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*Full Length Research Paper*

# The morphology and ultrastructure of glandular and non-glandular trichomes of *Pteronia incana* (Asteraceae)

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**The electron microscopical investigation of foliar appendages of *Pteronia incana* (Burm) has shown that there are two types of trichomes. The non-glandular type which consists of two-four cells forms a dense mass of long fibrous hairs, covering the entire surface of plant. The glandular trichome types which are club-oval shape and consist of several glandular cells. The gland cells of the glandular trichome are characterized by a dense cytoplasm containing osmophilic droplets, various organelles such as modified plastids, endoplasmic reticulum, a large nucleus with a dense cytosol. The secreted material accumulates in a cavity beneath a wall derived from separation of the cuticularized outer wall surface of the top tier of secretory cells and are released to the outside when the cavity ruptures. Only the apical pair of cells participates in secretion. Cells of both types possess plastids without thylakoids. These active compounds secreted by *P. incana* might be the reason why this plant is unpalatable to livestock.**

**Key words:** *Pteronia incana,* trichomes, oil glands, electron microscope.

## INTRODUCTION

*Pteronia incana* (Burms) of the Asteraceae family is small bush like perennial shrub which is widespread in Southern Africa (Webber et al., 1999). It has small greyish leaves with often ramified branches reaching a height of approximately 100 cm and has invaded an estimated land of 60 000 hectares of semi arid areas of the Eastern Cape in South Africa (Bruns and Meiertorens, 1987; Webber et al., 1999). It is considered to be a weed in this area; as a result this plant has occupied a large space which can be utilized for cultivation. The exudates of this plant are believed to be unsuitable for a variety of livestock and are also reported to render plant cultivation unnecessary. Its stem and leaves are covered by densely arranged whitish epidermal trichomes that reflect the plants visibility from far away as grey patches in grassland. The trichomes are well known to be responsible for the primary production of bioactive secondary products which may function as plant growth regulators and also act as a defence mechanism for the plant against insects, other pathogens and possibly livestock (Croteau, 1977; Bell, 1981; Kelsey et al., 1984; Wagner, 1991; Duke and Paul 1993; Werker, 1993). The essential oil produced by this plant is pale-yellow and is not extensively studied by Bruns and Meiertorens (1987) and Webber et al. (1999), and the worldwide production value of this oil is still unknown. The investigation on morphology and ultrastructure of these trichomes has not yet been reported.

In this article, we examine the morphology and ultrastructure of glandular and non-glandular trichomes of *P. incana* in order to relate our findings to their possible functional role in the production of essential oil for commercial exploitation and to open future investigations on medicinal implications of their products.

## MATERIAL AND METHODS

### Scanning electron microscopy

Sections of leaves and stems (0.1 x 0.5 mm thick) of *P. incana* were randomly collected and immediately fixed in 6%

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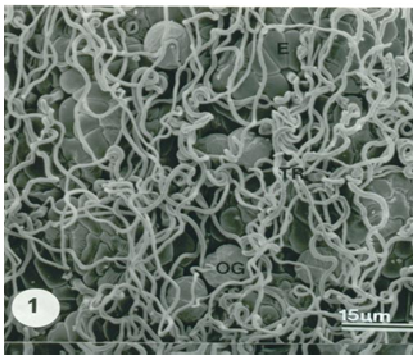


**Figure 1.** This is an electron micrograph of the *P. incana* leaf at low magnification showing the surface with a high distribution of glandular and non-glandular trichomes. TR = Trichome, OG = Oil gland.

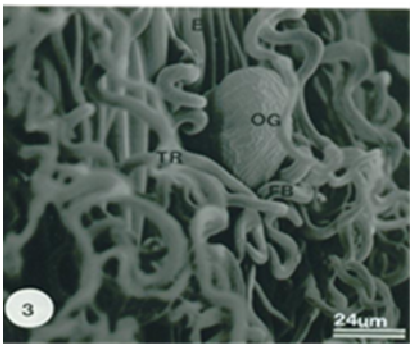


**Figure 3.** This is an electron micrograph of an old *P. incana* stem showing the surface of the stem with a dense network of fibrous non-glandular trichomes. **Note** the low distribution of the glandular trichome. TR = Trichome, FB = Fibrous end, OG = Oil gland, E = Epidermis.

