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Different Trichome Types on the Leaves of Styrian Oil Pumpkin

By

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With 5 Figures

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Summary

KOLB D. & MÜLLER M. 2003. Different trichome types on the leaves of Styrian oil pumpkin. – *Phyton* (Horn Austria) 43 (2): 365–379, with 5 figures. – English with German summary.

Conventional chemical fixation and histochemical preparation with Schiff reagent were used to investigate the ontogeny of four different types of glandular and non-glandular trichomes of *Cucurbita pepo* L. subsp. *pepo* var. *styriaca* GREB. and their distribution on the leaf surface.

The trichomes originate from single epidermal cells, which first undergo a periclinal division. A continuous series of divisions lead to the formation of the different trichome types. On the leaf surface of Styrian pumpkin, three glandular trichome types, digitiform hairs and bristle hairs can be distinguished. All capitate types consist of a basal, a stalk and a head region and these parts differ in the number of cells. The first trichome type, type I, consists of a basal cell, a short stalk and a four-celled head region. Type II, the so called “neck-cell” type is characterised by a long stalk region and a two-celled head region. The third investigated trichome type, type III, the “acuminate-digit”, consists of a short stalk and a bicellular head region, which shows only a small constriction and no clear distinction between the head and the stalk area. The fourth described trichome, type IV, the so called “stipitate-capitate”, is the biggest one and visible without the microscope. This hair type is characterised by a multicellular base, a uniseriate stalk and a multicellular head region. The above

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described trichomes and the bristle hairs are fully developed, when the leaf reaches a size of 3mm. Investigations were carried out with light microscope (LM) and scanning electron microscope (SEM).

Zusammenfassung

KOLB D. & MÜLLER M. 2003. Unterschiedliche Trichomtypen an den Blättern von Steirischen Ölkürbissen. – *Phyton* (Horn Austria) 43 (2): 365–379, mit 5 Abbildungen. – Englisch mit deutscher Zusammenfassung.

In dieser Arbeit wurde die Ontogenese von drei köpfchenförmigen Trichomen und einem nicht sekretorisch tätigen Haar, welche an der Blattoberfläche von *Cucurbita pepo* L. subsp. *pepo* var. *styriaca* GREB. vorkommen, untersucht. Die Trichome finden ihren Ursprung in einer einzelnen Epidermiszelle, die sich periklin teilt. Eine kontinuierliche Serie von Teilungen führt zu den unterschiedlichen Haartypen. An der Blattoberfläche des Steirischen Ölkürbis befinden sich neben Borstenhaaren, besonders köpfchenförmige Haare mit unterschiedlicher Morphologie. Diese besitzen immer eine Basalzelle, eine unterschiedliche Anzahl von Stielzellen und einen Köpfchenbereich. Die zuletzt genannte Region unterscheidet sich bei den einzelnen Haaren durch eine sich ändernde Zellanzahl. Der erste Haartyp, Typ I, ist der charakteristische *Cucurbitaceen*-Drüsenhaartyp und besteht aus einer Basalzelle, einem kurzen Stiel und aus einem vierzelligen Köpfchenbereich. Typ II, der sogenannte „neck-cell“ Typ ist charakteristisch für seinen langen Stiel und sein zweizelliges Köpfchen. Der dritte untersuchte Haartyp, Typ III, der als „acuminate-digit“ bezeichnet wird, beinhaltet einen kurzen Stiel, eine zweizellige Köpfchenregion, welche eine kleine Einbuchtung am Ende dieses Bereiches aufweist, jedoch keine klare Abgrenzung zwischen Köpfchen- und Stielbereich. Der zuletzt beschriebene Trichomtyp, Typ IV, genannt „stipitate-capitate“, ist der größte und ohne Zuhilfenahme eines Mikroskops sichtbar. Das Haar ist charakteristisch für seinen multizellulären Sockel, einen wenigzelligen Stielbereich und ein mehrzelliges Köpfchen. Diese beschriebenen Trichome, sowie die Borstenhaare, sind bereits bei einer Blattlänge von 3 mm voll entwickelt. Die Untersuchungen wurden mit dem Licht- und Rasterelektronenmikroskop durchgeführt.

Introduction

Cucurbita pepo is native in central America especially in Mexico and it is one of the oldest crops of the world. After the Spaniards had discovered America, pumpkin was imported to Europe, where it was welcomed as a cheap and nutritional vegetable. At the end of the 19th century a mutation introduced the variation *Cucurbita pepo* L. subsp. *pepo* var. *styriaca* (TEPNER 2000). Most, if not all species possess glandular and non-glandular trichomes and these epidermal hairs are widespread anatomical features of higher plants. The morphology of such structures can vary greatly between tissues and species (MC CASKILL & al. 1992). The botanical literature contains more than 300 descriptions of different trichome types to characterise the morphological types. Trichomes are defined as epidermal appendages of diverse form, structure and function. Glandular and non-glandular trichomes are an integral element of the plant surface.

