Acta bot. bras. 24(4): 909-915. 2010.

Characterization and ontogeny of the glandular trichomes of *Ocimum selloi* Benth. (Lamiaceae)

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Recebido em 2/09/2009. Aceito em 19/08/2010

RESUMO – (Caracterização e ontogenia dos tricomas glandulares de *Ocimum selloi* Benth. - Lamiaceae). *Ocimum selloi* Benth. (Lamiaceae) é uma espécie nativa da América do Sul e na medicina popular tem sido usada devido suas propriedades analgésica, anti-inflamatória e antiespasmódica. O objetivo do presente trabalho foi identificar os tipos de tricomas glandulares que ocorrem nos órgãos vegetativos e reprodutivos de *O. selloi* e determinar a ontogenia desses tricomas. Ramos laterais em início de formação, folhas totalmente expandidas, flores em diferentes estádios de diferenciação, amostras de caule e do eixo das inflorescências foram analisados em microscopias de luz e eletrônica de varredura. Tricomas glandulares do tipo peltado e capitado subséssil foram observados no caule, nas folhas, no eixo da inflorescência e na superfície adaxial das sépalas. Nas sépalas foi encontrado, além dos tricomas secretores peltados e capitados subsésseis, o tricoma glandular capitado pedunculado. A ontogenia inicia-se com a expansão de uma célula protodérmica que, de acordo com a seqüência de divisões periclinais e anticlinais (ora simétricas, ora assimétricas), dá origem aos tricomas. A diferenciação dos tricomas glandulares peltados e capitados não é sincrônica e ocorre muito cedo no desenvolvimento da folha, do caule e do eixo floral.
Palavras chave: alfavaca, elixir paregórico, estruturas secretoras, plantas medicinais

ABSTRACT – (Characterization and ontogeny of the glandular trichomes of O*cimum selloi* Benth. - Lamiaceae). *Ocimum selloi* Benth. (Lamiaceae) is native to South America and in traditional medicine has been used due to its analgesic, anti-inflammatory, and antispasmodic properties. The aim of this study was to identify the types of glandular trichomes that occur on the vegetative and reproductive organs of *O. selloi* and to determine trichome ontogeny. Lateral branches at the initial formation phase, fully opened leaves, flowers at different differentiation stages, and stem and inflorescence axes were analyzed under light and scanning electron microscopy. Glandular trichomes of the peltate and subsessile capitate types were observed on the stem, leaves, inflorescence axis and the adaxial surface of the sepals. On the sepals, in addition to the peltate and subsessile capitate secretory trichomes, the stalked capitate glandular trichome type was detected. Ontogeny began with the expansion of a protodermic cell, which according to the sequence of periclinal and anticlinal division (either symmetric or asymmetric) gave rise to the glandular trichomes. Differentiation of the peltate and capitate glandular trichomes was not synchronized and occurred very early in the leaf, stem and floral axis.
Key words: basil, paregoric elixir, secretory structures, medicinal plants

Introduction

Lamiaceae is rich in species that produce essential oils whose compounds are largely used in food (as flavorings), cosmetics (fragrances and aftershaves), and medicine (Burt 2004). The essential oils are lipophilic complexes synthesized and stored in different secretory structures, including the glandular trichomes in the Lamiaceae (Simões & Spitzer 2002).

Ocimum selloi Benth. is a perennial shrub, native to South America where it is known as "paregoric elixir", "basil" or "atroveran" (Lorenzi & Matos 2002). In traditional medicine *O. selloi* has been used as analgesic, anti-inflammatory, and antispasmodic. The essential oil extracted from leaves, stem and flowers contain anethole and methyl chavicol as their major components (Moraes *et al*. 2002; Gonçalves *et al*. 2003; Paula *et al*. 2003). The *O. selloi* essential oil is an efficient repellent of the *Anopheles braziliensis* mosquito (Paula *et al.* 2003) and it has modest antimicrobial activity against strains of *Escherichia coli* and *Staphylococcus aureus* (Farago *et al*. 2004).