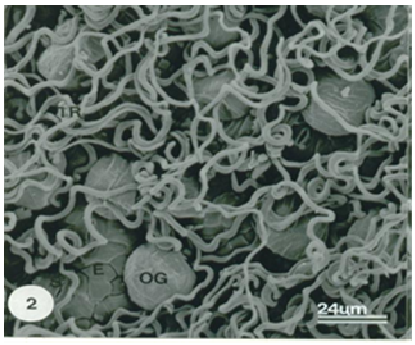


**Figure 2.** This is an electron micrograph of the *P. incana* leaf at high magnification showing the distribution pattern of glandular and non-glandular trichomes in relation to stomata. TR = Trichome, OG = Oil gland, E = Epidermis, S = Stomata.

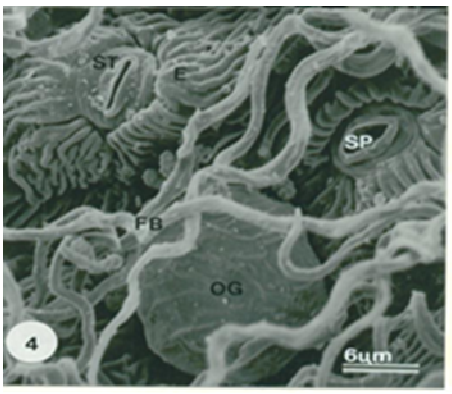


**Figure 4.** This is an electron micrograph of the *P. incana* leaf at high magnification showing the characteristic shape of stomata, the protective nature of non-glandular trichomes over the grooved epidermal surface, which is assumed to absorb the essential oils. FB = Fibrous end, E = Epidermis, SP = Stomatal pore, ST = Stomata

glutaraldehyde in 0.05 mM sodium cacodylate buffer (pH 7.3), washed in 0.05 mM sodium cacodylate for 12 h. Sections were then dehydrated in an ethanol series. The leaves were dried in a Hitachi HCP-2 critical point dryer, coated with gold using a sputter coater and viewed at 15 kV with a Hitachi S-450 Scanning Electron Microscope.

**Transmission electron microscopy**

Young and mature leaves and stems of *P. incana* were randomly selected from the natural environment. The leaf portions were cut into small segments approximately 2-3 x 5 mm in cold 50 mM sodium cacodylate buffer, (pH 7.3). The plant segments were fixed in a buffered 6% glutaraldehyde (50 mM sodium cacodylate, pH 7) and stored overnight in a refrigerator.

After rinsing in a 50 mM Na-cacodylate buffer, the samples were then post fixed in 2% osmium tetroxide ($OsO_4$) in 50 mM Na-cacodylate buffer, pH 7.3, overnight at 4 $^{o}$C, infiltrated in a graded series resin (Spurr, 1969).

Thin sections (0.5 - 2.0 µm) were cut with glass knives on an LKB Ultramicrotome, stained with Uranyl acetate followed by lead citrate and observed in a Hitachi at 75 - 100 kV. Some of the sections were stained with 0.05 % toludine blue and examined with a Zeiss photo-microscope III.

## RESULTS

Scanning electron microscopy (SEM) observations have shown that the leaves and stems of *P. incana* are characterized by uniseriate non-glandular and multicellular glandular trichomes. The non-glandular trichomes form a dense covering that completely cover a large portion of the epidermal surface and they seem to be obscuring the glandular trichomes (Figures 1 - 7). These non-glandular appeared to be tubular and fleshy in nature at the early stages of development when viewed with SEM (Figure 5). They seemed to be formed by the crystalline aggregates of cellulose molecules,

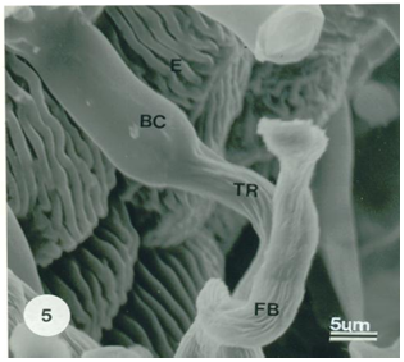


**Figure 5.** This is an electron micrograph of the *P. incana* stem showing a similar pattern of grooved epidermis. Note the fibrous thread-like structure of non-glandular trichomes due to progressive basipetal development. TR= Trichome, FB = Fibrous end, BC = Basal cells, E = Epidermis.