All outgrowths from the epidermis are termed as trichomes (ESAU 1965, FAHN 1979, JOHANSON 1975, WERKER 2000). These appendages arise from a series of anticlinal and periclinal divisions to form specialised trichomes that are glandular or not. Differences in the habitus of plant trichomes can be used in plant classification, they are taxonomically useful. Functionally, trichomes can protect the plants from herbivores or from heat and sunlight etc. (CROTEAU 1977, DUKE 1994, WERKER 1993). WERKER & al. 1985 postulated that capitate and peltate hairs are involved in the defence against pathogens. Further, they control the leaf temperature as well as the water loss. Especially glandular trichomes produce chemical substances, which are stored at the plant surface (WAGNER 1991, GRAYER & al. 1996). They are found as unicellular as well as multicellular and stalked structures. However, the majority consists of a foot, a stalk and a head region.

Most of the morphological and structural investigations and the resulting deliverables are generally made by species of *Asteraceae* (MONTEIRO & al. 2001) and *Lamiaceae* (ASCENSAO & al. 1999, BISIO & al. 1999), but only few of these structural observations include ontogenetical aspects.

There is only one study of a trichome ontogeny of *Cucurbitaceae* for *Cucumis* (UPHOF 1962) with long and uniseriate trichomes, which exist on the corolla of the pumpkin flower.

The aim of this work was to carry out the ontogenetical study of three different capitate trichome types and one digitform hair type of Styrian pumpkin. In this work light microscope (LM) and scanning electron microscope (SEM) were used to determine the ontogeny of the various types. The bigger part of the investigations was carried out with LM and histochemical procedures were used to localise the nucleus in different cell division stages (UPHOF 1962). SEM observations were added for a further characterisation of the morphology, ontogeny and structure of these types.

Material and Methods

Plant material

Leaves of *Cucurbita pepo* L. subsp. *pepo* var. *styriaca* GREB. were collected from two weeks old plants grown in climate chambers of the Institute of Plant Physiology, Graz. To establish the experiments seeds were grown on Perlite under defined climatic conditions with a photoperiod of 12 hours (PAR 400–700 $\mu\text{mol m}^{-2} \text{sec}^{-1}$), day and night temperature were 22 and 18°C, respectively, the relative humidity was 70%.

Light microscopy

Leaves were collected and fixed in ethanol:glacial acidic acid (3:1=v/v) for at least 24 h. After fixation the plant material was hydrolysed in 1 M HCl for 10 min at 60°C and stained in freshly prepared Schiff reagent for 60 min (modified according to MÜLLER & al. 1991).

After the preparation steps the epidermis from the leaf surface was drawn off. The investigations were conducted under a Zeiss microscope: Zeiss Axioskop was used to obtain digital images with colour video camera (Sony DXC 930 P with Sony-control-system) and a frame grabber (ITI MFG-3M-V, Imaging Technology Inc. with variable scan module AM-VS-VP and colour recording module AM-CLR-VP) was used. The images were obtained through Zeiss 40 $\times$, Zeiss 63 $\times$ dry objectives and Zeiss 100 $\times$ oil immersion objective and an image analysis system, Optimas 6.5.1. BioScan Corp., was used.

The number of trichomes per mm² surface area was counted directly on LM images at 40 $\times$ magnification.

