Chapter

Essential Oil and Glandular Hairs: Diversity and Roles

Zakaria Hazzoumi, Youssef Moustakime and Khalid Amrani Joutei

Abstract

The accumulation of essential oils in plants is generally limited to specialized secretory structures, namely, glandular trichomes (hairs) which are multicellular epidermal glands, found in some families such as Lamiaceae, Asteraceae, and Solanaceae, and which secrete terpenes in an extracellular cavity at the apex of the trichome. Storage of terpenoids in these structures can also be used to limit the risk of toxicity to the plant itself. The morphology of these structures varies according to the conditions of irrigation and also according to the toxicity of intracuticular contents and can be changed with the phenology of the plant. The secretory glands of aromatic plants come in different shapes and sizes, in order to ensure a specific function. This function consists mainly in the protection of different plant organs and the attraction of pollinators. Some scientist classified these glands into peltate hairs and capitate hairs, based on morphological criteria; however, others classified them into short-term glands and long-term glands, based on the mode of secretion. Short-term glands are glands that secrete rapidly to protect young organs. The long-term glands are glands in which the secretory substance accumulates gradually in the subcuticular space and play a role in the protection of mature organs such as the flower, as well as in pollination. According to this definition, he inferred that the capitate hairs are the short-term glands, while the peltate hairs are long-term glands. The difference between these two types of glands consists several aspects like structure, mode of secretion, and timing of secretion. In this object, this chapter includes some microscopic observation to glandular hairs and their combination with mode of secretion, nature of contents, and phenology of plant to give a good comprehension and classification.

Keywords: capitate, peltate, essential oils, glandular hairs, long term, short term

1. Introduction

Essential oil presents a complicated and heterogenic composition, with some molecules which can cause an injury to the plant itself, as there is evidence that many terpenoids are potentially toxic to plant tissues, when monoterpenes are released to proximate cells [1]. Injury has also been found when some sesquiterpenes are artificially deposited on leaves during tests of their ability to deter herbivores [2]. Therefore, the sequestration of terpenoid in specific compartments by sensitive metabolic processes may be essential to avoid adverse effects. The morphology of these structures varies according to the conditions of irrigation and also according to the toxicity of intracuticular contents [3].

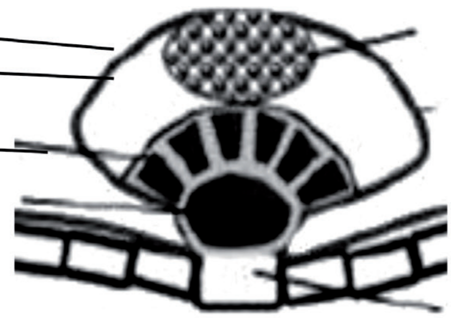

Figure 1.
Glandular hairs structure (Iriti et al. [12]).

These risks implicate the presence of specialized structures for the storage and the secretion of these compounds, those structures changed with the content and function. Largely named glandular trichomes which are multicellular epidermal hairs, found in some families such as Lamiaceae, Asteraceae, and Solanaceae, which secrete terpenes in an extracellular cavity located at the apex of the trichome [4, 5].

Previous studies have been able to observe these structures as well as its different constituents (**Figure 1**). The glandular trichome is composed of several cells performing different functions: the terpenes synthesized by the secretory cells pass into a subcuticular space located at the apex of the trichome for accumulation, and the basal cells ensure the attachment of the structure to the epidermis. These glands vary morphologically, biochemically, and secretionally.

The secretory glands of aromatic plants come in different shapes and sizes, in order to ensure a specific function. This function consists mainly in the protection of the different organs of the plant and the attraction of pollinators. These glands are subdivided into peltate and capitate hairs. Werker et al. [4] classified glands into short-term glands and long-term glands; short-term glands are glands that secrete rapidly to protect young organs. The long-term glands are glands in which the secretory substance accumulates gradually in the subcuticular space and play a role in the protection of mature organs such as the flower, as well as in pollination. According to this definition, he inferred that the capitate hairs are short-term glands, while the peltate hairs are long-term glands. The difference between these two types of glands consists of several aspects like structure, mode of secretion, and timing of secretion.

Capitate usually consists of a single or bicellular head and rarely more than two cells in some species with lipophilic content. This content is ready to be released just after its production via a porous cuticle [3].

2. The glands' location depends on the function

The glands of secretions are localized in all the plant organs, leaves, and stems and even at the root. The location of these structures depends on the organ in which they are located and the function and nature of the substances stored and secreted by these glands.

Due to the enormous diversity of these structures, morphology, origin, size, location, microstructure of the head, secretory capacity, secretion mode, function, etc., their classification is made difficult. The use of one of these criteria renders the classification incomplete which requires a method based on different types of criteria to classify these glands.

The major classification divides the glands into two groups: glandular hair and nonglandular hair. The main characteristic of distinction between these two types is the morphology as well as the nature of the substances to be secreted.

3. Non-glandular trichome

Nonglandular trichomes differ in morphology, anatomy, and microstructure. Essentially, they are classified according to their morphology. They can be unicellular or multicellular and branched or unbranched. The unbranched multicellular trichomes can be uniseriate, biseriate, or multiseriate. They can be distinctly articulated between cells or transverse walls which make the distinction of these structures impossible on the surface. They may differ in length, size, and shape of cells and may be symmetrical or asymmetrical. This type of gland provides a protective function as a mechanical barrier and does not ensure secretion of any substance.

4. Glandular trichome

The term "glandular hair" refers to a wide variety of glands. They differ according to the chemical composition of the substances they secrete, accumulate, or absorb; according to their mode of production, structure, and location; and according to their functions. All of these differences serve a certain level, which overlaps the classification.

