. tomentosa* (Fig. 2a).

On the surface of non-glandular trichomes there was cuticular ornamentation in the form of stripes lying along the branch of the trichome (*K. beharensis*, *K. millotii*, *K. orgyalis*, *K. tomentosa*) (Fig. 3c,h,i), or irregular ornamentation (*K. hildebrandtii*, *K. orgyalis*, *K. rhombopilosa*). Wax occurred in the form of lumps of different sizes, scattered (Fig. 3c) or dense in some areas (Fig. 3h,i). Cell wall protuberances were found on the surface of the branched trichome in *K. millotii* (Fig. 3i). The cuticle of trichomal elements of the epidermis is coarsely stratified. Sometimes ruptures are visible.

The longest protective trichomes (bushy three-branched) were found in *K. tomentosa*, and the shortest (peltate) in *K. rhombopilosa* (Tab. 2). The average length of a *K. rhombopilosa* trichome is about 3.5% the average length of a *K. tomentosa* trichome. The length of non-glandular trichomes is practically the same on both sides in the examined species, except for *K. beharensis* (Tab. 2). In this taxon, trichomes of the abaxial surface are ~91% the length of those on the adaxial

TABLE 1. Types of trichomes occurring on the leaf surface of 8 examined species of *Kalanchoë*

	Type of trichome	Species
Non-glandular	Bushy three-branched	<i>K. beharensis</i> , <i>K. millotii</i> , <i>K. tomentosa</i>
	Peltate	
	Stellate	<i>K. hildebrandtii</i>
	Sagittal-hastate	<i>K. hildebrandtii</i> , <i>K. orgyalis</i>
	Rhomboi	<i>K. rhombopilosa</i>
Glandular	Clavate	<i>K. gastonis-bonnierii</i>
	Capitate	<i>K. beharensis</i> , <i>K. manginii</i> , <i>K. millotii</i>
	Peltate	<i>K. millotii</i>
	Truncate	<i>K. orgyalis</i>

surface. The largest number of non-glandular trichomes are produced by the epidermis of *K. millotii*, and the fewest by *K. beharensis* (Tab. 2).

GLANDULAR TRICHOMES

As listed in Table 1, structurally the glandular trichomes are clavate (*K. gastonis-bonnierii*) (Figs. 1h,i,

4e), capitate (*K. beharensis*, *K. manginii*, *K. millotii*) (Figs. 1e–g, 2j–m,o,p, 4a,b,i), peltate (*K. millotii*) (Fig. 4h) or truncate (*K. orgyalis*) (Fig. 4g). They form 2-cellular (*K. beharensis*, *K. gastonis-bonnierii*, *K. millotii*, *K. orgyalis*) (Figs. 1h, 2k,o,p, 4g) or 4-cellular (*K. gastonis-bonnierii*, *K. manginii*, *K. millotii*) (Figs. 1i, 2m, 4a,e,h) gland structures on top of the stalk, which probably secrete ethereal oils (Sudan III treatment) (Figs. 1f, h, i, 2j–m, o, p). One seriate glandular trichome stalk contains 2 to 9 cells (Tab. 2). In contrast to non-glandular trichomes, the surface of glandular trichomes is smooth or wavy (Fig. 4i), and the coarsely stratified cuticle is sometimes covered with globules of wax (Fig. 4b, g, h).

The localization of glandular trichomes on the leaf surface of *Kalanchoë* varies greatly between species. In *K. beharensis* and *K. millotii*, glandular trichomes occur in higher density on petioles than on leaf blades. In *K. beharensis* there are more on the top side of the leaf blade than on the bottom; together with non-glandular trichomes they form separated, non-uniformly arranged groups on the adaxial side. The largest number of glandular trichomes are produced by the epidermis of *K. manginii*, and the fewest by *K. beharensis* (Tab. 2). The shortest gland trichomes were found in *K. orgyalis*, 5.4 times shorter than the longest trichomes observed in *K. manginii* (Tab. 2).