Scanning electron microscopy

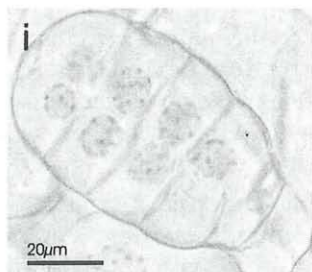
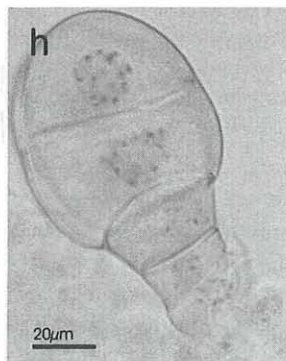
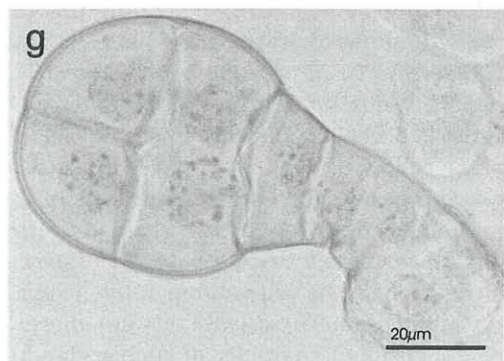
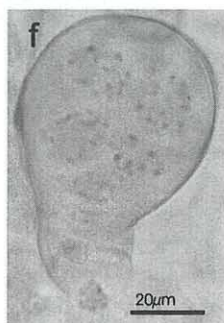
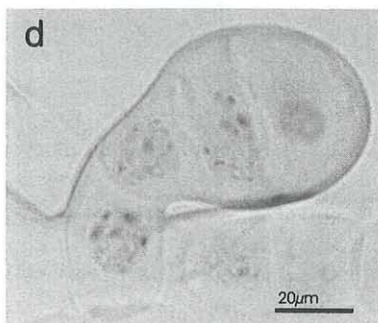
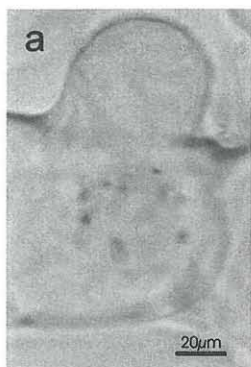
The leaves were fixed in 2.5 % glutardialdehyde in 0.1M phosphate buffer (pH 7.2) for 24 h at 4°C. After fixation, the leaves were subsequently dehydrated in a graded acetone series, critical point dried with CO₂ and the specimens were sputter-coated with a thin layer of gold. Observations were carried out on a Philips XL 30 ESEM operating at 20 KV under high vacuum conditions (ROBINSON & al. 1987).

Results

The development of the different trichome types of Styrian pumpkin starts very early in the ontogeny of the plant leaf, which is visible in the overview of Fig. 5a, showing the density of trichomes on a young leaf. By the investigations with light and scanning electron microscopy four different and ontogenetical independent capitate trichome types could be observed. Distinctions are visible in the structure, in the spreading on the leaf surface and also in their function.

The adaxial and abaxial surface of young leaves of Styrian pumpkin shows numerous glandular and non-glandular trichomes. The investigated trichomes can be categorised into four different types. Typ I is the "characteristic" short stalked Cucurbita type with four cells in the head region (Fig. 1g). A mature and fully developed glandular trichome is about 110 $\mu\text{m} \pm 33$ (mean value $\pm$ standard deviation) in height. Another glandular trichome type is type II, the "neck-cell" type with a long stalk

Figs. 1. a-i Trichome type I of *Cucurbita pepo* L. subsp. *pepo* var. *styriaca* (Greb.). Developing and mature stages of glandular trichomes of drawn off leaves, short stalked trichome type: a) protruding epidermal cell; b) product of cell division; two-celled stage; c) dividing three-celled stage; d) four-celled stage; e) cells in the stalk region are dividing periclinal and four cells are achieved; f) differentiation in four-celled head region, "middle-cell" and stalk region; g) fully developed trichome with four cells in the head region, one "middle-cell" with two following stalk cells and a basal cell; h) lateral view of a fully developed trichome; i) modification with eight cells in the head region.