In many of the Lamiaceae, two main types of glandular trichomes are encountered, the capitate and the peltate. They differ according to the shape of their secretory head and according to the morphology as well as the nature of the substances to be secreted. The head of the capitate glands consists of 1–4 more or less rounded secretory cells, generally oriented horizontally; a stem, one to several long cells; and a basal cell. The head cell can sometimes be very large, as in some species of *Salvia* [5]. The peltate hairs' head consists of 4–18 more flattened cells on a horizontal plane, a stem cell, and a basal cell. Thus, intermediate shapes can be encountered.

5. Variability and classification

There is great variability in the secreted materials of glandular trichomes: polysaccharides, sugars, salts, lipids, essential oils, resins, proteins, etc. Uphof [6] proposed to classify glandular trichomes according to the nature of their secretory products. Fahn [7] classified secretory substances in plants in general into two groups:

1. Unmodified or slightly modified substances, such as salts secreted by certain glands, as well as nectar.

2. Substances synthesized by secretory cells. This can be hydrophilic (as in trichomes which secrete mucilage and glandular trichomes of digestive carnivorous plants) or lipophilic (such as in the glandular trichomes of Lamiaceae, Asteraceae, Geraniaceae, Solanaceae, and Cannabaceae).

The difficulty with this type of classification is that some glands secrete more than one type of substance. For example, the glands of *Inula viscosa* secrete lipophilic substances, polysaccharides, and proteins at different stages of life and by different organelles [8]. In some carnivorous plants, the same glandular hairs produce both seductive (nectar) and digestive substances (enzymes).

In Lamiaceae, in addition to lipophilic substances, relatively large amounts of polysaccharides, which vary in amount between species, are secreted by certain capitate glands [8]. Many of these secreted materials are phytotoxic.

6. Glandular hair functions

The function of glandular trichomes varies according to their location, the substances it secretes, and the moment of secretion. Structurally, similar trichomes can produce different materials, but even when similar materials are produced, when the trichomes are located differently, they may have different functions. For example, the functions of seed mucilage trichomes differ considerably from those of leaves.

Different types of glandular trichomes may differ according to the stage of development of the organ. In Lamiaceae, from a functional viewpoint and according to their mode of secretion, the secretion materials of certain types of capitate glands are released outside just after production, when the leaves are still young and developing, often with a porous cuticle or mechanical breakage. The lipophilic fraction acts as a repellent on young leaves even before being touched. In the peltate glands, the secretory material is gradually secreted from the glandular cells in a space formed by elevation of the cuticle. The cuticle can break through a predator, releasing secreted material, which can then act as repellents. The glandular hairs can also be classified in "short term" corresponding with the first group of capitate glands and "long term" corresponding with the peltate glands [3].

a. **Protection**: the plant needs protection against various external factors such as herbivores and pathogens, extreme temperatures, excessive loss of water, allelopathy against competing plants, etc. When nonglandular hairs are densely distributed (sometimes forming a carpet thicker than the leaf itself, found in many plants growing in arid conditions), they can serve as a mechanical barrier against most of the factors externally. A correlation between trichome density and pest resistance has been demonstrated by Levin [9]. The glands, which secrete lipophilic substances, can be used in chemical protection against various types of herbivores and pathogens by repulsing or poisoning them. Secreted mucilage can trap insects by sticking.

b. **Absorption of water**: ensure a permanent function of water absorption and soil minerals. They are usually short-lived, unicellular, unbranched, and well elongated or with one or more swellings.

The epiphytic plants, which have no contact with the soil, as well as the plants that grow in xeric conditions, sometimes have other types of glands for the collection of fog water such as pineapple (*Ananas comosus*) [10].

c. **Salt secretion**: consist of cells that actively secrete a solution of different minerals.

d. **Seductive trichomes**: secretory glands of certain nectars, such as the unicellular glands of *Lonicera* and *Tropaeolum* and the multicellular glands of *Abutilon*. The most striking examples are carnivorous plants that have special requirements to catch their prey; they need to seduce and trap the various preys (sensory-triggering, digestion, and absorption devices). These functions are mainly fulfilled by trichomes [11].

6.1 Histological variations of the glandular hairs of three aromatic and medicinal plants: *Ocimum gratissimum*, *Salvia officinalis*, and *Pelargonium* sp.

6.1.1 Histological study of glandular structures of Salvia officinalis

The microscopic observations made on the *Salvia* plants (**Figure 2**) show the existence of two types of structures (secretion glands and protective hairs) which play various roles during the growth of the plants.