Even though some of the glandular trichomes of *O. selloi* have been described by Martins (1996) and Costa *et al*. (2007a) information is still scarce.

Glandular trichomes, frequently called glands, are epidermal appendices formed by the head of a single cell or pluricellular secretory cells and a non-glandular stalk (Fahn 1990). The number of secretory cells, number and length of the stalk cell(s), and the density, location and arrangement of these glandular trichomes in the epidermis can vary. Their structure and ultrastructure in vegetative and reproductive organs have been widely described in the literature (Werker *et al*. 1985; Maffei *et al*. 1989; Werker *et al*. 1993; Ascensão *et al*. 1995; Serrato-Valentin *et al*. 1997; Milaneze-Gutierre *et al*. 2007; Martins *et al*. 2009).

Increased interest in the therapeutic use of *O. selloi* has motivated researchers to investigate not only its biology regarding reproduction (Facanali *et al*. 2009) but also optimal growth conditions, *e.g.* cultivation (Costa *et al.* 2007b, 2010), harvest time, and temperature for dryness, that will lead to improved content and composition of the essential oil (David *et al*. 2006; Costa *et al*. 2007c). Studies on the occurrence, location and characterization of the glandular trichomes can provide important insights regarding harvest, post-harvest and quality control of essential oil producing plants. Furthermore, the adaptive and taxonomic value of the glandular trichomes, and consequently the essential oils, is of great importance in botanical studies (Abu-Asab & Cantino 1987; Martins *et al*. 1997). The present study was undertaken to identify the types of glandular trichomes that occur on the vegetative and reproductive organs of *Ocimum selloi* Benth. and to characterize trichome ontogeny.

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Materials and methods

Seed-derived plants of *Ocimum selloi* Benth. (Lamiaceae) were collected in the "Grupo Entre Folhas Medicinal Plants", located at Universidade Federal de Viçosa (UFV), Viçosa (20°45´20" S; 42°52´40" W), Minas Gerais state, Brazil. The climate of the region is the "Tropical Altitude" type (Cwb), with warm summers and temperatures in the hottest month below 22°C (Köppen 1948).

Seedlings (average 3 cm tall) were collected and placed in plastic bags containing soil, sand and manure (1:1:1), and were initially kept partially shaded (50% light reduction) and watered on a daily basis. After 41 days, seedlings with 4 nodes (approximately 7 cm tall) were transplanted to six-liter polyethylene containers, filled with soil, manure and sand (3:1.5:1 ratio). After transplant, six plants were kept under greenhouse conditions. The substrate was kept at 80% of field capacity. Maximum and minimum temperatures were recorded daily.

Voucher materials were prepared according to standard herbarium protocol and placed in the VIC Herbarium at the Plant Biology Department, Viçosa, MG (# 23,642).

Lateral branches at the initial formation stage were collected and embedded in paraffin. Fully opened leaves were used for clarification, embedding in paraffin, and for scanning electron microscopy. The samples were collected from the mid-region of leaves located at the second node, from tip to base, of the main axis of the plants. Stem and inflorescence axis samples were prepared for embedding in paraffin and scanning electron microscopy. Buds and open flowers were embedded in paraffin and sepals from open flowers were prepared for scanning electron microscopy. In addition, freshly prepared sections were made from stem and fully expanded leaves.

The samples were fixed in FAA50 for 24 hours, dehydrated in progressive ethylic-butyric series and embedded in paraffin according to the usual techniques (Johansen 1940). Transverse sections were made in the inflorescence axis, leaves (petiole and blade) and in the stem. Transverse and longitudinal sections were made in the buds, opened flowers, and branches at the initial formation phase. Thick sections (12 μm) from all samples were obtained in a rotating microtome. The inflorescence axis, leaves and stem were stained with astra blue 1% (for 2 minutes) and ferric hematoxylin (for 30 minutes), while the branches at initial formation phase and flowers were stained with ferric hematoxylin (for 120 minutes). The sections were mounted between a slide and slide cover in Canadian balsam.