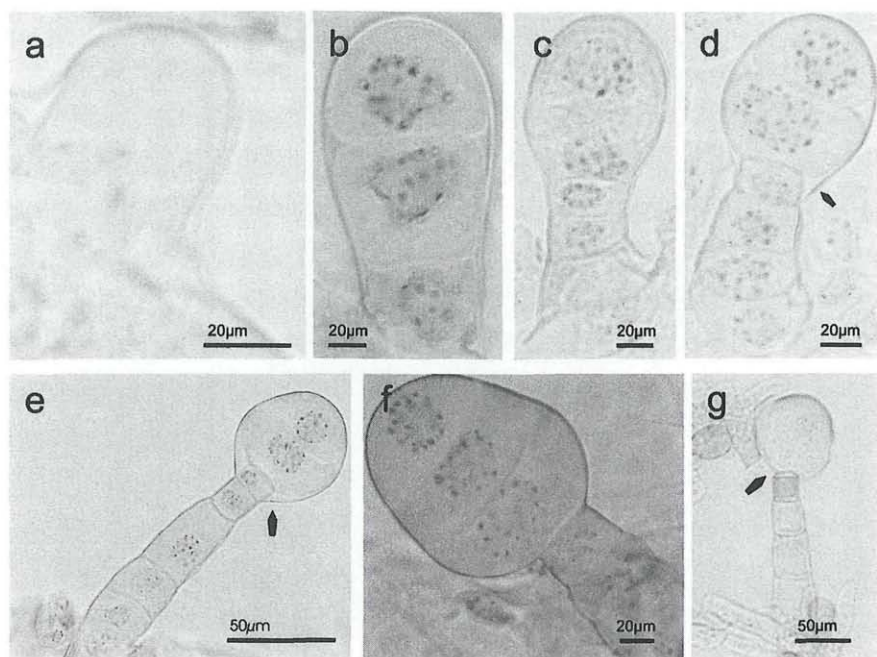


and a two-celled head area (Fig. 2e). The fully developed trichomes vary in length between $345 \mu\text{m} \pm 41$. The third trichome type, type III, is non-glandular and called "acuminate-digit" (Fig. 3c), which shows a length between and $235 \mu\text{m} \pm 49$. The last observed trichome type, type IV, is the biggest of the four types and is called the "stipitate-capitate" type, which is a glandular hair (Fig. 4f). The fully developed trichome measures $1466 \mu\text{m} \pm 253$ and the semi-developed stages at about $868 \mu\text{m} \pm 107$. On a leaf section with a dimension of 18 mm^2 of 3 mm long leaves 1071 different capitate and digitiform trichomes can be observed. In older leaves with a size of 8 cm in length only the characteristic short stalked four-celled trichome type and bristle hairs could be investigated: a section of 28 mm^2 contains only 50 glandular trichomes.

The ontogeny of the type I, also the best described trichome type in literature (UPHOF 1962) of *Cucurbitaceae* is shown in Figs. 1a–h. A single epidermis cell undergoes a periclinal division (Fig. 1a), the outer wall is softened and the turgor pushes the wall outward into the structure of a papille. The volume increases and the result is a two-celled trichome stage (Fig. 1b) with an upper cell, which is the apical cell and a lower cell. Afterwards both cells divide themselves and a trichome pre-stage with four cells can be observed. This splitting does not always process at the same time, which means that the upper or the lower cell in the two-celled stage can divide previously (Figs. 1c, 1d).

This four-celled stage will be followed by further dividing processes and finally the two lower cells will show divisions and four cells in the lower region can be observed (Fig. 1e). Each of these cells is exactly assigned to a special trichome region. The first cell in stalk of the four lower cells in line under the head region is becoming the "intermediate cell" and is part of the trichome-stalk. The following two cells are also part of the stalk and the last one in line is the basal cell. The two apical cells show anticlinal divisions and a glandular head with four cells is finally formed (Fig. 1f). After the head area had reached the four-celled stage and the cells in the uniseriate stalk are fully developed, the cell volume in the head area increases and also the trichome elongation. These two facts are enormous in the head region and a three dimensional character of such a glandular trichome is given (Figs. 1g, 1h). All these steps lead to a fully developed trichome. In Fig. 5b, a SEM micrograph shows the mature secretory trichome. Sometimes "special" types of this hair type can be seen (Fig. 1i). In this case, the cell division in the head region does not stop at the four-celled stage but such variations are rare. Because of their tallness they can be identified easily.

Type II, also a glandular hair, is called the "neck-cell" type and its developing process is shown in Figs. 2a–f. The ontogeny starts with a single epidermal cell division (Fig. 2a). After a periclinal division a two-celled



Figs. 2. a–g Trichome type II of Styrian pumpkin, long stalked “neck-cell” type. a) periclinal dividing epidermal cell; b) three-celled stage in line; c) five-celled stage with the two-celled head region; d) lateral cuticle rupture in the head region (arrow) and six cells in line; e) fully developed trichome type with two cells in the head region, five stalk cells and one basal cell, a cuticle rupture in the head region is visible (arrow); f) glandular head with a third cell area; g) glandular head is detached at the weak point (arrow).

stage could be observed, followed by the division of the lower cell, which results in a three-celled stage (Fig. 2b). Dividing of the two lower cells is responsible for the five-celled stage (Fig. 2c). Afterwards the head region is including two cells, which are bigger compared to the pre-stalk cells. The volume of the two head cells is increasing. However, the basal cell is dividing again and the cell number increases until a six-celled stage is reached (Fig. 2d). After these splitting steps a cuticle rupture in the head region is observable (arrow in Fig. 2d). The characteristic “neck-cell”, which is the first cell in line of the stalk under the glandular head, holds the size and the head and stalk cell volume is increasing and an elongation of the stalk is visible. The diameter of the head is bigger in comparison to the stalk and the “neck-cell” is smaller than the following stalk cells. The trichome can be easily characterised, because of the two head cells, which are separated from the small uniseriate stalk. A comparable SEM picture is shown in Fig. 5e. The stalk contains normally five cells and one

