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Ontogenesis of trichome-like cavities in *Dictamnus dasycarpus*

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ABSTRACT

The ontogeny of a special type of glandular hairs, namely the trichome-like cavities in *Dictamnus dasycarpus*, characterized by many morphological similarities to non-glandular hairs, capitate glandular hairs, and secretory cavities, was studied using light and electron microscopy. These trichome-like cavities originate from a single, initial epidermal cell that undergoes a periclinal division, with one cell developing into the internal cells and the other into the outer, epidermal cells. A beak-shaped apex is formed on the head of the trichome-like cavity. The histochemical test shows that the trichome-like cavities are important sites for lipid production. By ultrastructural analysis it becomes evident that formation of these trichome-like cavities starts with a disorganization of the cytoplasm that is accompanied by formation of odd shaped nuclei with condensed chromatin. The process continues bringing about plasmolytic processes, and disintegration of the plasma membrane system follows leading finally to autolysis, when mitochondria and degenerated plastids with disorganized membrane systems are engulfed by vacuoles, multivesicular bodies, and double-membranous autophagosomes within the vacuoles. A strong structural twist and swelling of the internal cell walls ultimately leads to complete breakdown of the structures. Nuclei of the inner internal cells within the trichome-like cavity become TUNEL-positive and DAPI-negative first; later this is detected also in the outer internal cells, indicating a centrifugal nuclear degradation process. On the basis of this work, it can be assumed that the lysigenous formation of the trichome-like cavity is a typical programmed cell death process.

Introduction

Secretory structures are well known to be critical sites for accumulation of secondary plant substances. In case of secretory cavities of Rutaceae, much attention has been dedicated to their original location, the number of initial cells, and their further differentiation. Fohn (1935) studying secretory cavities in *Citrus*, concluded they were of subprotodermal origin, but did not identify the number of initial cells. According to Bosabalidis and Tsekos (1982a), secretory cavities of *Citrus deliciosa* originate from a pair of meristematic cells, including an epidermal cell and a subepidermal cell. Bennici and Tani (2004), however, report that the secretory cavities of *Citrus sinensis* and *Citrus limon* are both initiated from clusters of meristematic cells under or including the epidermal cells. Rafiei and Rajaei (2007), studying the oil cavities in *Citrus aurantifolia*, also conclude that the glands originate from both epidermal and subepidermal cells. Rauter (1871) studying *Dictamnus*, reported that both secretory cavities and trichome-like cavities originate from a lower daughter cell formed from a single protodermal cell that undergoes periclinal division. A similar interpretation was offered by Sprecher (1956) for *Ruta* secretory cavities. In contrast, Frank (1883) argued that secretory cavities of *Dictamnus* originate from clusters of meristematic cells located under the protoderm.

Concerning the manner by which secretory cavities form in Rutaceae, some authors concluded that they occur by an autolytic process of the internal cells within the oil gland, as in *Citrus* (Bosabalidis and Tsekos, 1982b; Esau, 1977; Rafiei and Rajaei, 2007; Turner, 1999). Other authors disagreed, claiming that these glands typically are the result of a schizogenous process (Fahn, 1979; Knight et al., 2001, 2002; Thomson et al., 1976; Turner, 1999). Still other authors interpreted these secretory cavities to be of schizolysigenous origin (Bennici and Tani, 2004; Buvat, 1989; Tschirch and Stock, 1933). For other genera of Rutaceae Heinrich (1969) reported that the formation of oil glands in *Ruta graveolens*

Abbreviations: PCD, programmed cell death; TUNEL, terminal deoxynucleotidyl transferase-mediated dUTP nick end labeling.

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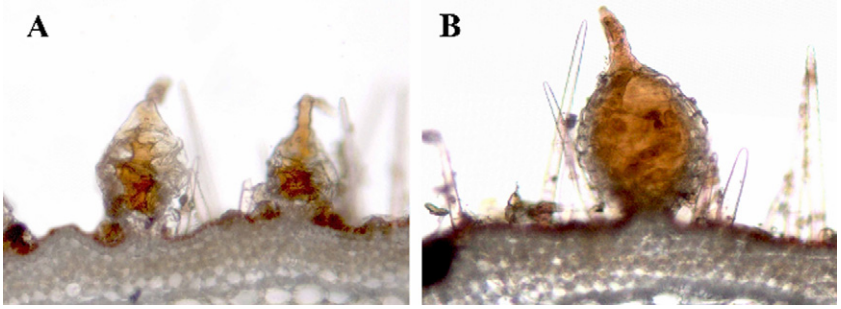

Fig. 1. Histochemistry with Sudan III of trichome-like cavities. (A and B) Trichome-like cavities with positive reactions for lipids.

is a typical schizogenous process, but is a lysigenous phenomenon in *Poncirus*. Liu and Hu (1997) and Liu et al. (1998) studied the formation of the secretory cavities in *Zanthoxylum bungeanum* and *Evodia rutaecarpa* and concluded that they are formed schizogenously. In *Dictamnus*, Rauter (1871) and Martinet (1872) reported that the formation of secretory cavities in *Dictamnus fraxinella* and *Dictamnus albus* is a purely lysigenous process of internal cells.