For clarification, some samples were placed in 50% ethanol, stored in 70% ethanol and further processed according to the procedure adapted from Johansen (1940): 10% NaOH solution, for 3h, 3% sodium hypochlorite solution until bleached, and 10% hydrated chloral ($CCl_3CHO.H_2O$) until the material was completely translucent. The material was stained with safranin 1% (for approximately 24 hours), and after dehydration was mounted between slide and slide cover in Canadian balsam. The remaining samples were placed directly in hydrogen peroxide until bleached, stained with safranin and hematoxylin for a few seconds, and mounted between slide and slide cover in hydrated glycerin (3:1).

Photographic documentation was done by an Olympus microscope model AX-70 with the U-PHOTO system.

The samples for scanning microscopy were fixed in 2% glutaraldehyde and 1% osmium tetroxide and after using 1% thiosemicarbazide and post-fixed with 1% osmium tetroxide (Silveira 1989). The material was dehydrated in a progressive ethanol series, dried to the critical point with liquid CO_2, fixed on a support with silver glue and covered with metallic gold (10 nm).

Photographic documentation was done by a JEOL-T 200 scanning microscope at 15 Kv.

The types of glandular trichome were classified according to Werker *et al.* (1985) and Werker *et al.* (1993).

Results

Peltate and capitate glandular trichomes were detected in *O. selloi.* The *O. selloi* capitate type was further divided into subtypes designated here as subsessile capitate and stalked capitate.

Peltate and subsessile capitate glandular trichomes (Figure 1) were detected in the stem, leaves (petiole and blade), inflorescence axis and sepals.

The peltate type consists of four cells in the secretory head, one cell in the stalk (low and necklace-shaped) and a base cell. This type of glandular trichome was frequently observed in depressions in the epidermis (Figure 1A-B). The subsessile capitate glandular trichome consists of two cells in the secretory head, one cell in the stalk and one basal cell (Figure 1C-D).

The stalked capitate type glandular trichome is formed by two cells in the stalk and one secretory cell (forming the head) (Figure 2A-B), where small droplets were observed (Figure 2B). The stalked capitate type was observed on the adaxial surface of the sepals (Figure 2C-D), however it was not found on the petals, stamens and gynoecia.

Several events were defined in peltate and capitate glandular trichome ontogeny (Figure 3). Firstly, a protodermic cell expands, differentiating itself from the other cells and the nucleus migrates to the distal pole of the cell. The equal distribution of cytoplasm was visible at this point, with the vacuole located almost completely on the opposite side of the nucleus (Figure 3A). Secondly, the cell divides periclinally giving rise to a more vacuolated basal cell and an apical cell with fairly dense cytoplasm and voluminous nucleus (Figure 3B-C). Thirdly, the apical cell divides periclinally originating the cell from which the secretory head and the stalk cell will derive (Figure 3D-E); there was an anticlinal symmetric division with the subsequent formation of the two secretory cells (Figure 3F-G). These two apical cells and the stalk cell expand without further division and the final product is a capitate glandular trichome with two head cells (Figure 3H). Two apical cells, displaying typical voluminous nucleus and dense cytoplasm, divide again anticlinally, and form four secretory head cells, thus creating the stalked capitate type glandular trichome (Figure 3I). It was observed whether the division of the two cells into four occurred simultaneously. Cells in anaphase and telophase were observed in several of the events (Figure 3).

The *O. selloi* peltate and subsessile capitate glandular trichome differentiation occurred very early in leaf, stem and flower development. These glandular trichomes were observed at various differentiation stages even before the differentiation of stomata mother cells. Protodermic cells were observed in expansion in very young primordial leaves and in the internodes farthest from the stem apex, and occasionally, glandular trichomes at more advanced differentiation stages. Glandular trichomes at different differentiation stages were also observed in the same region of these primordial leaves or the stem, showing that development was not synchronized.