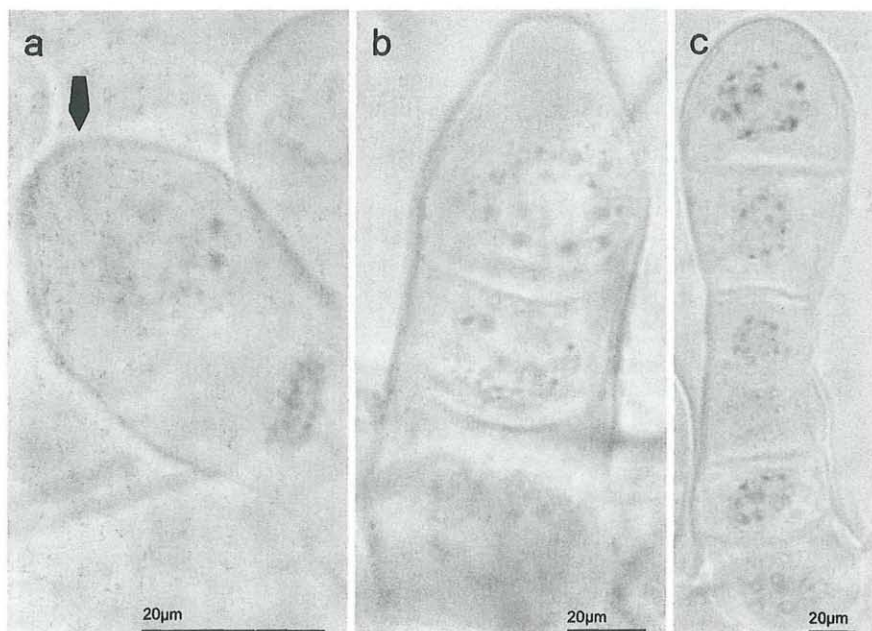
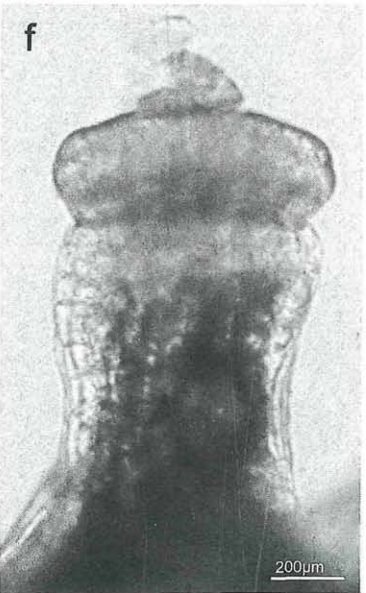
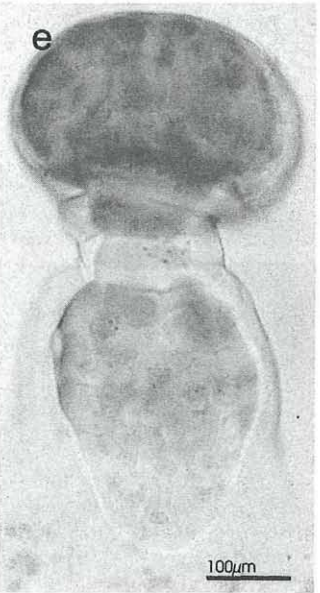
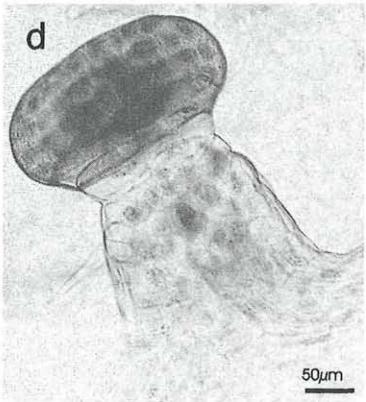
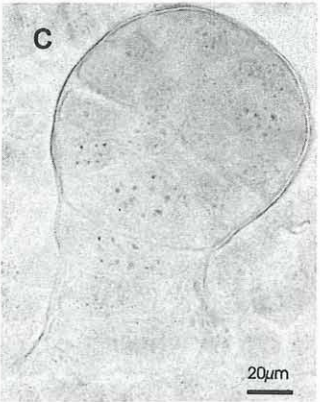
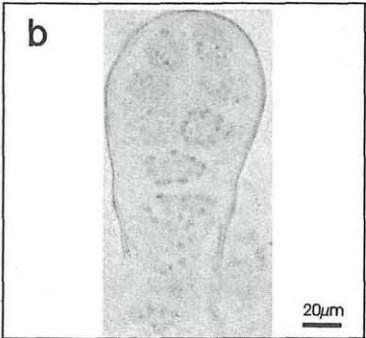
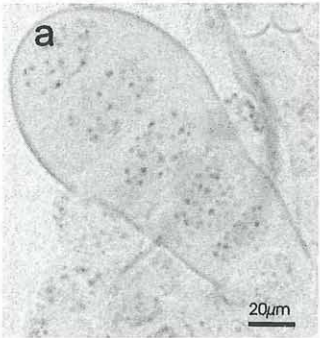


Fig. 3. a–c Trichome type III of Styrian pumpkin, “acuminate-digit” trichome type. a) the first developing cell is acuminate (arrow); two-celled stage; b) three-celled stage; c) fully developed trichome type with one basal cell, three stalk cells and a two-celled head region.

basal cell (Figs. 2e, 5c). In some cases the two head cells also divide and a third cell area is visible (Figs. 2f, 5d). Specifically the “neck-cell” is a weak point and the head is breaking off in this area (Fig. 2g).