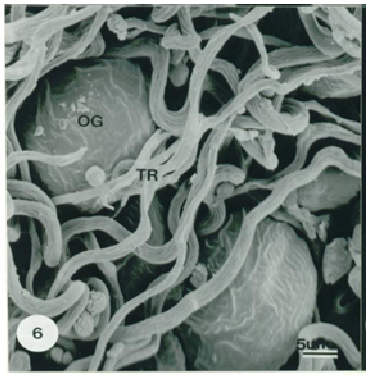


**Figure 6.** This is an electron micrograph of the *P. incana* stem showing a cluster of advanced cauliflower-like spongy structures attached to fibrous non-glandular trichomes. TR = Trichome.

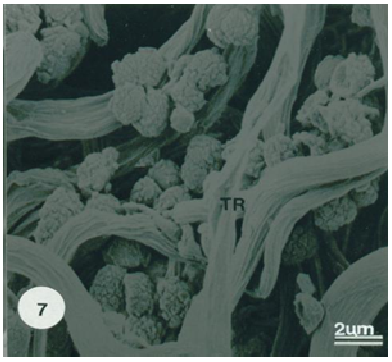


**Figure 7.** This is an electron micrograph of the *P. incana* stem showing a cluster of advanced cauliflower-like spongy structures attached to a fibrous non-glandular trichome. TR = Trichome.

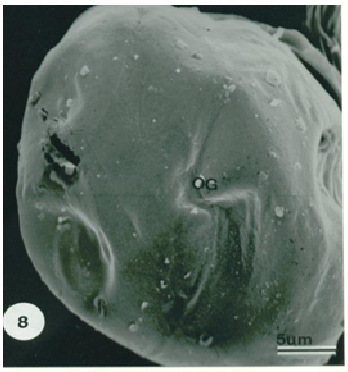


**Figure 8.** This is an electron micrograph of the *P. incana* stem showing the characteristic glandular cell, which is about to release essential oil. Note the distended cuticular sac. OG = Oil gland.

which constituted well-organized macrofibrils (Figures 4 - 7). These fibrous threadlike non-glandular trichomes, which are appeared to be dead at maturity, appeared to be shielding and protecting the glandular trichomes, epidermal layer and the stomata (Figures 1 - 4 and 6) possibly against foraging insects and airborne propagates of fungi.

The mode of development of non-glandular trichomes appeared to be basipetal (Figure 5). As this basipetal development proceeded from the terminal end to the base of the non-glandular trichome, the mature portion of the trichome became dehydrated and fibrous (Figures 4 - 7). However, the basal portion of the non-glandular trichome remained alive without being dehydrated (Figure 5).

Another common characteristic, which is associated with the maturation of the non-glandular trichome, is the development of sponge-like structures (Figures 6 and 7). These structures appeared to be more dominant where the epidermal layer of leaves or stems were characterized by a number of matured non-glandular trichomes and also associated with the oil glands. In some instances, a complete growth of these non-glandular trichomes often resulted in their removal from the stem's epidermis, as the epidermis was substituted by the periderm during the development of the secondary growth; meanwhile the basal cell remained alive as the progressive growth continued in a basipetal direction (Figures 4 and 5).

The ultrastructure of the non-glandular trichome has indicated that in the early stages of trichome development, all the cells of the trichome are metabolically active (Figures 9 - 12). At this early stage of development, the basal cell was characterized by a large nucleus surrounded by a dense cytoplasm (Figures 10 - 12). As these non-glandular trichome cells matured, progressive growth occurred through anticlinal divisions (Figures 10 - 12). At maturity, it appears that

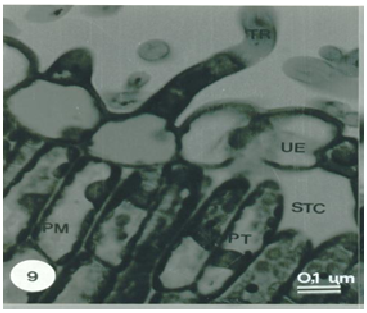


**Figure 9.** The transverse section of the *P. incana* leaf showing mature non-glandular trichomes and photosynthetic palisade mesophyll tissues below. TR = Trichome, UE = Upper epidermis, PT = Parenchymatous tissues, PM = Palisade mesophyll cells.