TABLE 2. Some structural features of trichomes on the leaf surface of the examined species of *Kalanchoë*

Species	Non-glandular trichomes				Glandular trichomes				Number of cells in one seriate trichome stalk	
	Average length (µm)		Average number in 1 mm ²		Average length (µm)		Average number in 1 mm ²		Non-glandular	Glandular
	AD	AB	AD	AB	AD	AB	AD	AB		
<i>K. beharensis</i>	852.5 ±47.29	776.9 ±45.13	19.1 ±1.61	21.2 ±1.03	51.2 ±3.87	50.6 ±3.11	0.63 ±1.45	0.40 ±0.72	3–6	2–3
<i>K. gastonis-bonnierii</i>	-	-	-	-	100.1 ±12.26	105.4 ±12.58	0.47 ±2.36	0.49 ±2.17	-	3–4
<i>K. hildebrandtii</i>	46.1 ±8.48	47.1 ±7.92	49.6 ±1.58	51.9 ±1.72	-	-	-	-	2–4	-
<i>K. manginii</i>	-	-	-	-	155.3 ±17.34	150.7 ±18.13	7.08 ±2.15	8.49 ±2.49	-	6–9
<i>K. millotii</i>	536.7 ±46.84	539.1 ±49.30	42.5 ±0.93	52.4 ±1.15	50.7 ±3.61	52.3 ±3.82	0.71 ±0.58	0.65 ±0.81	5–12 (to 20)	4–5
<i>K. orgyalis</i>	114.7 ±11.38	120.3 ±12.04	26.2 ±1.21	39.6 ±0.83	28.7 ±2.49	29.1 ±2.73	1.36 ±0.71	1.73 ±0.94	2–4	3–4
<i>K. rhombopilosa</i>	42.8 ±6.89	43.4 ±7.23	17.7 ±1.08	27.6 ±1.33	-	-	-	-	3–5	-
<i>K. tomentosa</i>	1249.7 ±88.69	1258.9 ±91.43	35.4 ±0.75	42.5 ±0.48	-	-	-	-	4–8 (to 12)	-

-- trichomes do not occur; ± – standard deviation; AD – adaxial surface; AB – abaxial surface.