The ontogeny of type III, the “acuminate-digit” is shown in Figs. 3a–c. This type is smaller compared to the “neck-cell” type or to type IV and may be non-glandular. The development also starts with a single epidermal cell and results in a two-celled stage. However, these cells are acuminate in the apical region (Fig. 3a, arrow). The upper cell remains constant and the lower one divides, resulting in a three-celled stage (Fig. 3b), followed by a five-celled stage, where the two lower cells of the three-celled stage divide again. If the trichome shows a head with two cells and a stalk with two

Figs. 4. a–f Trichome type IV of Styrian pumpkin, “stipitate-capitate” trichome type. a) structure with six cells in line; b) #/and c) periclinal and anticlinal cell divisions; d) differentiation between stalk, head and basement with mesophyll cells; e) not fully developed stage, however, an elongation of the pre-trichome structure is visible; f) fully developed “stipitate-capitate” trichome type with a secretion process.



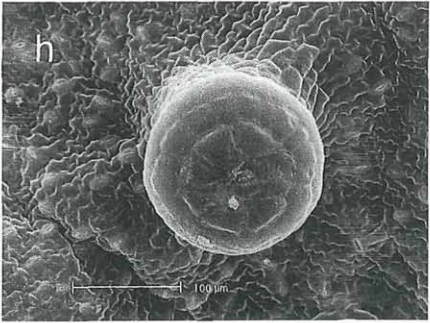
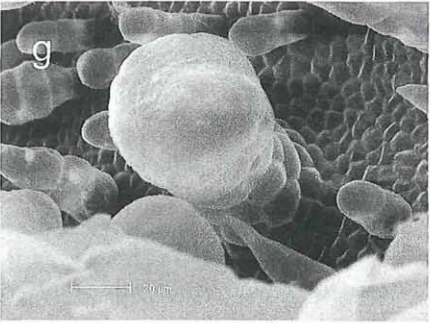
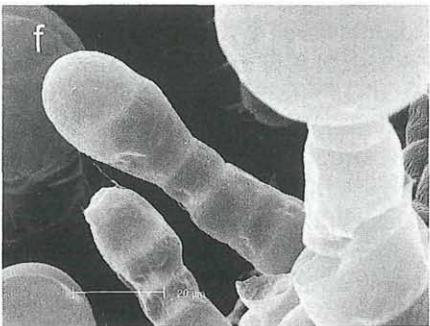
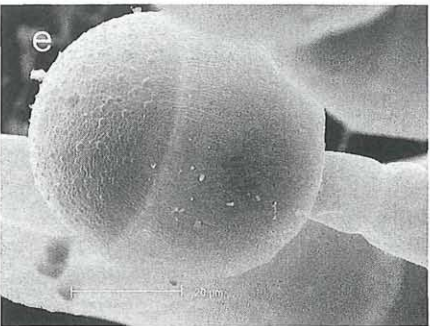
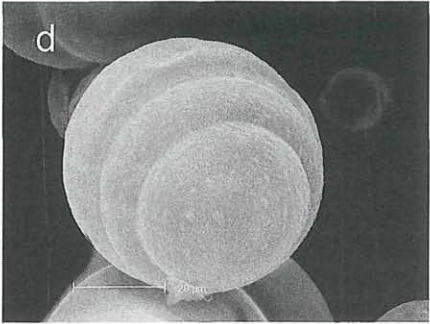
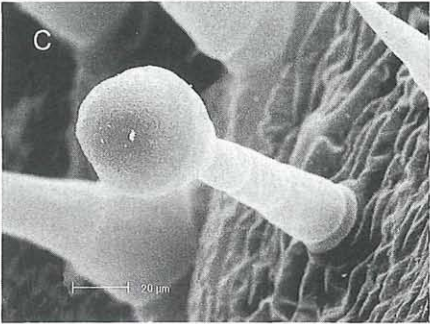
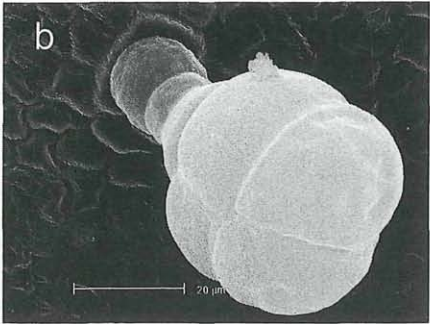
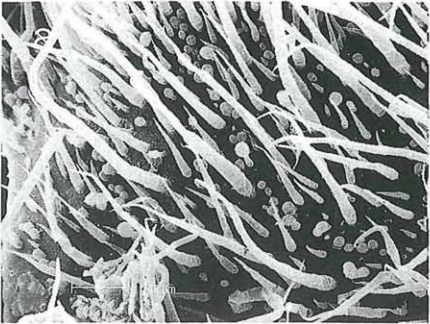
cells and one basal cell, a constriction under the head region could be observed (not shown). Finally the size of the "acuminate trichome" is increasing, a stalk cell divides once again and an elongation is the final stage (Figs. 3c, 5f).