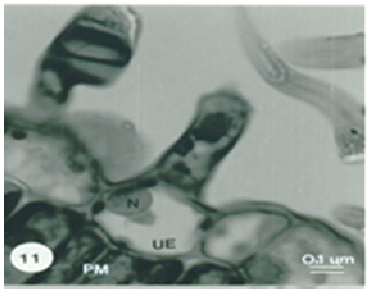


**Figure 11.** A transverse section of the leaf showing the developing trichomes and compact palisade mesophyll cells. TR = Trichome, N = Nucleus, UE = Upper epidermis, STC = Stomatal cavity, PM = Palisade mesophyll cells.

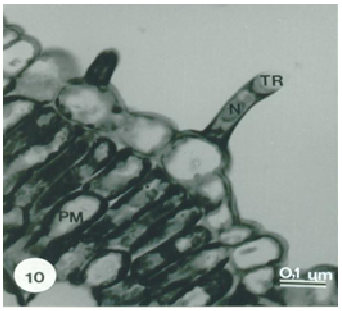


**Figure 10.** Section of the leaf showing an early stage of non-glandular trichome development, palisade mesophyll cells beneath the upper epidermis containing chloroplasts. PM = Palisade mesophyll, N = Nucleus, TR = Trichome.

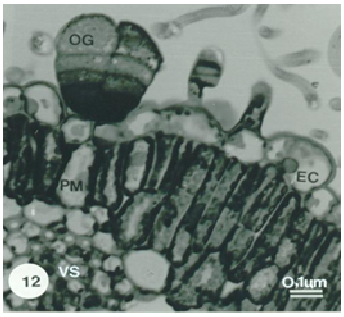


**Figure 12.** This is an electron micrograph of a *P. incana* leaf showing the epidermal cells, a portion of the palisade tissue and glandular trichome with no cuticular sac. EC = Epidermal cell, OG = Oil gland, PM = Palisade mesophyll cells, VS = Vascular tissue.

the initial non-glandular trichome cells, which were produced, collapsed and died, thereby giving the non-glandular trichomes a more or less fibrous appearance (Figures 9 and 12).

In contrast, the glandular trichomes resembled club-shaped, sac-like structures that formed a protrusion outside the epidermal layer (Figures 6 and 8). These are multicellular and biseriate, globular to oval in shape (Figures 6, 8, 12 - 14).

During the early stages of plant development, glandular trichomes appeared to be dense and scattered in a random pattern (Figures 1, 2, 6 and 12). When the leaf matures, the glandular trichomes appeared to decrease progressively, and their distribution became far apart. The development of the oil glandular trichome resulted in the appearance of the cuticular sacs which appeared to be intact, shrivelled or hard during the early stages of gland development (Figures 3 and 6). As they approached maturity, the surface seemed to be smooth, as the oil gland cell walls were transformed to cuticular sacs (Figure 8). A further development resulted in the accumulation of the essential oil in the cuticular sac. The secretory products are usually released through pores in the cuticle or through rupture of the cuticle caused by external pressure (Figures 8 and 14).

Transmission electron microscopy revealed that, in the initial stages of trichome development, the expanding epidermal cell had an electron cytosol, with a clearly evident of a large basal nucleus (Figure 12). At this stage, it was difficult to distinguish whether the cell might be a non-glandular or a glandular trichome, because there was no clear indication of periclinal or anticlinal division with the exception of the bulgeness of the epidermal cell, which would have formed the trichome initially.

The glandular trichome appeared to originate from two epidermal cells as a result of a periclinal division which was subsequently followed by an anticlinal division to give rise to six or ten glandular head cells which are supported by two stalk cell (Figure 12). At full maturity, the upper surfaces of the oil gland cells were covered with a cuticular sac (Figure 13). The latter appeared to be the modified cell wall of glandular cell(s) which occurred on the terminal position. The subcuticular sac became distended due to the accumulation of the essential oils which were produced

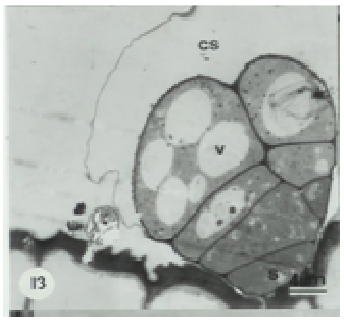


**Figure 13** Ultrastructure of glandular trichome of *P. incana* showing lateral view of an oval-club shape trichome with several glandular cells. **Note** the cuticular sac (CS); with several vacuoles (V), S = Stalk cell.