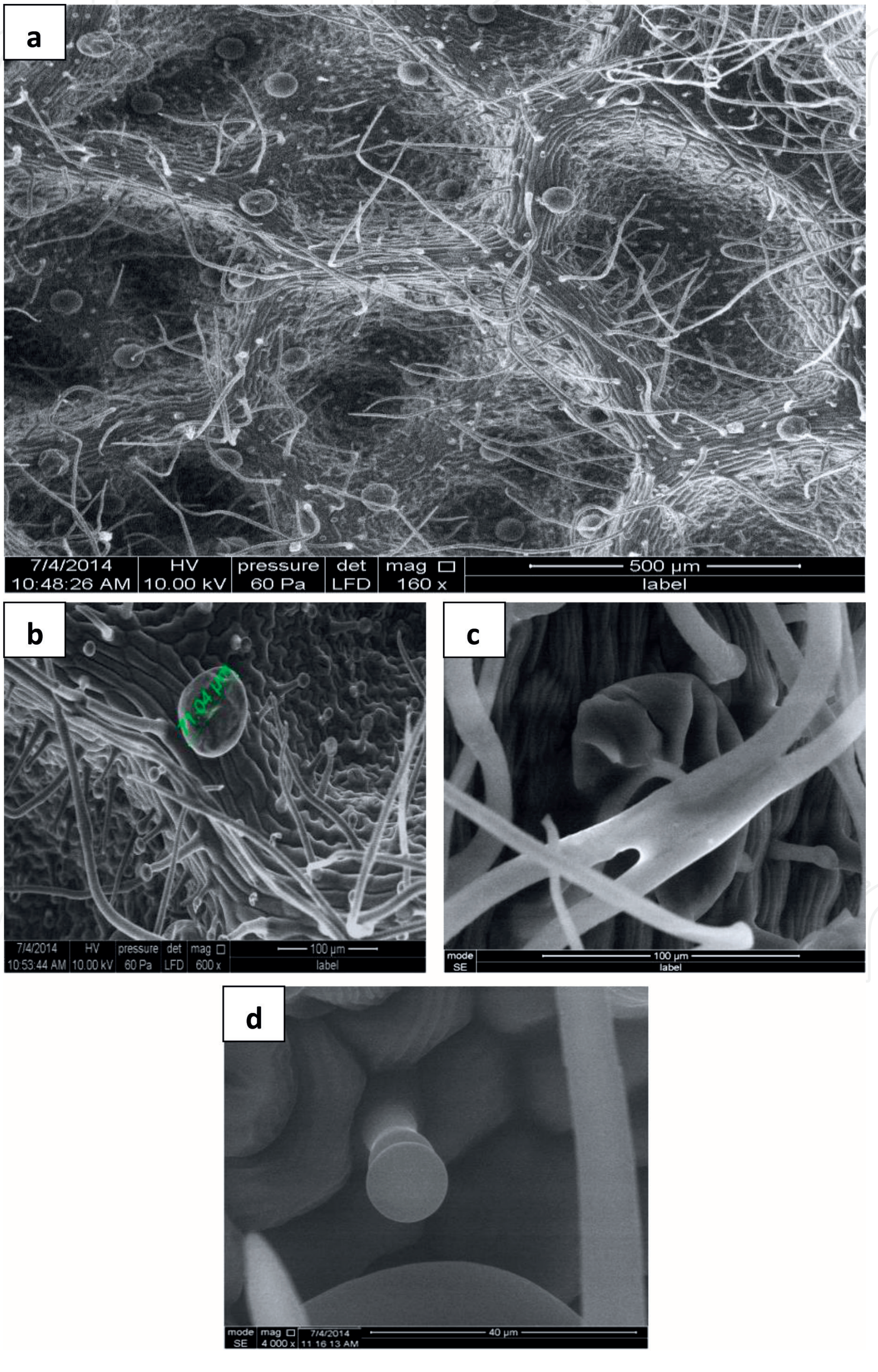

Figure 2.
Scanning electron microscope observations of the central region of Salvia officinalis leaf (a), showing the presence of two types of glands: peltate glands (b, c) and capitate glands (d) with GP (peltate glands) and P (protective hairs).

Glandular hairs consist of a base cell, a short unicellular stem, and a secretion head generally composed of 12 cells (sometimes 16) arranged in the form of a shield of 4 central cells surrounded by 8 peripheral cells (**Figure 2a, b**). Moreover, **Figure 2c** shows a sessile gland with multiple cells of the head. These structures are called peltate glands.

The second category of glands or capitate glands have a variable morphology since one distinguishes two types of glands: glands consisting of a short stem with one or two cells (**Figures 3a** and **4a–c**) and a head that can be unicellular or bicellular. In this type of gland, the cuticle is thin, with the presence or absence of a small subcuticular space. The second type consists of glands observed in old leaves at the end of flowering (**Figure 5**) and has a thin cuticle with the presence of a large subcuticular space directly to the epidermis. This structure is characterized by the presence of an accumulation pocket which is used to store the secretory material suggesting the presence of secretory cells below this pocket and whose synthesis products would arrive at the accumulation pocket through a structure (channel or pore) located under this pocket. The absence of this structure in young leaves and their appearance in old leaves suggests that these structures have a specific function related to the age of the leaf and are therefore specialized in the accumulation of a different substance.

Capitate glands are usually characterized by a single-cell head (**Figure 4a, b**). However, the light microscopic observations of the *Salvia officinalis* leaves show the presence of capitate glands that can present a two-celled head (**Figure 4c**).

According to the classification proposed by Werker et al. [4], the capitate glands are short-term glands specialized in the synthesis of non-terpenic substances frequently found in young leaves to provide a protective function against predators.

Figure 3.
Light microscopic observations of the different glands in Salvia officinalis. (a) Capitate gland, (b) detached peltate gland, (c) peltate gland in secretion phase, and (d) post-secretion peltate gland.