Hair type IV is the biggest one and also a glandular trichome on the leaves of Styrian pumpkin, the development is shown in Figs. 4a-f. This remarkable "stipitate-capitate" glandular trichome type starts its development with a single epidermal division. This cell divides periclinal and quickly a structure is built with five or six cells in line (Fig. 4a).

At first three apical cells divide repeatedly anticlinal, their volume is increasing in comparison to the lower stalk cells, so that a separation of a developing multicellular head region could be detected (Fig. 4b).

In Figs. 4c and 5g a young ontogenetical stage is featured where a clear differentiation between head, stalk and the basement is already visible. The head is separated from the stalk through a "middle-cell", the basement is not developed in this stage. The head in this stage is characterised, because of more anticlinal divisions, the stalk consists of two cells and lower a sem-circle of epidermal and mesophyll cells is observable. These epidermal cells divide henceforth and their function is to surround the basement structure in future with its mesophyll cells. The mesophyll cells elongate and an enormous trichome swelling primary in the lower region can be observed and so the volume of the basement is increasing (Fig. 4d). The basement as a whole is surrounded from epidermal cells (Fig. 4d), inside this mesophyllical basement an area, which shows a similarity to a bulbus is built, where maybe the secret production takes place (Fig. 4e). The growth of typ IV continues, because the cells from the basement and the stalk cells elongate and a long trichome with a secretory head is formed. In the middle of the head area, at the final stage of the trichome development, a secret release is observable (Figs. 4f, 5h with the central region of the secret release). This trichome can be seen without a microscope because of its large size.

Figs. 5. a-h: SEM micrographs of Styrian pumpkin showing the morphology of the four different trichome types on the leaves. a) overview about the high trichome density on a leaf surface; b) short stalked trichome type with a four-celled head region; c) long stalked "neck-cell" type with two cells in the head region; d) "neck-cell" type with three cells in the head region; e) the characteristic "neck-cell" region; f) "acuminate-digit" trichome type consisting of three cells in the stalk and two cells in the head region; there is not a clear distinction between the apical (head-like cell) and the other cells; g) and h) "stipitate-capitate" trichome type; g) multicellular basement, h) view above of the head region.



Discussion

The majority of ontogenetical studies are related to many *Asteraceae* and *Lamiaceae* species (MONTEIRO & al. 2001, ASCENSAO & al. 1999). Only a small part of hairs of *Cucurbitaceae* is known and described. But only few ontogenetical studies on glandular and non-glandular trichomes in *Cucurbitaceae* were made. The investigations of different trichome types, which were described by UPHOF 1962 were made on the flowers of *Cucurbitaceae* and not on leaf surfaces as it has been carried out in this study. In this study of UPHOF 1962 short stalked trichomes, which are characteristic for *Cucurbitaceae*, are described and especially the "intermediate cells" of this trichome type were observed. The intermediate cell is also called "middle-cell" because this cell part separates the head from the rest of the hair. If the trichome is touched the head is separated from the stalk at this weak point. Type I, described as the well known *Cucurbitaceae* type, shows such an intermediate cell. This type is not only found on the leaves and flowers of Styrian pumpkin, but also on the flowers of *Trichosanthes*, which is described by UPHOF 1962. The flowers show glandular hairs with the same habitus as type I of Styrian pumpkin. They have four cells in the head area and this region is followed by an intermediate cell and further two stalk cells and one basal cell.