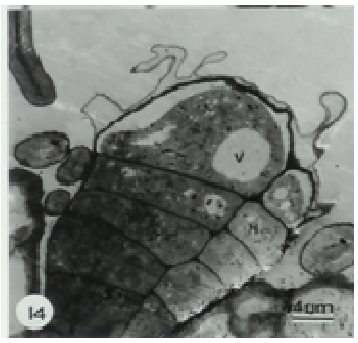


**Figure 14** A glandular trichome that has already secreted the material to the outside environment. V = Vacuole; H = Head cells.

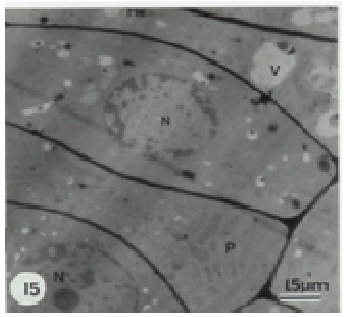


**Figure 15** High magnification of the middle cells of the apical cell prior to secretion. Note an electron dense nucleus (N), and the plastids (P).

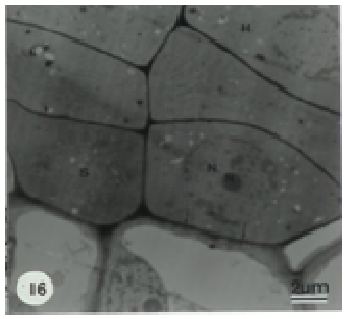


**Figure 16** Another high magnification of a trichome between the stalk cell an the basal cell of the epidermal cell characterized with plasmodesmata (arrows), S = Stalk cell; H = Head cell; N = Nucleus.

by the cells of the oil gland. As the progressive production of the essential oil continued, it resulted in the slow disintegration of the subcuticular sac. The essential oil was subsequently released through pores of the cuticle or more likely after the rupturing of the cuticular sacs (Figure 14). The cell walls of secretory cells are electron dense with reticulate ingrowths (Figure 19).

The ultrastructure of the apical cells of the glandular trichome shows a dense cytosol, with poorly developed vacuoles containing small osmophilic droplets (Figures 14, 15, 18 - 20). It was also noticed that there were numerous highly elongated granular structures which were considered to be modified plastids. The latter appeared to occupy most of the volume of the cytoplasm of the cells above stalk cells, but below the apical cells of the developing glandular trichome (Figures 15, 18 and 20). These plastids displayed complex tubular structures (Figure 20). Another interesting feature is the presence of endoplasmic reticulum system which appeared to surround the plastids in the oil gland cells (Figures 15, 16 and 18). The most interesting features were the presence of plasmodesmata between the stalk cells and basal epidermal cell of the glandular trichome (Figures 16 and 17). However, these plasmodesmata were absent in the suberized cell walls of the matured glandular trichome cells. The presence of these channels at the early stage of development suggested an energy input mechanism to stalk-epidermal cells transport system. However, the cell wall between the stalk cells of the glandular trichome and also the cuticular sac showed no signs of the presence of plasmodesmata or the transport system (Figures 15 and 19).

## DISCUSSION

The non-glandular trichomes were composed of uniseriate cells. The terminal cells of the non-glandular trichomes were the first cells to mature but thereafter there was no further growth. Further progressive maturity resulted in continuous death of the uniseriate cells until on many occasions there were approximately one or two cells, which remained active at the basal ends of the trichome. The dead cells resembled fibre-like clothing threads, which covered the epidermis (Bosabalidis and Tseko, 1984).

The observation indicated that, the basal or the terminal cells of the non-glandular trichomes were

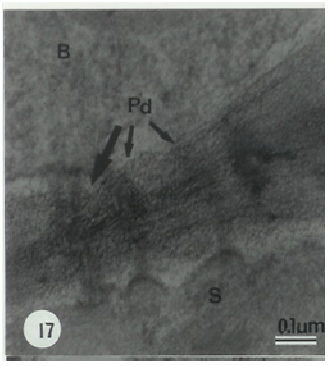


**Figure 17.** High magnification of the cell wall between the basal cell (B) and the stalk cell (S) of the trichome showing the presence of plasmodesmata (Pd). The presence of these plasmodesmata suggests a movement of materials from cell to another.

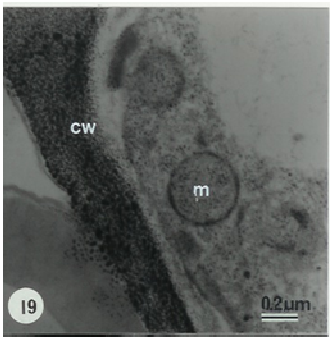


**Figure 19.** Part of the gland cell prior to secretion. Note the dense cuticle along the cell wall (cw), m = mitochondria.