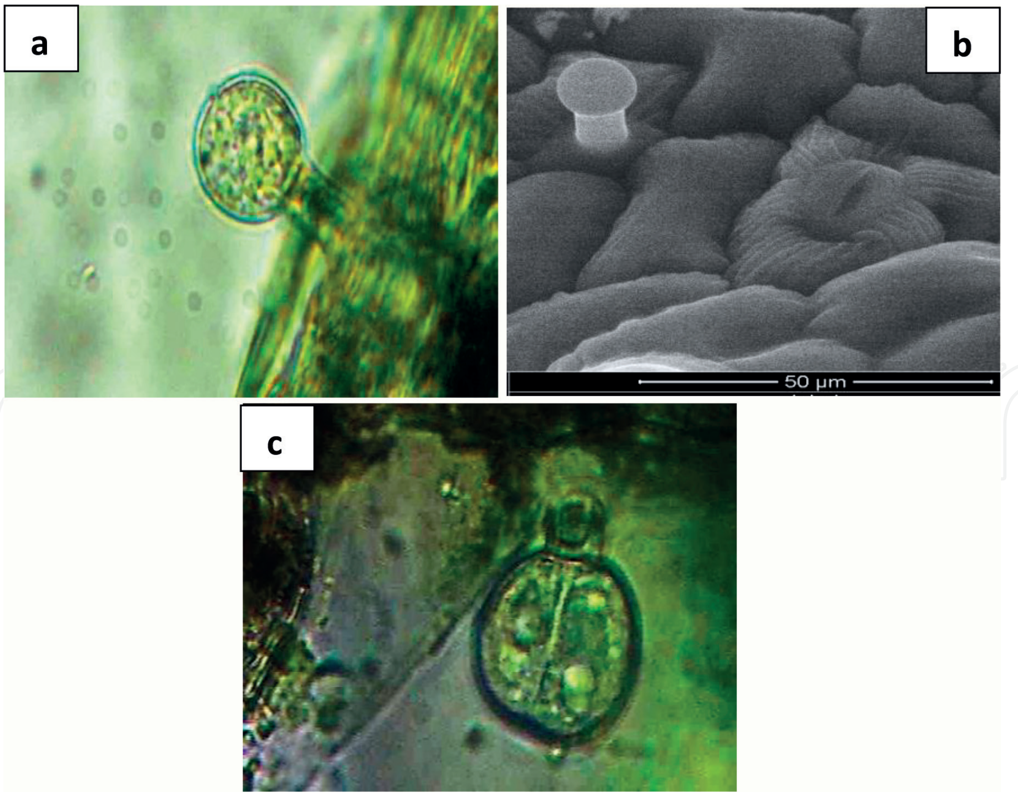

Figure 4.
Observations in light and scanning electron microscopy of capitate glands in Salvia officinalis. (a & b) Glands with single-cell head; (c) Gland with two-cell head.

The peltate glands are called long-term glands that are present in the leaves throughout the growth phases and whose number increases at flowering and are specialized in the synthesis of terpene substances.

Observations by the LM as well as SEM of the peltate glands (**Figure 3c, d**) do not reveal the presence of pores through which the secretory material can exude, which makes the material not released until the break of the cuticle, whether due to mechanical events or at the end of gland life.

6.1.2 Histological study of Pelargonium sp. glandular hairs

As in the case of sage, light microscopy observations made on *Pelargonium* sp. leaves show that this plant is characterized by the presence of two types of secretory glands, the peltate glands or long-term glands and the capitate glands or short-term glands, as well as protective hairs or non-secretory glands (**Figure 6**).

Capitate glands (short-term glands) are divided into two categories according to their forms: capitate glands with a stem consisting of four cells (**Figure 7b**) and capitate glands with one head and unicellular stem (**Figure 7c**). At the level of these glands, the synthesized secretion material is ready to be released just after its production via a porous cuticle (**Figure 7b**).

Moreover, we could only meet one type of peltate glands (long term), with a multicellular stem and a large head in which one finds the cells of synthesis as well as a storage pocket of essential oils. The appearance of these glands varies with their stage of maturity. **Figure 8a** shows a gland that has an empty aspect of any content and confirms the juvenile condition of the gland. These glands are gradually filled by the EO as they mature (**Figure 8b, c**), and their cuticle eventually breaks to release their contents at the end of their maturation (**Figure 8c**).

These peltate glands have a thick and rigid cuticle, but along the maturity stages of these glands, the thickness of this cuticle decreases to facilitate bursting and

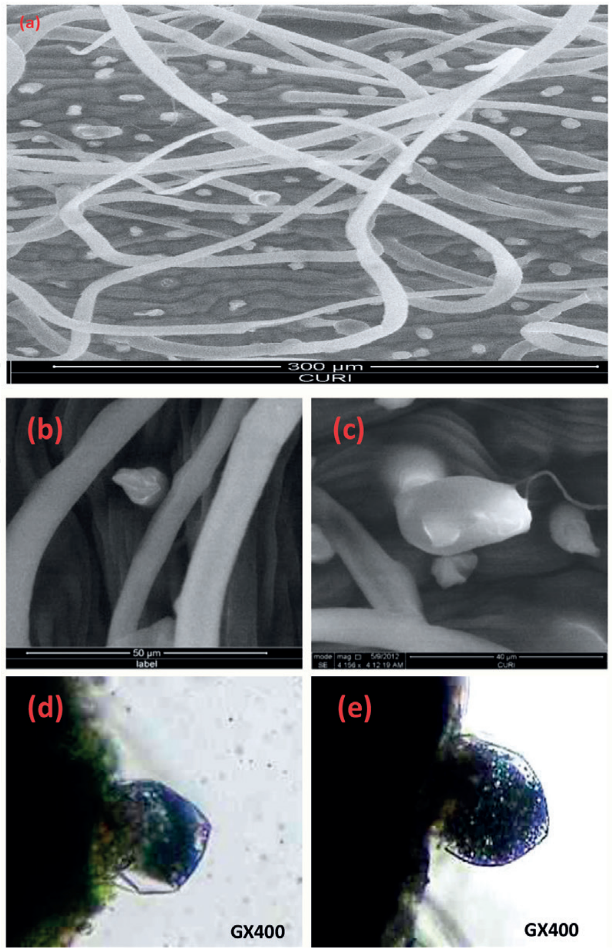

Figure 5.
Observations with light microscopy and scanning electron microscopy of capitate glands in Salvia officinalis. (a) Distribution of the pocket; (b&d) empty pocket; (c&e) pocket fill with secretory material.

release of contents toward the end of the maturity of the gland or by contact with some insects (**Figure 8**).

6.1.3 Histological study of Ocimum gratissimum glandular hairs

Environmental scanning electron microscopy observations of basil leaves show the presence of two types of glands (**Figure 9**), peltate gland and capitate gland. The peltate glands have a round shape and a fairly large diameter that can exceed 70 microns. The capitate glands are small not exceeding 40 microns and come in two forms, glands capitate with one head (CH) and two bilobed heads (C2H).