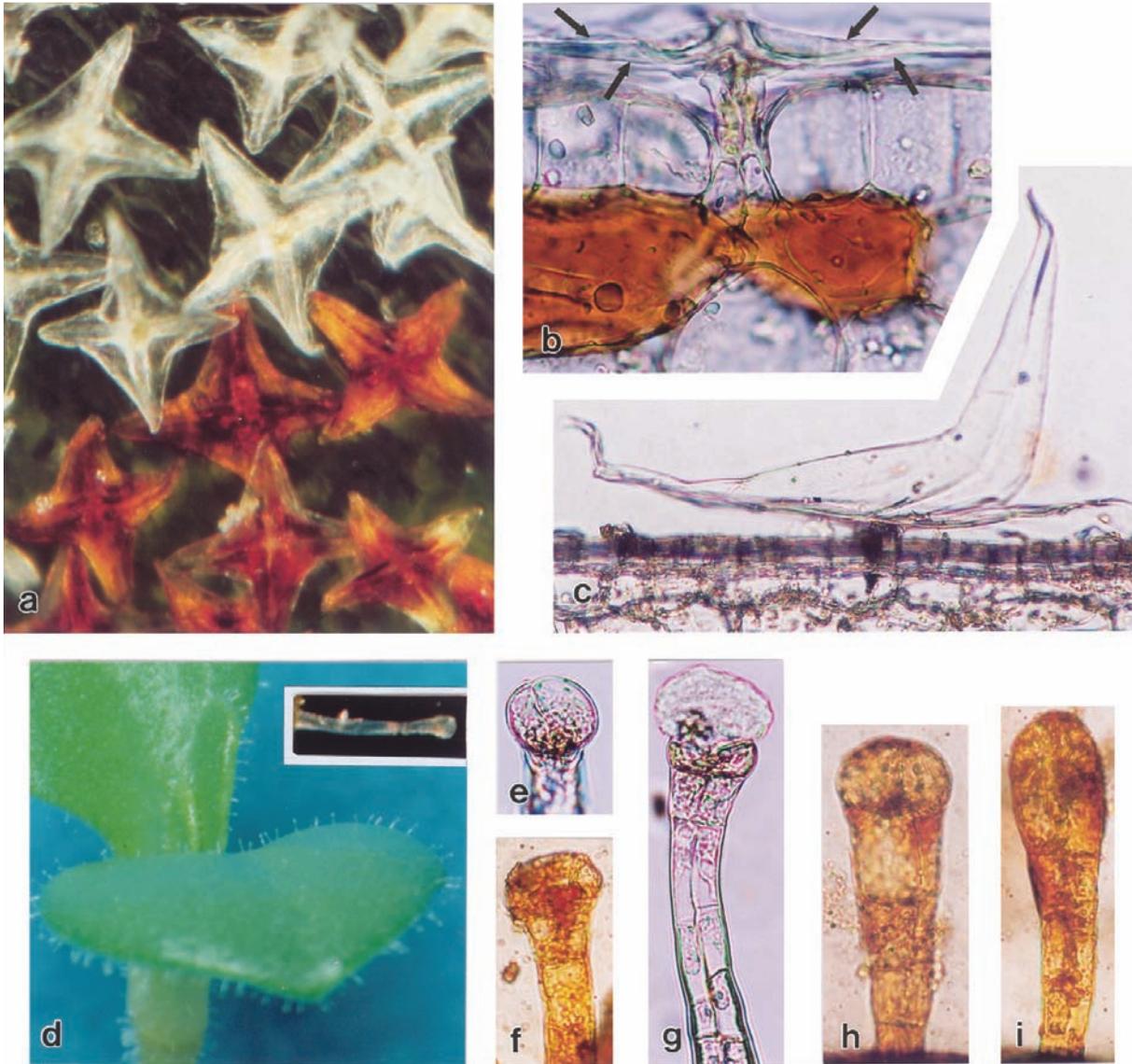


Fig. 1. Fragments of leaf surface of two *Kalanchoë* species, showing structure of glandular and peltate non-glandular trichomes of four *Kalanchoë* species. **(a,b)** *K. rhombopilosa*: **(a)** Peltate trichomes of rhomboid shape (quadrilateral star) with concave external walls from adaxial surface of leaf. Trichome anthocyanins in vacuoles are visible. $\times 150$, **(b)** Transverse section of leaf fragment, with peltate trichome visible (arrows), with biseriate stalk between cells of the epidermis. $\times 600$, **(c)** *K. orgyalis*: peltate trichome on leaf transverse section. $\times 200$. **(d-g)** *K. manginii*: **(d)** Fragment of top of seed leaves covered with small trichomes. $\times 9$, at right is multicellular glandular trichome. $\times 130$, **(e-g)** Capitate glandular trichomes at different phases of maturation. $\times 480$, **(e)** Top view of glandular structure of trichome, **(f)** Adaxial part of the trichome, stained with Sudan III, **(g)** Fragment of multicellular biseriate stalk; head with secretion after splitting of cuticle is also visible. **(h,i)** *K. gastonis-bonnierii*: multicellular glandular trichomes of clavate shape, stained with Sudan III. $\times 480$.

DISCUSSION

These results demonstrate the considerable variety of trichomal structures on leaf surfaces in the examined species of *Kalanchoë*. These trichomes were divided into eight types (Tab. 1). Our findings supplement and systematize the existing data on trichome structure (Hamet, 1907, 1908; Solereder, 1908; Berger, 1930;

Boiteau and Mannoni, 1948, 1949; Uphof, 1962; Metcalfe and Chalk, 1965; Jacobsen, 1981; Boiteau and Allorge-Boiteau, 1995; Rauh, 1995; Descoings, 2003). It should be pointed out that the well-known "three-armed" type of trichome of *K. beharensis* and *K. tomentosa* has not previously been characterized in detail; the present work discusses this issue. This paper also gives the first report of the occurrence of glandular trichomes