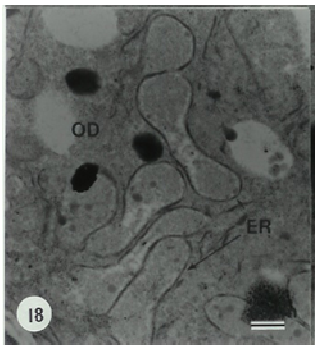


**Figure 18** The organelles within the apical cell of trichome. OD = Oil droplets; ER = Endoplasmic reticulum.

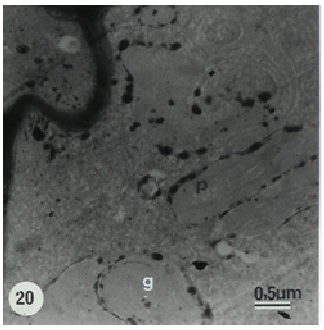


**Figure 20.** Bottom cell of a glandular trichome with high distribution of plastids (P) with granum (G).

characterized by suberin similar to the root endodermal cells. It was assumed that these suberin barriers on the dead cells of the non-glandular trichomes were able to prevent apoplastic water flow into the trichomes (Gunning, 1977; Werker et al., 1985). When such uniseriate cells retained living protoplasts, it was assumed that the transpiration stream of the trichomes might continue through the symplast. The same assumption was supported by Fahn and Shimony (1998).

However, a possibility existed that when a water deficit balance developed, incipient plasmolysis might have occurred in the trichome cells. The detachment of the protoplasts from the cell wall or a complete death of the terminal cells might minimize the effect of the symplastic water transport to the uncutinized walls of the upper or the adjacent cells of the trichomes. This stage of non-glandular trichome development occurred in great abundance in mature leaves and stems (Wagner, 1991).

It appeared that the high distribution of non-glandular trichomes in *P. incana* foliar appendages might be regarded as an adaptation associated with arid conditions. The trichomes were assumed to affect transpiration by influencing the water diffusion boundary layer of the transpiring leaf surface. In addition, they might also indirectly influence the water economy of the leaves or young stems through temperature. This might also occur either through reduction energy dissipation by trichomes, which have high reflectance properties, or else the non-glandular trichomes were able to shield the stomata and oil glands from extensive heat during the dry and hot seasons. Such basic phenomena involved in the characterization of the boundary layer resistance have also been observed in xeromorphic species (Gates, 1968; Johnson, 1975).

Such a relationship between the stomatal and boundary layer resistance was also of great significance in attempting to assign an adaptive role to the indumentum layer shown by *P. incana*. The greyish-white cast which occurs in the dead non-glandular trichomes of the leaves supports the contention that high reflectance of visible radiation was frequently associated with the pubescence (Johnson, 1975). The dead non-glandular trichome cells and the epidermis appeared to have wavy anticlinal walls and an

undulation, which covered the entire depth of the walls of the leaf and stem epidermis, and the non-living portion of the non-glandular trichome. This differentiation has resulted in a thick fibrous epidermal layer and thick fibrous thread-like and rod-like non-glandular trichomes. It has been suggested that the undulation and waviness of the epidermal and dead non-glandular trichomes might be related to the development of stresses during the leaf non-glandular trichome and cuticle differentiation in the xeromorphic species (Fahn, 1986; Esau, 1953). Since these characteristics were also present in *P. incana*, it appeared that this species might also be adapted to a xeromorphic environment.

The non-glandular trichomes appeared to originate from the epidermal layer by periclinal division. This process continued by periclinal division until several cells, which formed the uniseriate trichomes, was produced. A similar uniseriate trichome ontogeny was observed in several species (Bosabalidis and Tsekos, 1984).

The ultrastructure of the non-glandular trichome cells was characterized by a large nucleus surrounded by the cytoplasm, which contained oil globules, and phenolic compounds that were associated with the cell wall. It appeared that these phenolic compounds and oil globules found in living cells of non-glandular trichomes might be ascribed for defence and wound healing processes (Webber et al., 1999). This physiological aspect had been observed in the trichomes of many species by Beckman et al. (1972).