The observations made by the light microscopy of the capitate glands confirm those made by scanning electron microscopy, with the presence of capitate glands with a single head (**Figure 10a**) and capitate glands with two heads (**Figure 11b**). On the other hand, the glands with a single head can be unicellular (**Figure 10a**) or bicellular (**Figure 10b**).

In basil plants, the peltate glands show a variability in the number of secretory cells. There are large glands with four cells (**Figure 12a**). In addition, we have been able to highlight the presence of glands that have eight secretory cells (**Figure 12b, c**). A thick cuticle covers both types of glands. With the filling of the essential oil structure, this cuticle becomes thinner to facilitate the release of the contents.

Figure 13 shows peltate glands of basil after bursting and release of their terpenic contents; according to this figure, we notice the existence of four secretory cells

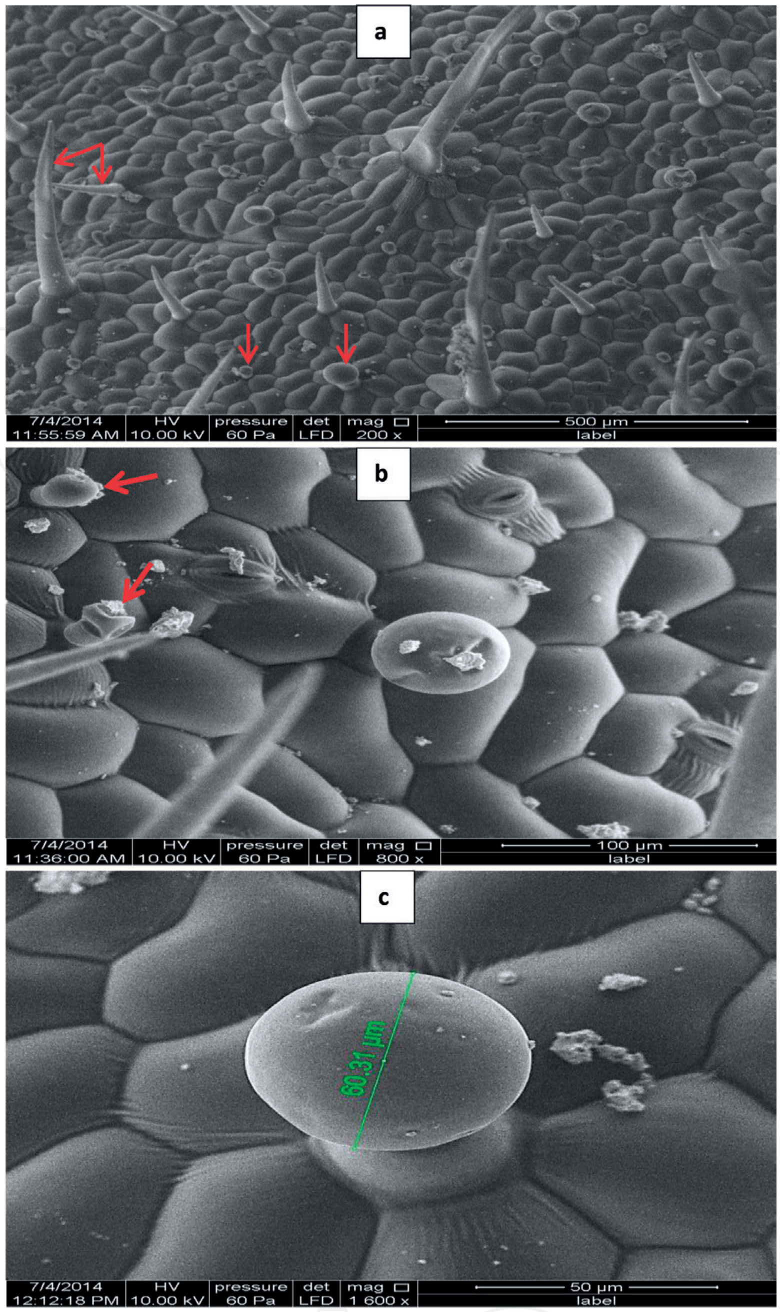

Figure 6.
Scanning electron microscopic observations of the ventro-central part of a Pelargonium *sp. leaf, showing the presence of two types of secretion glands, peltate. (a): observation of non glandular hairs and glandular hairs (c) and capitate (with red arrow).*

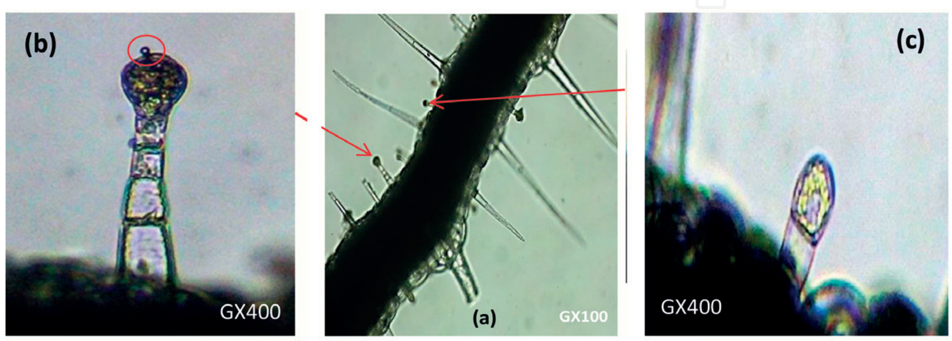

Figure 7.
Observations made by light microscopy on Pelargonium sp. leaf showing the two types of capitate glands. (a) Global vision; (b) capitate glands with a stem consisting of four cells; (c) capitate glands with one head and unicellular stem.