The initial events of the stalked capitate glandular trichome ontogeny are probably similar to those of peltate and subsessile capitate ones. However, stalked capitate glandular trichomes were observed only in the end stage of

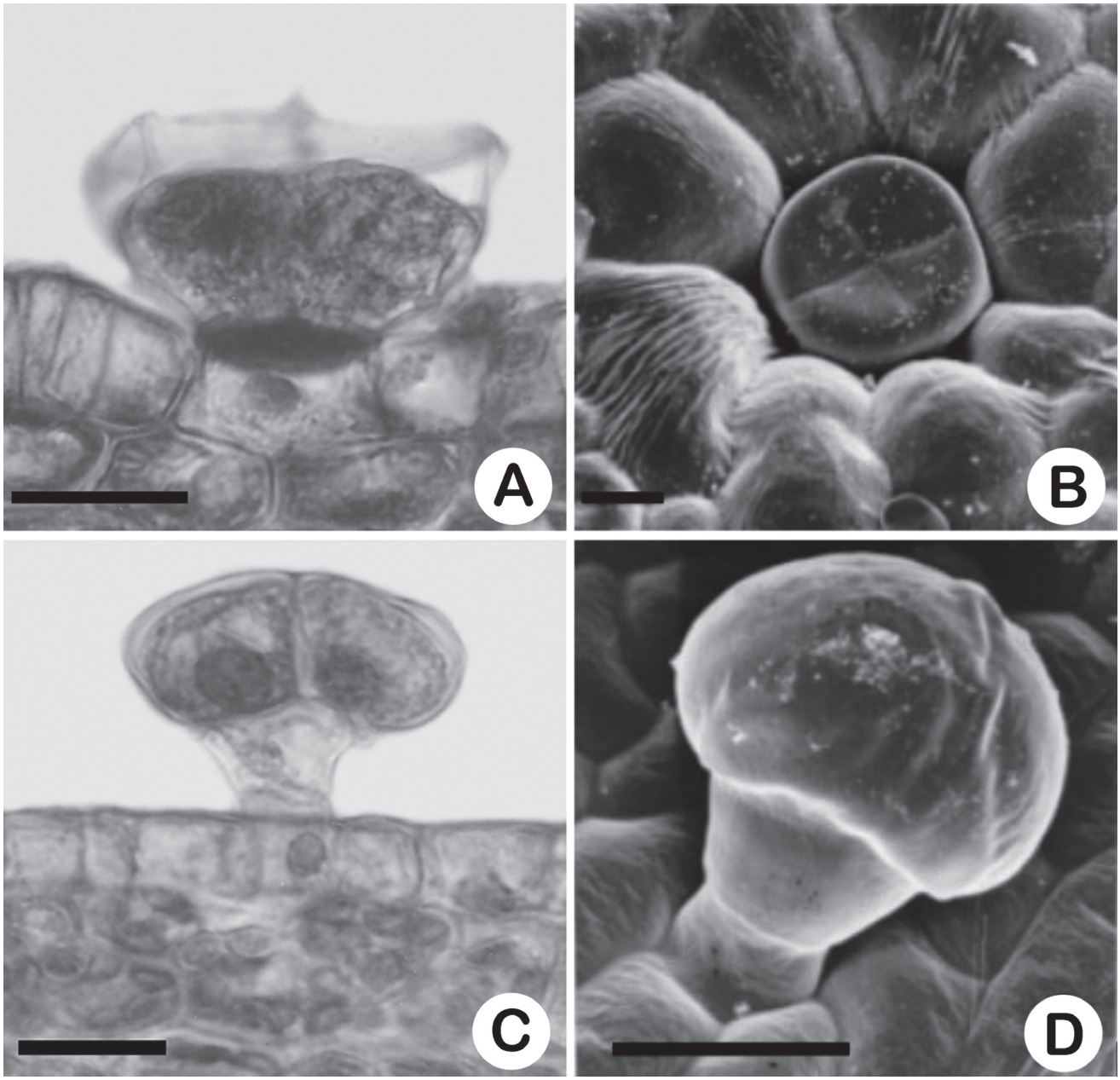

Figure 1. Glandular trichomes present in the *Ocimum selloi* Benth. stem, leaves and flowers. A and C, transverse sections in light microscopy. B and D, scanning electron microscopy. A and B, peltate type. C and D, subsessile capitate type. Bars = 20 μm.