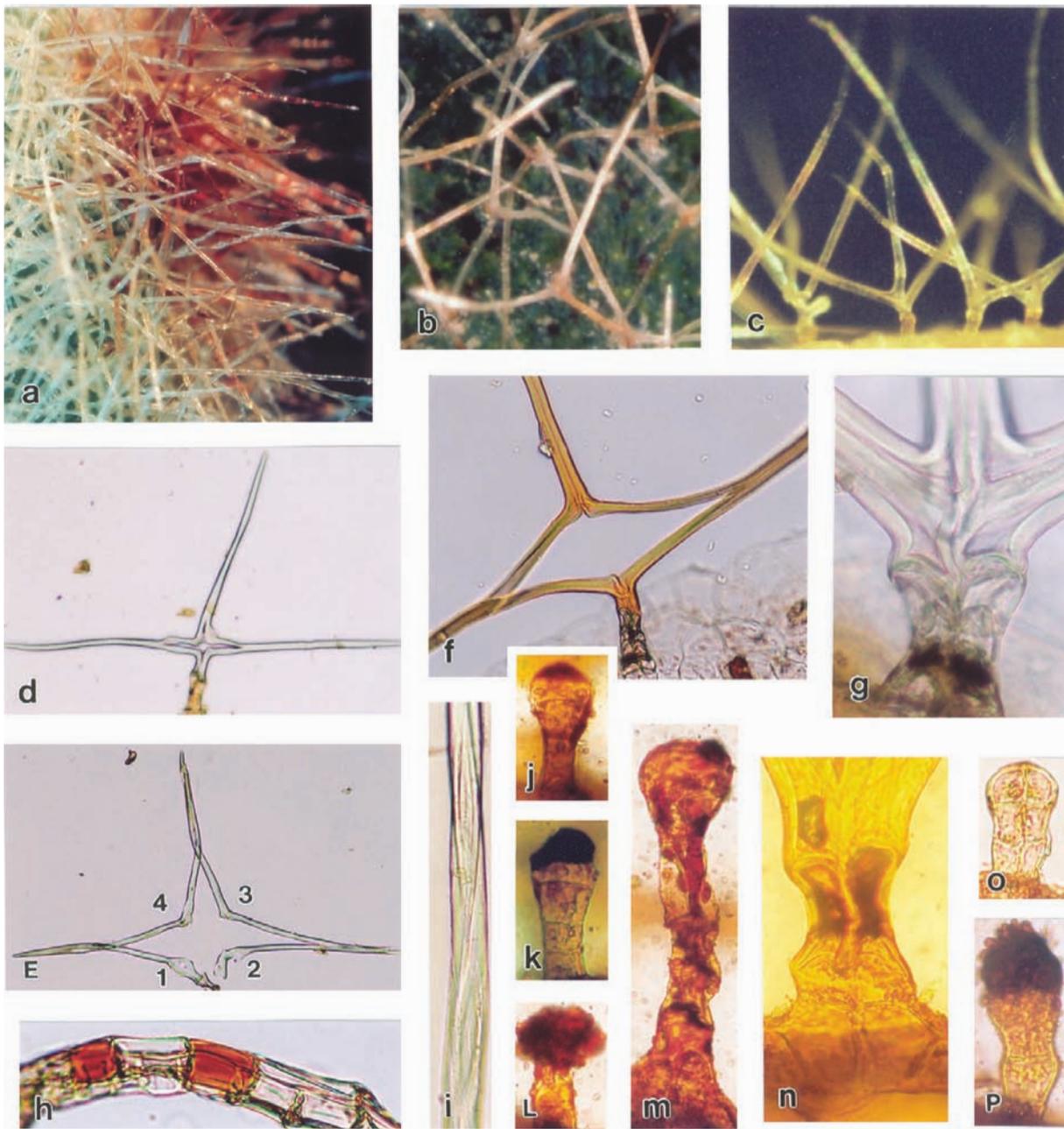


Fig. 2. Fragments of leaf surface of two *Kalanchoë* species, showing structure of glandular and bushy three-branched non-glandular trichomes of three *Kalanchoë* species. **(a,g,i)** *K. tomentosa*: **(a)** Tooth on leaf rim with trichomes, the cells of which probably contain anthocyanins. $\times 40$, **(g)** Basal part of trichome, showing stalk with fragments of three ramifications. $\times 480$, **(i)** Segment of dead trichome with fragment of two interlocked cells. $\times 300$. **(b, c, n-p)** *K. beharensis*: **(b)** Top view of non-glandular trichomes of adaxial surface. $\times 80$, **(c)** Bushy three-branched non-glandular trichomes on leaf transversal section. $\times 90$, **(n)** Basal part of multicellular non-glandular trichome. $\times 480$, **(o, p)** Capitate glandular trichomes at different phases of maturation, stained with Sudan III. $\times 480$. **(d-f, h, j-m)** *K. millotii*: **(d)** Bushy three-branched trichome. $\times 90$, **(e)** Adaxial part of non-glandular three-branched trichome with radial prosenchyma cells separated and numbered. $\times 90$, **(f)** Fragment of young non-glandular trichome stained with Lugol liquid after separation of branching cells. $\times 200$, **(h)** Part of multicellular stalk of non-glandular trichome with two cells accumulating tannins, stained with potassium bichromate. $\times 480$, **(j-m)** Multicellular glandular trichomes with capitate glandular structure at different phases of maturation, stained with Sudan III. **(j-l)** $\times 480$, **(m)** $\times 600$.