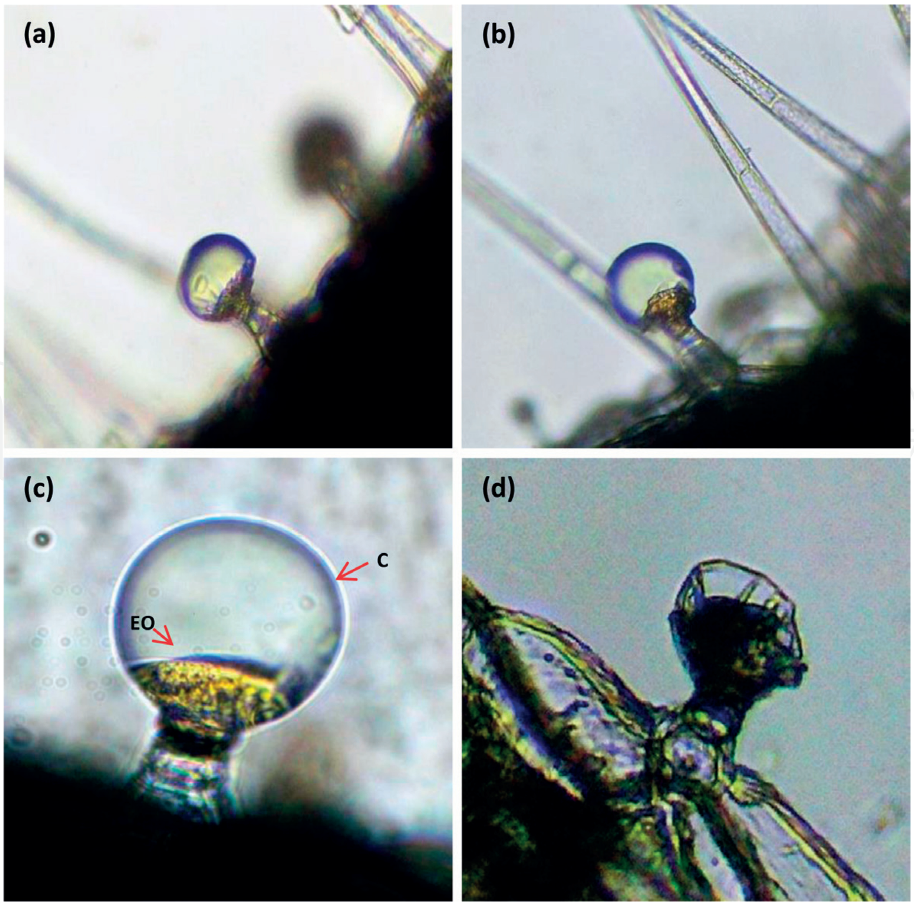

Figure 8.
Observations in light microscopy of peltate glands, secreting essential oils at different stages of maturity in Pelargonium *sp. (a) Beginning of maturation, (b, c) filling with the EO, and (d) bursting of the gland. C, cuticle; EO, essential oil (Gx 400).*

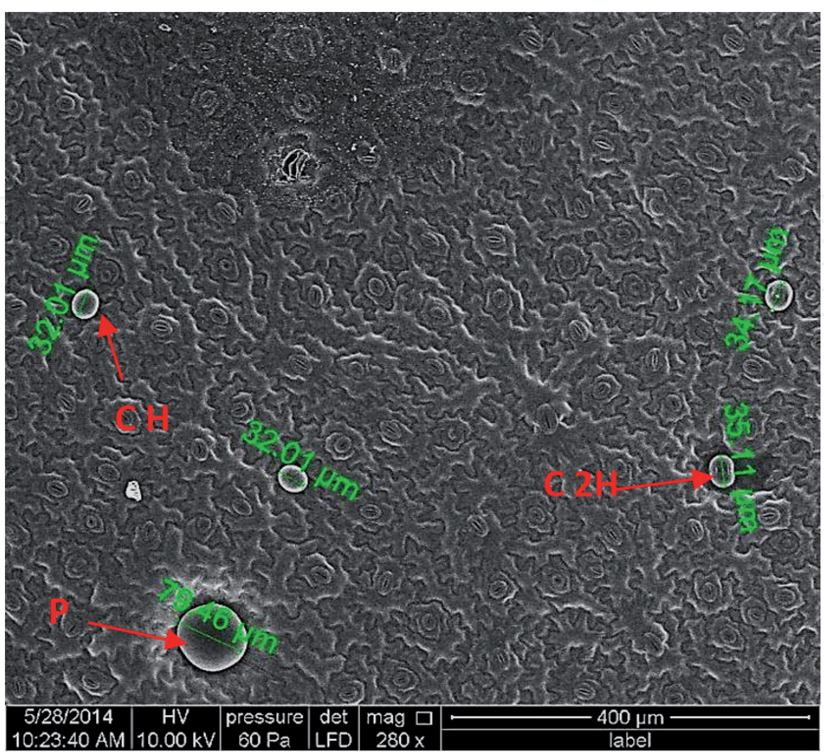

Figure 9.
Observation by scanning electron microscopy of basil leaf showing the presence of pelt glands (P) and capitate glands (CH: capitate gland with one head and capitates gland with head bilobed C2H).