differentiation, with short stalk cells (Figure 3J), and it was not possible to define the precise sequence of development.

The maximum and minimum average temperatures throughout the experiment were 33.5°C and 15.5°C, respectively.

Discussion

Although the number of species examined in detail in the Lamiaceae family is considered small, peltate and capitate glandular trichomes are common to the species already studied in the family and have been described in detail in the literature.

The occurrence of capitate and peltate glandular trichomes in leaves of *Ocimum selloi* has been documented by Martins (1996) and Costa *et al*. (2007a; 2010). In the present study, besides confirming previous findings, further work was accomplished in characterizing the types of trichomes that occur on the vegetative and reproductive organs of *O. selloi*.

According to Werker *et al*. (1985) the capitate type glandular trichomes are less variable than the peltate glandular trichome regarding the length of the stalk cells and the shape of the secretory head. The secretory head of the peltate trichomes consists of four cells in the middle and variable number of cells surrounding them. Others consist

of four secretory cells only. The capitate trichomes are generally formed by one or two cells in the stalk and by one or two secretory cells. Werker *et al*. (1985) classified the capitate glandular trichomes in the Lamiaceae family in three subtypes. The subsessile and pedunculated capitate glandular trichomes observed in *Ocimum selloi* are similar to subtypes I and III described by these authors, respectively. Type I consists of 1-2 cells in the stalk and 1-2 secretory cells, whereas type III consists of 2-5 cells in the stalk and one cell in the secretory head.