This proposition on the physiological specialization of non-glandular trichomes was also confirmed in some genera of the Asteraceae family (Duke and Paul, 1993; Afolayan and Meyer, 1995). Furthermore, it appeared that, such a phenomenon has been demonstrated in young leaves of *Olea europaea* (Fahn, 1986). The essential oils and oil globules found in the non-glandular trichomes of *P. incana* might be associated with defence function related to alkaloids which were present in the same compartments in other species (Robinson, 1974).

The glandular trichomes were also the characteristic feature of the *P. incana* leaves. These trichomes were multicellular and uniseriate. The glandular trichomes ranged from club to oval shape and they were composed of a basal cell and, a short stalk cell with a large six to eight celled head. The orientation of the glandular trichome is not uniform, however, a different orientation has been observed in the leaves.

Morphological studies have shown that the distribution of these glandular trichomes was high during the vegetative growth period prior to the flowering period. At this stage of development high glandular trichome distribution was present on both the abaxial and adaxial surfaces of the leaf. These glandular trichomes were also found in the old stems, but their distribution frequency was lower in comparison to the mature leaves.

It appeared that the glandular trichomes occurred in abundance during the early stages of leaf and stem differentiation. However, these glandular trichomes seemed to decrease in the old stems.

What is not yet known from the literature is whether the new glandular trichomes, which exist throughout the lifetime of the leaf or stem, are formed in the same position as the previous glandular trichomes by regeneration of new cuticular sacs. To our knowledge there is no literature available, which dealt with this aspect. It appeared that there is strong evidence that after the essential oil has been released due to the rupture of the cuticular sac, there was a regeneration of the new oil glands, which would replace the old cells (Bosabalidis and Tsekos, 1984; Ascensão et al., 1987). It was proposed that the process occurred in the following sequence.

The initial event was the apical oil gland cell lysis. Thereafter the first layer of the oil gland cells, beneath the apical oil gland cells undergo a process of differentiation and replace the former apical oil gland cells. It is also, proposed that, the new stalk cells are regenerated from the basal epidermal cells by periclinal and anticlinal divisions. However, the possibility of glandular trichome ontogeny in other parts of the epidermis due to ordinary expansion of leaf or stem as the result of growth and differentiation is not excluded. Some authors have also suggested that there is a high-density occurrence of glandular trichomes during early leaf differentiation (Ascensão et al., 1987; Fahn, 1988). However, other authors have observed that there is a high glandular trichome distribution throughout all stages of leaf or stem development (Bosabalidis and Tsekos, 1982, 1984; Vermeer and Peterson, 1979; Bosabalidis, 1990).

These glandular trichomes of *P. incana* are regarded as long term glandular trichomes in which the secretory material appeared to accumulate gradually and consistently under elevated cuticular sacs during the development and growth of the aerial parts of *P. incana*. Similar glandular trichomes, which occur in some species of most genera, are believed to play a vital role in defensive mechanisms against the pathogens and herbivores (Werker, 1993). The metabolites which were present in the glandular trichomes of the stems and leaves were also found in the various floral parts. The function of such glandular trichomes is attributed to the attraction of pollinators (Werker et al., 1985).

In contrast to the varieties of uniseriate, biseriate and capitate, short-term glandular trichomes commonly found in some genera of the *Asteraceae*, and *Lamiaceae* (Hammond and Mahhlberg, 1977), *P. incana* is only characterized by the long term peltate glandular trichomes (Bosabalidis and Tsekos, 1984; Wagner, 1991). These short-term glandular trichomes are assumed to function for a very short period during the early development of young organs (Fahn, 1988; Duke and Paul, 1993). The other common characteristic of *P. incana* glandular trichomes was that when the

glandular trichome matured, the stalk cell showed clear cutinization of the lateral wall. This cuticular sac is believed to enclose the secondary metabolites such as essential oil, and when this sac raptured due to the external pressure exerted on the wall, it released the content. It was suspected that these glandular trichomes did not only accumulate and store essential oil, but also the phytotoxic compounds which rendered these species unpalatable to herbivores.

Consequently, *P. incana* has successfully invaded a large area in the Alice and Peddie districts in the Eastern Cape. A similar notion was supported by Wagner (1991) when he demonstrated that the toxic compounds were able to defend the plants as these phytotoxin were excreted to the surface of the plants. The secreted metabolites appeared to be adsorbed by the fibrous non-glandular trichomes which shielded the glandular trichomes and epidermal layer.

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