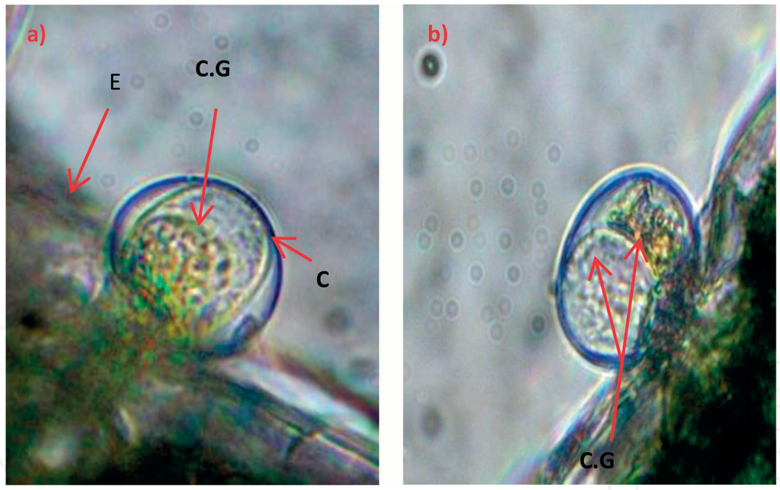

Figure 10.
Light microscopy observations of a capitate gland with a single head and a single cell (a) and with two cells (b). C, cuticle; E, epidermis; CG, glandular cell (GX400).

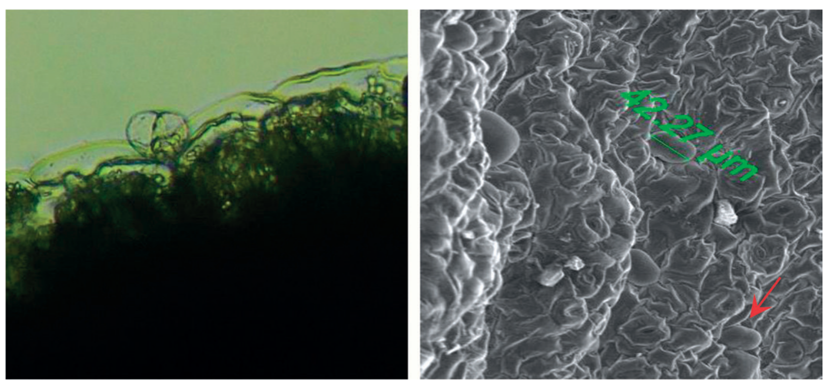

Figure 11.
Observations made by light microscopy and scanning electron microscopy of a double-headed gland in basil plants.

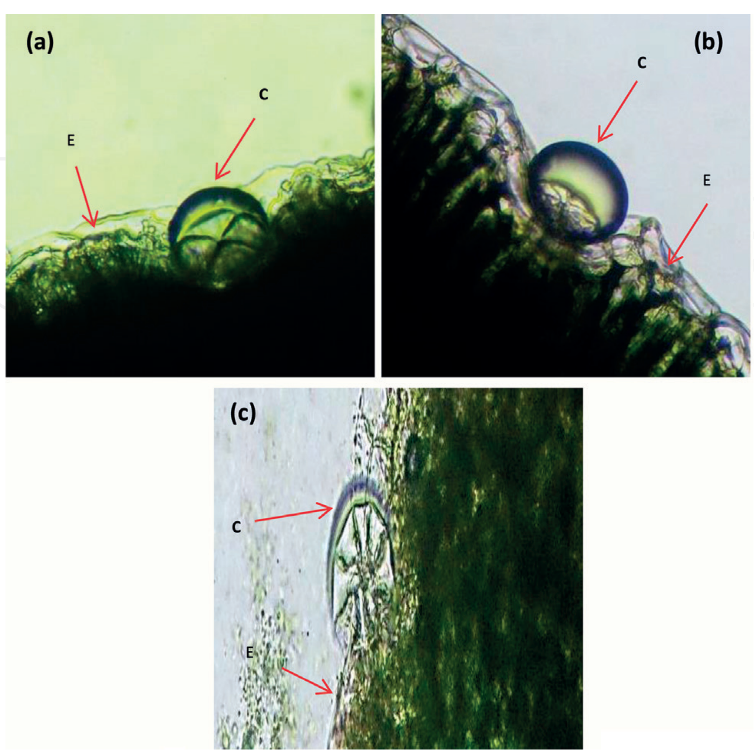

Figure 12.
Light microscopic observations of a cross section (central part of a basil leaf O. gratissimum*) showing two types of peltate glands: glands with four secretory cells (a) and glands with eight secretory cells (b, c).*

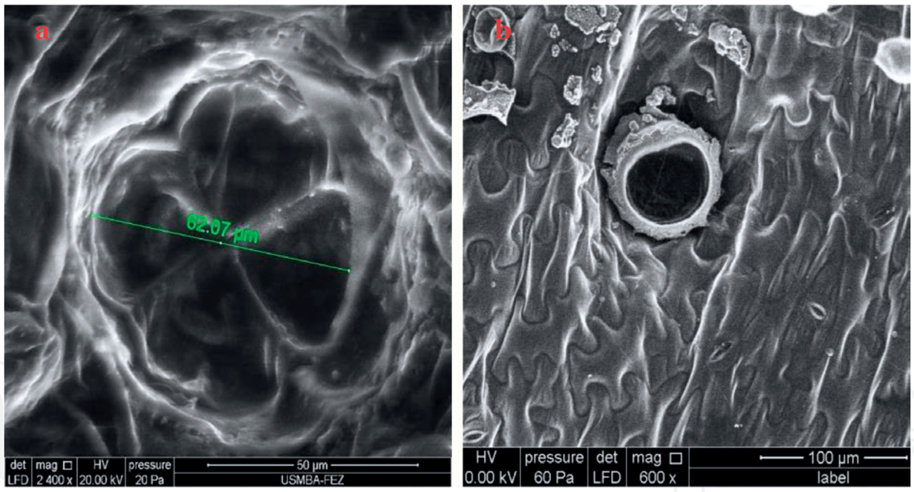

Figure 13.
Observation by scanning electron microscopy of a pelted basil gland after natural bursting (a) and mechanics (b).