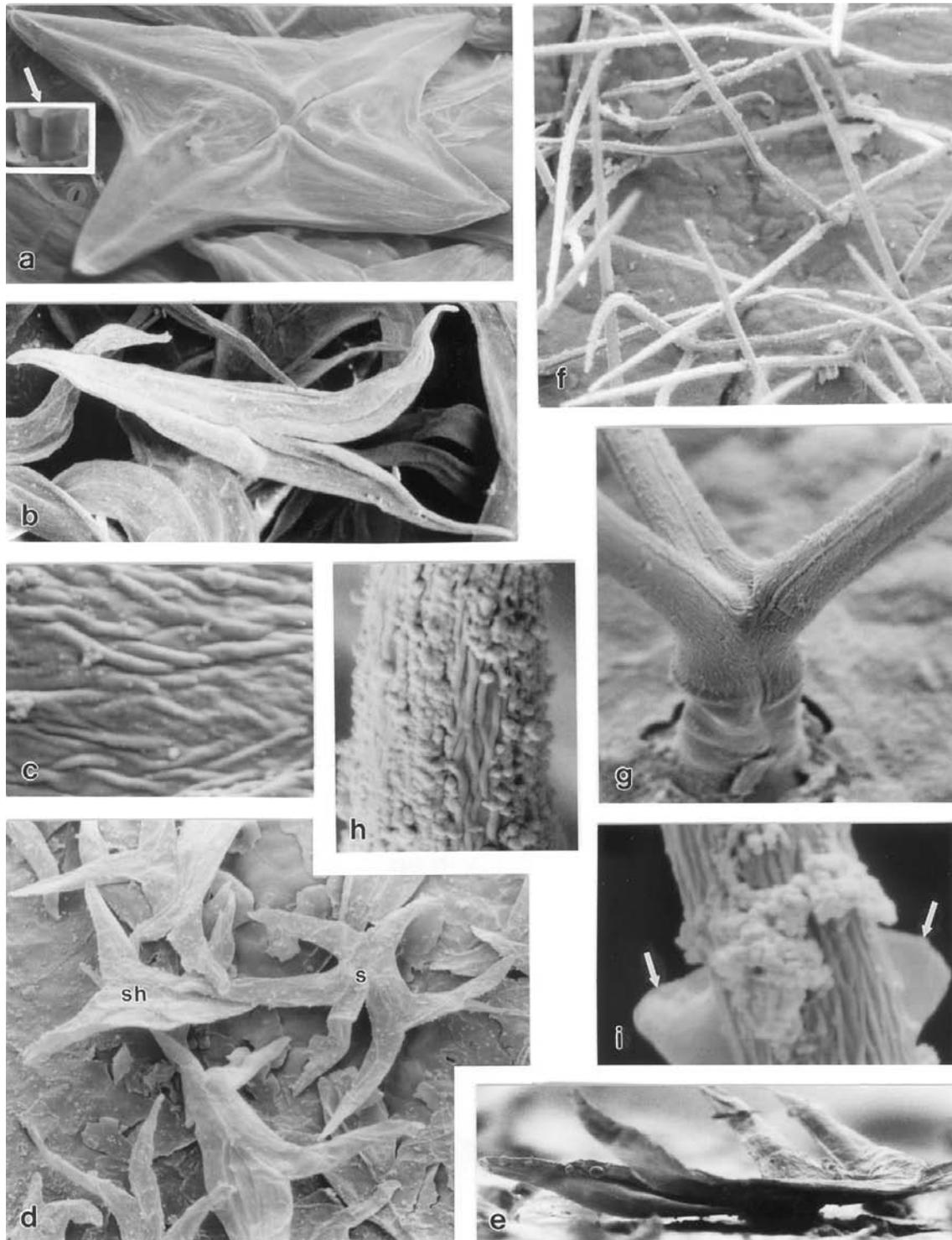


Fig. 3. Structure of non-glandular trichomes of five *Kalanchoë* species (SEM). **(a)** *K. rhombopilosa*: adaxial part of peltate trichome formed from four cells. $\times 420$. Arrow indicates biseriate leaf stalk. $\times 650$. **(b, c)** *K. orgyalis*: **(b)** Adaxial view of leaf of sagittal-hastate shape. $\times 250$, **(c)** Fragment of adaxial surface of trichome with striped cuticle. $\times 4500$. **(d, e)** *K. hildebrandtii*: **(d)** Fragment of prepivotal surface of leaf, with peltate trichomes of irregular shape: stellate (s), sagittal-hastate (sh). $\times 280$, **(e)** Lateral view of peltate trichome. $\times 620$. **(f-h)** *K. beharensis*: **(f)** Fragment of leaf surface with non-glandular trichomes. $\times 130$, **(g)** Basal part of trichome with visible ramification. $\times 650$, **(h)** Fragment of trichome ray with cuticular striae covered with lumps of wax. $\times 4500$, **(i)** *K. millotii*: part of trichome ray with visible cuticular striae, concentration of wax lumps and protuberances (arrows). $\times 4500$.