Early work by Bosabalidis and Tsekos (1982b) detected multivesicular lomasomes and autophagic vacuole-like structures during the lysigenous formation of secretory cavities in *Citrus deliciosa*, which are considered to be events involved in programmed

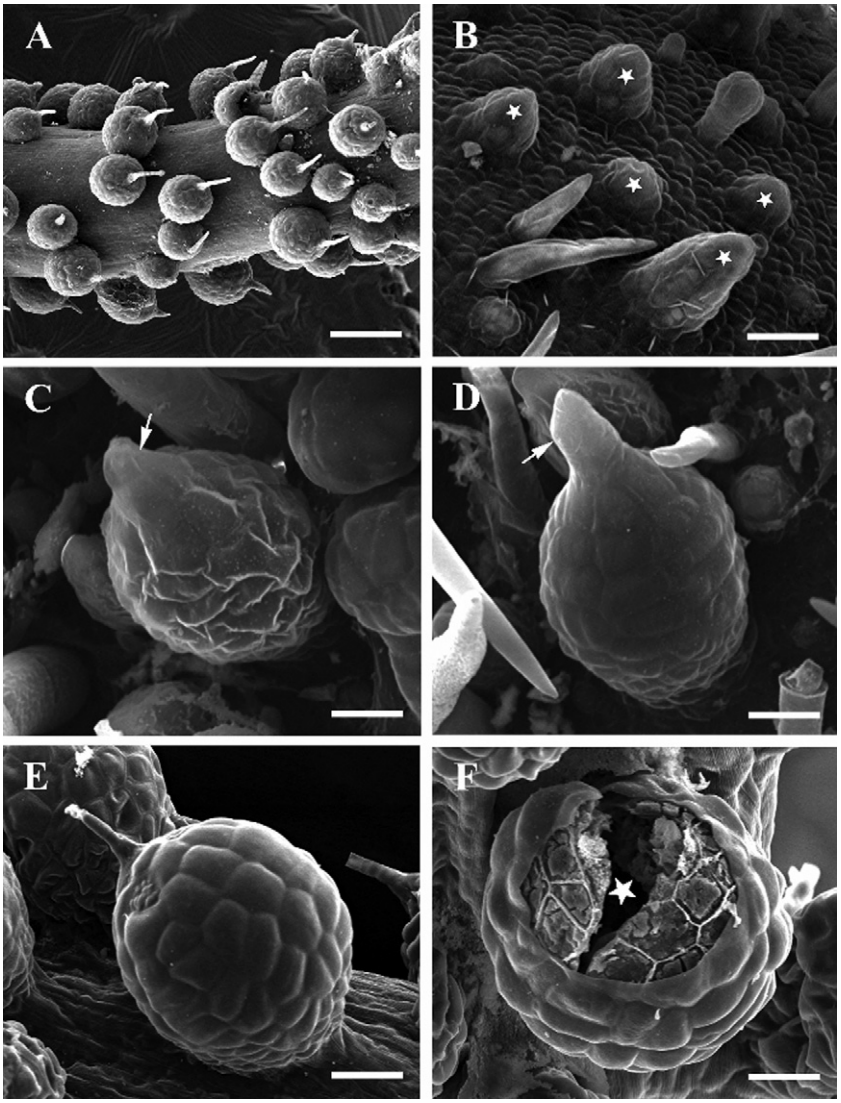

Fig. 2. Scanning electron micrographs of trichome-like cavities. (A) High density of trichome-like cavities distributed on a filament; bar = 200 μm. (B) Stage 1, trichome-like cavities (asterisks) with no obvious beak-shaped apices; bar = 30 μm. (C) Stage 2, initial location of the apex (arrow); bar = 20 μm. (D) Stage 3, an evident beak-shaped apex (arrow) has formed; bar = 30 μm. (E) Stage 4, mature trichome-like cavity determined by oblong shaped head with a long, evident beak-shaped apex; bar = 60 μm. (F) Stage 4, a sub-epidermal cavity (asterisk) within the head; bar = 30 μm.