(**Figure 13a**) with an internal diameter (without the cuticle which encompasses the gland) that touches 62 µm. Furthermore, **Figure 13b** shows an immature gland, but burst under pressure (exerted by SEM), and shows a thick cuticle which confirms the state of non-maturity that has already been reported.

7. Discussion

The microscopic observations made in this work show the presence of two major groups of secretory glands in the three plants (sage, pelargonium, and basil). The first group is peltate glands or long-term glands, and the second group is capitate glands or short-term glands. Within the same group, we can see a morphological variation from one plant to another, depending on the content, the role, and the phenological stage of the plant, which makes the classification difficult. But to ensure a credible classification, various authors are mainly based on the morphological criterion, the content, as well as the mode of secretion [4–8, 12].

In this context, scientists have given a definition to these two names; they have described a short-term gland as any gland whose secretion is rapid to protect young organs and a long-term gland as any gland in which the secretory substance accumulates gradually in the subcuticular space and serves for the protection of mature organs in the flower, as well as for pollination. The difference between the two types consists of several aspects, namely, the structure, the mode of secretion, and the moment of secretion.

The microscopic observations made on our plants go in the direction of this classification and show the two groups of glands, peltate and capitate. Moreover, two major types of peltate glands could be determined in this study, peltate glands with stem consisting of a single-cell and peltate glands glued directly to the epidermis. In the latter group, there is a major difference in the number of cells of each gland, since there are 4 and 8 cells in *O. gratissimum* and up to 12 in *Salvia*. These results are confirmed by the work of Tissier [13], Werker [8], and Gang et al. [14]. According to these authors, the peltate glands can have a large number of cells that can reach 16 cells.

These peltate glands are generally characterized by a large subcuticular space and a rigid cuticle which thins during the maturation of the gland which facilitates bursting at maturity or after mechanical contact with predators.

The captioned glands are subdivided into several categories according to their forms:

- Capitate glands possessing a basal cell and a united or multicellular stem (1–3 cells) and a head
- Capitate glands with a stem cell and a united or bicellular head
- Capitate glands with a basal cell and a head with one or two cells
- Capitate glands in the form of a pocket glued directly to the epidermis

These capitate glands are characterized by a thin cuticle with the synthesized secretory material which is ready to be released just after its production via a porous cuticle and usually consist of a united or bicellular head with lipophilic content.

Similar observations have been found in *Salvia* [15], since according to these authors the capitate glands are morphologically very variable and four types can be distinguished. Type I has a single or double bicellular stem and a united or bicellular head. The cuticle is thin and there is no subcuticular space. The secretory material is released slowly through the cuticle and can be released suddenly if the cuticle is broken. Type II is very small, possessing a unicellular stem and a small subcuticular space. The secretory material is probably secreted by a pore. Type III is a large gland with a long stem made up of several cells (about three or more), a neck cell, and a unicellular head, which probably releases the secretory material often collected as a drop on the head. Type IV is a large gland with a long thin stem, made up by four cells.

According to these authors, each type of gland is responsible for the synthesis of a distinct substance. Venkatachalam et al. [16] found a correlation between the increased number of peltate glands and increased camphor and thujane synthesis.

These observations are in agreement with those of Pedro et al. [17] who deduced the presence of three types of glands, a peltate type and two capitate types. According to these authors, the glands with a unicellular stem represent a distinct capitate gland with a specific content different from that of the peltate structure. According to the same work, these three types of glands ensure the synthesis of three types of different substances, terpenoids, phenols, and flavonoids.

In other works by Ko et al. [18], *Pelargonium*'s peltate and capitate glands all have a single basal cell. These two types of glands differ in the number of stem cells and in the diameter of the head depending on the stage of maturity [3]. According to these authors, the glands defined in our study as glands capitate to a head and a unicellular stem represent only one stage of the formation of the peltate glands. However, observations made in *Salvia* leaves show structures identical to this structure, possessing a small unicellular head and a single-celled stem. This structure has been classified as a capitate gland.

These kinds of peltate and capitate glands are found in several species (*Mentha piperita*, *Origanum dictamnus*, *Monarda fistulosa*, *Pogostemon cablin*, etc.) and have been described in ancient works [16]. In mint, the peltate glands have eight head cells, and the capitate glands have a single-stem cell and a head cell. In *Origanum dictamnus*, the head of the peltate glands has 12 cells, whereas in *Pogostemon cablin*, it has only 4 cells.

According to Werker [8], young basil leaves (*O. basilicum*) that are highly vulnerable to predators are heavily covered by capitate glands that are characterized by rapid secretion to repel herbivores. When the plants become older, the rate of the peltate glands increases; these terpenoid-rich glands will be used for defense against pathogens in case of injury and pollinator attraction.

8. Conclusion

The microscopic observations made on the three plants (basil, pelargonium, and sage) show the presence of two major types of secretory glands. The first type is peltate glands or long-term glands, and the second types are capitate glands or short-term glands. Within the same type of gland, we can see a morphological variation from one plant to another, depending on the content, the role, and the phenological stage of the plant.

In basil, we have demonstrated for the first time the existence of eight secretory cell glands in the peltate glands.

In *Salvia*, we noted the presence of two types of glands, capitate and peltate, the latter being constituted by 12–16 cells arranged in the form of a shield. On late flowering, we noted the presence of pocket secretions in older leaves. In this plant, we have mainly highlighted the presence of sessile glands, and this observation has never been confirmed in the literature.

Conflict of interest

The authors of this work (Zakaria Hazzoumi, Youssef Moustakime, Khalid Amrani Joutei) declare that they have no conflict of interest.

Notes/thanks/other declarations

"The scientist is not a person who gives the right answers, he is one who asks the right questions. Claude Levi-Strauss".

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