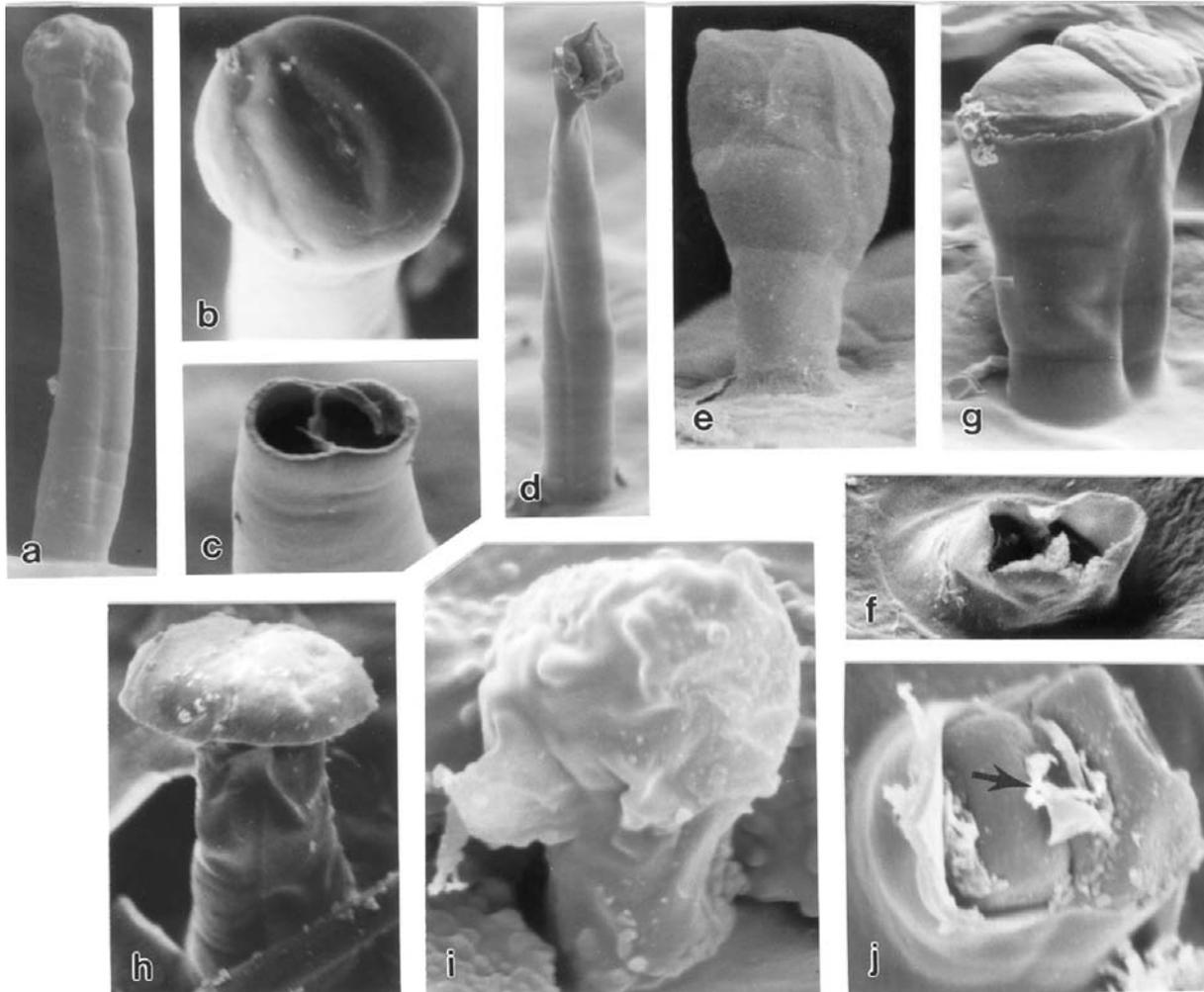


Fig. 4. Multicellular glandular trichomes of five *Kalanchoë* species (SEM). (a–d) *K. manginii*: (a) Trichome habit, with the head formed from four glandular cells set on a biseriate stalk. $\times 650$, (b) Top view of glandular part of trichome. $\times 1600$, (c) Fragment of transversal section of trichome stalk. $\times 1300$, (d) Trichome with broken cuticle after liberation of secretion. $\times 510$. (e, f) *K. gastonis-bonnierii*: (e) Clavate trichome. $\times 1000$, (f) Fragment of basal part of trichome stalk. $\times 1300$, (g) *K. orgyalis*, truncate trichome. $\times 1600$, (h) *K. millotii*, peltate trichome. $\times 1300$, (i, j) *K. beharensis*: (i) glandular trichome with head covered by visible layer of cuticle. $\times 1600$, (j) top view of glandular part of trichome with broken cuticle and dried secretion on the surface of gland cells (arrow). $\times 1600$.

on the surface of the leaves of *K. beharensis*, *K. gastonis-bonnierii*, *K. millotii* and *K. orgyalis*.

The non-glandular trichomes apparently are the most diverse in terms of length, density of occurrence, number of cells in the stalk (Tab. 2), shape of the upper part (Tab. 1), cuticle ornamentation, the presence of protuberances (*K. millotii*) and the occurrence of wax on their surface. The upper part of non-glandular trichomes of different shapes (sagittal-hastate, stellate, rhombus, bushy three-branched) is formed of four cells. Different secretory parts of gland trichomes vary in the number of cells, length, and density of occurrence on the leaf surface, and differ in many respects from non-glandular trichomes.

The presence of different types of trichomes on the leaf surface the examined species of *Kalanchoë* is adaptive. In natural conditions these plants grow in the south and more rarely in central Madagascar (Jacobson, 1981; Boiteau and Allorge-Boiteau, 1995; Rauh, 1995; Descoings, 2003). The examined *Kalanchoë* species occur in subarid hot climate (*K. beharensis*, *K. millotii*, *K. orgyalis*, *K. rhombopilosa*), semiarid hot climate (*K. beharensis*, *K. gastonis-bonnierii*, *K. hildebrandtii*, *K. manginii*, *K. millotii*, *K. orgyalis*, *K. rhombopilosa*, *K. tomentosa*), subhumid temperate-cool climate (*K. gastonis-bonnierii*, *K. hildebrandtii*, *K. manginii*, *K. tomentosa*) and subhumid hot and humid hot climate (*K. gastonis-bonnierii*) (Sokolov, 1990; Boiteau