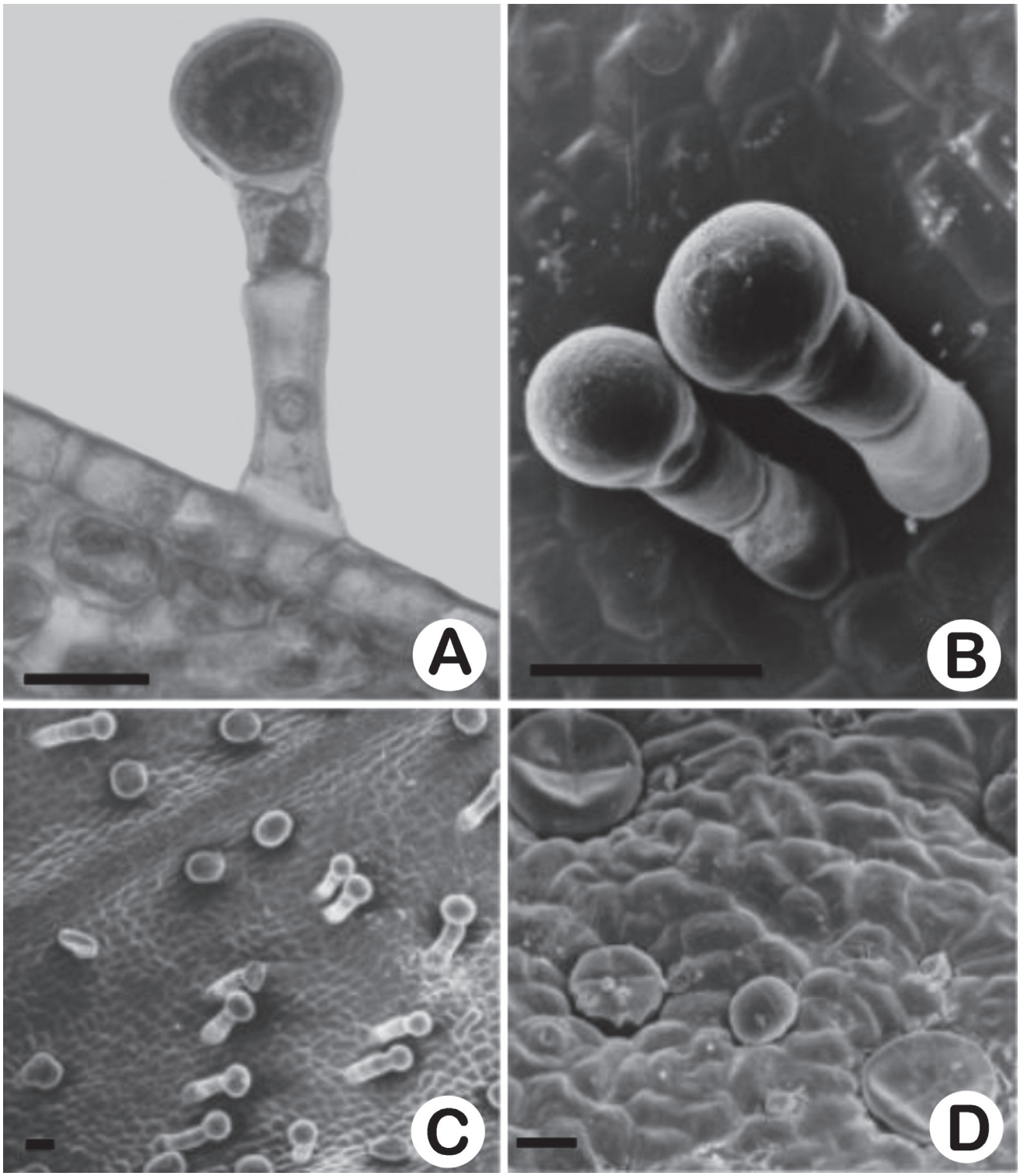

Figure 2. Glandular trichomes present in the *Ocimum selloi* Benth. flowers. A, transverse section in light microscopy. B-D, scanning electron microscopy. A and B, pedunculated capitate trichome, with one secretory cell. C and D, overall view of the adaxial and abaxial sepal surfaces, respectively. Bars = 20µm.