Trichome types that are similar to type I of Styrian pumpkin, because of their structure, size, head and stalk region are situated e.g. on the leaves and flowers of *Stevia rebaudiana* (BERT.) (MONTEIRO & al. 2001). The ontogenetical development of the biserial trichome type of *Stevia rebaudiana* is similar to the short stalked trichome type of Styrian pumpkin leaves, however, the first epidermal division of Styrian pumpkin is periclinal and not anticlinal. A similar trichome development, which starts with an outgrowth of an epidermal cell, could be observed for *Calceolaria adscendens*. There, the first periclinal division generates an upper and a lower cell, which results in a short stalk and a glandular head cell. The last one divides anticlinal and a two-celled secretory head (SACCHETTI & al. 1999) originates. In this *Astereaceae* species the ten-celled biserial type is also already fully developed at an early stage of development. Another similar glandular trichome type, which is also called "T-trichome" is situated on the flowers of *Artemisia annua* (FERREIRA & JANICK 1995). This type is biserial and arises from a pair of cells. It is identical to this one, which is described on the leaves of *Artemisia annua*.

The second observed trichome type, also called the long stalk "neck-cell" type was not described in earlier studies of *Cucurbitaceae*. A similar hair type, which is a touch-sensitive glandular trichome is known from a palaeontological study, which was made on *Sicana odorifera* (KRINGS & al. 2002). The hairs of *Sicana odorifera* consist, like the "neck-cell" type of *Cucurbita pepo* var. *styriaca*, of 3–6 cells in the stalk region and a two-

celled head. Also type II is touch-sensitive, because the head breaks off at the intermediate cell and a sticky exudate is released. Long stalked glandular trichomes are also described by ASCENSAO & al. 1999 on the leaves and flowers of *Plectranthus ornatus*. In this study short-stalked capitate and long-stalked capitate trichomes are described and the ontogeny of the long stalked types could be observed, because of a full description on SEM micrographs. During the development of this glandular trichome type the differences in their stalk-length are big, which is comparable with the ontogeny of "neck-cell" type of *Cucurbita pepo*. However, such capitate trichomes, with one to four stalk cells are also found on the leaves of *Salvia aurea* L. (SERRATO-VALENTI & al. 1997). The third hair is the "acuminate-digit" trichome and it shows six cells in line. Because of this habitus it has similarities with the digitform trichomes of *Plectranthus ornatus* (ASCENSAO & al. 1999), which consist of three to four cells. There is no clear distinction between the apical head cell and the following other cells. These hairs are not considered being capitate hairs, however, the apical cell is glandular in comparison to that of type III of Styrian pumpkin. The digit trichomes of *Plectranthus ornatus* consist of one basal cell, one or two stalk cells and one apical secretory cell, whereas the apical cells have a secretory function in comparison to the "acuminate-digit" trichomes of Styrian pumpkin.

Further observations on the leaves of Styrian pumpkin offered the presence of the fourth described trichome type. This trichome consists of an enormous multicellular base and a stalk with a pluricellular head. The "stipitate-capitate" glandular trichome is only semi-developed on young leaves, which means that the stalk region and the base with mesophyll cells divide henceforth. After the leaf has reached at least a length of about 4 cm, the fully development of these hairs can be observed. The pre-phase of this *Cucurbita* hair type is similar to the habitus of the glandular "stipitate-capitate" trichome of *Adenocaulon bicolor* (KARRFALT & KREITNER 1980). However, the earliest dividing condition shows a two-celled stage, which originates from an anticlinal cell division and not from a periclinal one-celled stage division as it could be observed by the "stipitate-capitate" trichome of Styrian pumpkin. In comparison the glandular trichome types of *Fagonia* L. species (FAHN & SHIMONY 1996) show an ontogenetical similarity, because the leaf basement of both hair types originates from the subtending mesophyll cells and the stalk develops from the epidermal cells, too. The structure inside the basement has a similarity to a bulbus of a stinging hair of *Urtica dioica*.

In Styrian pumpkin the diversity of glandular and non-glandular hairs is already present, when the leaf has reached a size of 3 mm in length. The density of the trichomes varies among species and varieties of different plant leaves, age and leaf size. For instance the number of trichomes of

Fagonia L. species leaves (FAHN & SHIMONY 1996) is per 1 mm² 25, but their density decreases towards maturation. This phenomenon is shown in Styrian pumpkin, too. On a leaf section with a size of 18 mm² of 3 mm long leaves 1071 different trichomes could be observed, however, on a leaf section with a dimension of 28 mm² of 8 cm long leaves only 50 hairs could be detected. These results show further, that in older leaves trichomes are broken off or dead. These broken hairs are not regenerated and so the leaf surface of older leaves is sparsely covered with hairs. Responsible for such a breaking off are often insects, which touch the trichomes and the structures are ruptured (KRINGS & al. 2002).

In conclusion we can summarise that on the leaf surface of Styrian pumpkin three different capitate trichome types and one digitform type and one bristle hair type could be observed. A continuous series of periclinal and anticlinal divisions lead to the formation of the ontogenetical independent trichome types.

Detailed histochemical and ultrastructural studies may be aided to interpret their part and function on the leaf surface.

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