and Allorge-Boiteau, 1995; Rauh, 1995). These succulents store water in the leaves and even in the stem, and in the course of evolution have also gained other features adapting them to conditions of high insolation. Thus, the surface of *Kalanchoë* leaves is covered tightly and protected from excessive transpiration and overheating by long, bushy three-branched non-glandular trichomes, which create a tomentum, as well as by plates of peltate structures. Some researchers report that plant surfaces densely covered by trichomes exposed to high insolation reflect light more than uncovered ones do, reducing the intensity of transpiration (Pearman, 1966; Wuenschel, 1970; Szwarcbaum, 1982; McClendon, 1984; Baldini et al., 1997). Other authors observed decreased transpiration in plants having dead trichomes (Shennikov, 1950; Grigorev, 1955). On the other hand, the presence of live non-glandular trichomes enlarges the plant surface and increases transpiration, because the cuticular transpiration of trichomes is considerably higher than that of epidermis cells (Miroslavov, 1974). Our observations of the non-glandular trichomes on the surfaces of the different kinds of plant leaves examined indicate that they are short-lived. Necrosis of the cellular content, connected with the filling of the interior with air, takes place in non-glandular trichome cells of *Kalanchoë* leaves that have not yet fully formed. The presence of dead non-glandular trichomes on the surface of *Kalanchoë* leaves can be considered a protective structure enabling maintenance of surface moisture (Miroslavov, 1974). It is one of the most important xeromorphic features. Secretion of different substances through glandular trichomes, which often have ecological importance, is also significant (Fahn and Shimony, 1996).

These results on the structure of trichomes on leaf surfaces in several species of *Kalanchoë* have no equivalents in the literature, and provide taxonomic characters of diagnostic value.

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