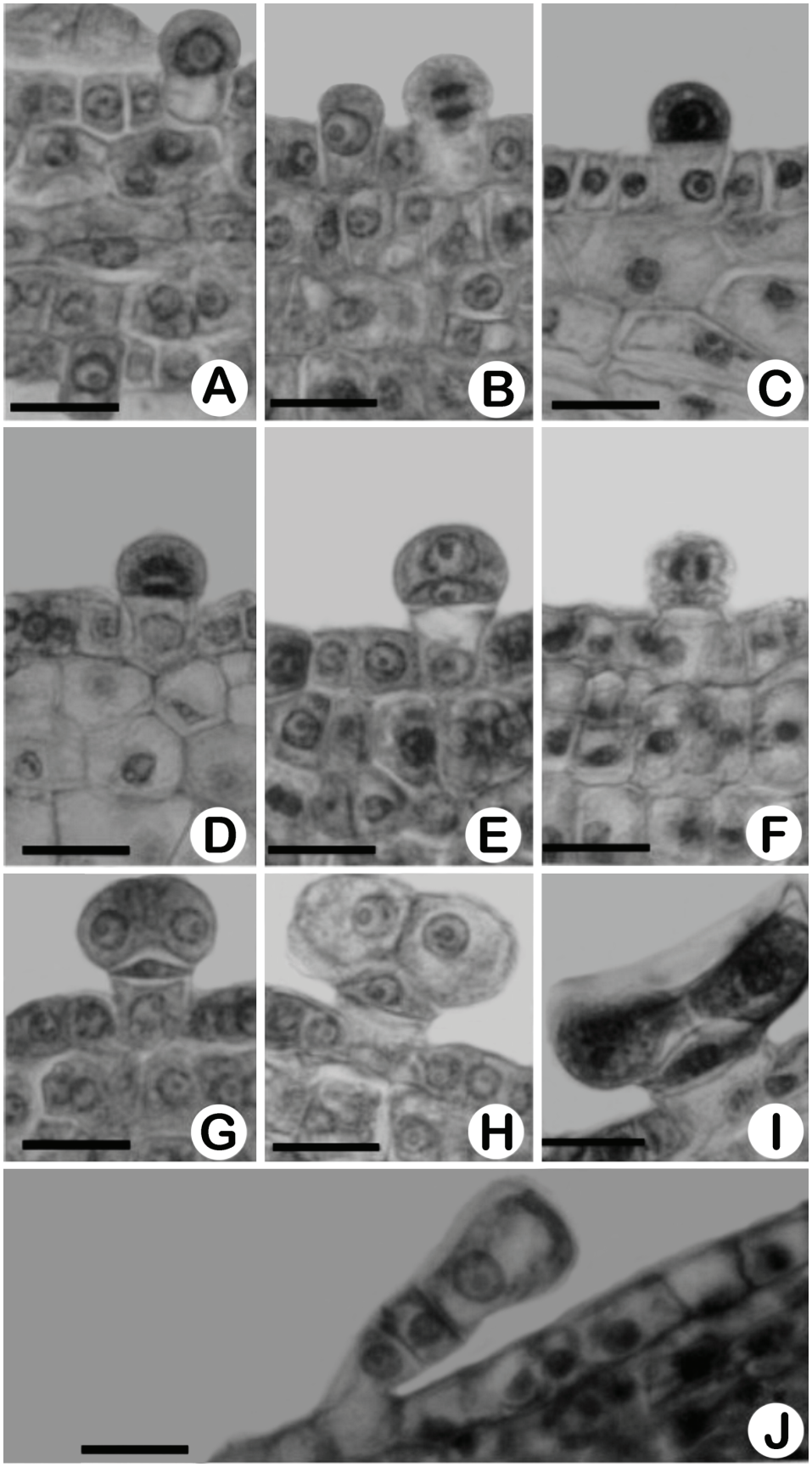

Figure 3. Differentiation pattern of the *Ocimum selloi* Benth. glandular trichomes. A, Initial diferenciation of the glandular trichome. B, C, D e E, periclinal divisions. F, anticlinal division. G and H, expansion of the two apical cells or, I, formation of the capitate trichome. J, stalked capitate with the stalk cells in expansion. Bars = 20µm.

Small droplets were observed in the stalked capitate glandular trichome, indicating that the secretion could be released without rupturing the cuticle. This type of secretion was reported in *Salvia aurea* L. and *S. blepharophylla* Brendegee ex Epling capitate glandular trichomes (Serrato-Valentin *et al.* 1997; Bisio *et al.* 1999).

The clarification process and paraffin embedding considerably damaged the peltate glandular trichome structure, which presented deformed secretory cells and subcuticle space, characteristic of this type of ruptured glandular trichome. However, the subcuticular space was observed in fresh sections of the stem and leaves, indicating one of the possible ways of storing and eliminating the material synthesized in this type of glandular trichome. According to Werker *et al.* (1985), in several Lamiaceae species a continuous layer, formed by the cuticle and by part of the external wall of the secretory head cells, detaches itself from the rest of the walls forming a space where the secretions are accumulated. External factors, such as high temperatures, low air humidity or aggression by animals, may break this layer leading to the release of the oil (Ascensão *et al.* 1995).

Glandular trichomes were not observed in the stamens and gynoecia of *O. selloi*. However, although few species have been examined, several authors have reported the occurrence of glandular trichomes in reproductive Lamiaceae organs. Glandular trichomes of the peltate and capitate types were detected on reproductive organs of *Leonotis leonurus* (L.) R. Br. Those of the capitate type were observed in the calyx, corolla, stamens and gynoecia, but the capitate type glandular trichomes occurred rarely and were numerous only on the abaxial surface of the calyx (Ascensão *et al.* 1995). It is possible that the number of glandular trichomes on the stamens and gynoecia of *O. selloi* is indeed small, or that the embedding process in paraffin may have contributed to damaging the structures, though impairing observation.

Capitate and peltate glandular trichomes also occur in other species of the genus *Ocimum*. In *O. basilicum* the capitate trichomes are composed of one basal cell, one stalk cell and the head of either one elongated, oval cell or two cells broad (Werker *et al*. 1993). In *O. gratissimum* (Martins *et al*. 2009), the capitate and peltate glandular trichomes on the leaves are similar to those found on the leaves of *O. selloi*, and cannot be used to distinguish the two species.

It is noteworthy that the oil produced on the leaves of *O. selloi* has repellent (Paula *et al*. 2003) and antimicrobial (Farago *et al*. 2004) activities, indicating the possible role of glandular trichomes and their essential oil in protecting the plant against herbivores and pathogens.

The ontogeny of glandular trichomes of *Ocimum selloi* follows the pattern described for other species of the Lamiaceae family such as *Origanum* sp. (Bosabalidis & Tsekos 1984), *Leonotis leonurus* (Ascensão *et al*. 1995), and *Mentha x piperita* (Turner *et al*. 2000b).

Bearing in mind the differentiation of the glandular trichomes in *Ocimum selloi*, it can be presumed that the number of glandular trichomes in this species is fixed at the initial development stages of the leaf and stem, similar to *O. basilicum* L. (Werker *et al*. 1993), *Leonotis leonurus* (Ascensão *et al*. 1995) and *Origanum* sp. (Bosabalidis & Tsekos 1984). In some species this fact has not been observed. It was shown that during *Mentha x piperita* L. leaf development the total number of peltate type glandular trichomes continued to form until leaf expansion ceased (Maffei *et al.* 1989; Turner *et al*. 2000a), indicating sustained gland production during leaf growth. Similar results were reported for *Salvia officinalis* L. (Croteau *et al.* 1981).

The ontogeny of the stalked capitate type glandular trichomes is probably similar to that of peltate and subsessile capitates ones. The hypothesis is that cell expansion occurs only after the formation of the secretory cell is completed. The stalked capitate glandular trichome probably forms later in the flower differentiation process. The peltate and subsessile capitate glandular trichomes are found on the sepals of incompletely differentiated buds to fully opened flowers. Conversely, the stalked capitate glandular trichomes were only observed in flowers just before anthesis.

It should be pointed out that in the flowers, the peltate and subsessile capitate glandular trichomes seemed to differentiate first in the most basal region of the abaxial surface of the sepals. The maximum number of these glandular trichomes was also observed in this region when the flowers were open. This fact can be explained considering the influence of light on glandular trichome differentiation. According to Maffei *et al.* (1989), for example, in *Mentha x piperita* the abaxial and adaxial surfaces of the epidermis generally present different development rates for glandular trichomes. The abaxial surface showed little change in the number of glandular trichomes during leaf development and the density quickly decreased with leaf opening, while the number of glandular trichomes increased on the adaxial surface. This difference between the numbers of glandular trichomes on the two epidermis during leaf development is caused by the influence of solar radiation on the differentiation of these structures. The abaxial surface of the leaf is directly exposed to solar radiation during the first stages of development; in the subsequent stages the situation is reversed. Consequently, glandular trichome development is inhibited on the abaxial epidermis and induced on the adaxial epidermis. The abaxial surface of *Ocimum selloi* sepals, unlike the adaxial surface, is exposed to light throughout the flower differentiation stages that probably induces the formation of the glandular trichomes first on the surface.

Acknowledgements

CNPq (National Council for Scientific and Technological Development) is acknowledged for the financial support.

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