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Tapetal Ultrastructural Changes During Pollen Development. II. Studies on *Pelargonium zonale* and *Kalanchoë obtusa*

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TAPETAL ULTRASTRUCTURAL CHANGES
DURING POLLEN DEVELOPMENT.
II. STUDIES ON *PELARGONIUM ZONALE*
AND *KALANCHOË OBTUSA*

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INTRODUCTION

We undertook a series of studies on the developmental stages of the tapetal cells, particularly as regards the meaning and origin of the many vesicles found in the tapetum before the beginning of meiosis. The first observations made on *Antirrhinum maius* have been reported in a previous paper (LOMBARDO and CARRARO 1976). Here we report the results of our studies on *Pelargonium zonale* and *Kalanchoë obtusa*, characterized, like *Antirrhinum maius*, by a typical secretory tapetum.

MATERIALS AND METHODS

Anthers of *Pelargonium zonale* and *Kalanchoë obtusa* were fixed in cacodilate-buffered 3% glutaraldehyde pH 6.9 at 4° for 2 hr. After washing in 0.1M cacodilate buffer, the specimens were postfixed in cacodilate-buffered 1% osmium tetroxide for 2 hr, at 4°, dehydrated in ethanol, and embedded in Araldite. When in 75% ethanol, the samples were impregnated with uranyl acetate in semisaturated solution.

Anthers of *Pelargonium zonale* were also fixed in a 1.5% aqueous solution of potassium permanganate at 4° for 2 hr, rinsed in distilled water, dehydrated and embedded as above-described (impregnation with uranyl acetate was omitted).

Ultrathin sections were cut with an LKB Ultratome III, stained with lead citrate and examined in a Hitachi H11B electron microscope.

RESULTS AND DISCUSSION

Kalanchoë. After glutaraldehyde fixation, in very young anthers the tapetal cells surrounding pollen mother cells showed a very dense cytoplasm rich in mitochondria and proplastids.

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In the cytoplasm many spherical bodies were seen bounded by a single membrane and containing cytoplasmic material. These bodies were always localized in saccules originating from dilations of the endoplasmic reticulum (ER) (Fig. 1).

Similar bodies were always visible also in the perinuclear space (Fig. 2).

Pelargonium. After glutaraldehyde fixation, the same spherical bodies, as described above, were found also in the tapetal cells of *Pelargonium* anthers in a similar stage of development. They were always localized in dilations of the ER and in the perinuclear space (Figs. 3 and 4).

In a later stage the cytoplasm appeared less dense and also the bodies had a more rarefied content. The plasmalemma was sinuous and many electron-dense droplets were seen adhering to the plasmalemma evaginations. The cell wall was still visible (Fig. 3).

The presence of the above-mentioned bodies was clearly detected also in permanganate-fixed preparations, where the phenomenon was particularly visible (Fig. 5). In a few cases some bodies were in connection with the nuclear content (Fig. 6).

As to the origin of these bodies it was suggested in a previous paper that they might derive from invaginations of the ER which circumscribe portions of cytoplasm. This hypothesis seems confirmed by the present results, because in a few cases it is possible to observe the connection between some of these bodies and the ER (see Figs. 1 and 3). Besides the aspect of the ER as seen in *Antirrhinum maius* (LOMBARDO and CARRARO 1976 and Fig. 7), suggests a proliferation of its membranes which might well give rise to the bodies seen elsewhere in its dilations.

It seems reasonable to suppose that the aim of this phenomenon is to increase the surface of contact between the ER and the cytoplasm.

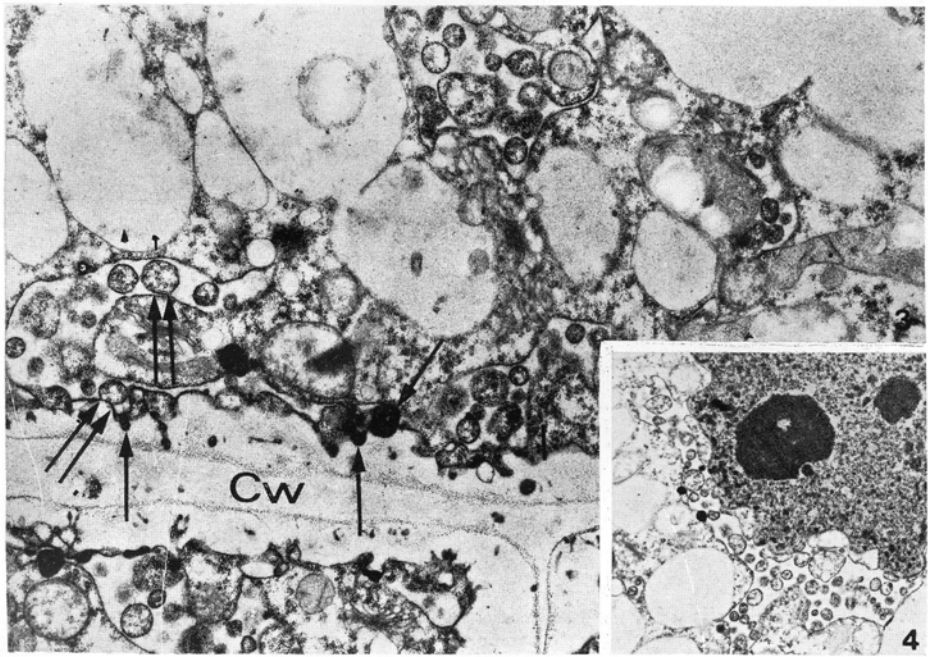
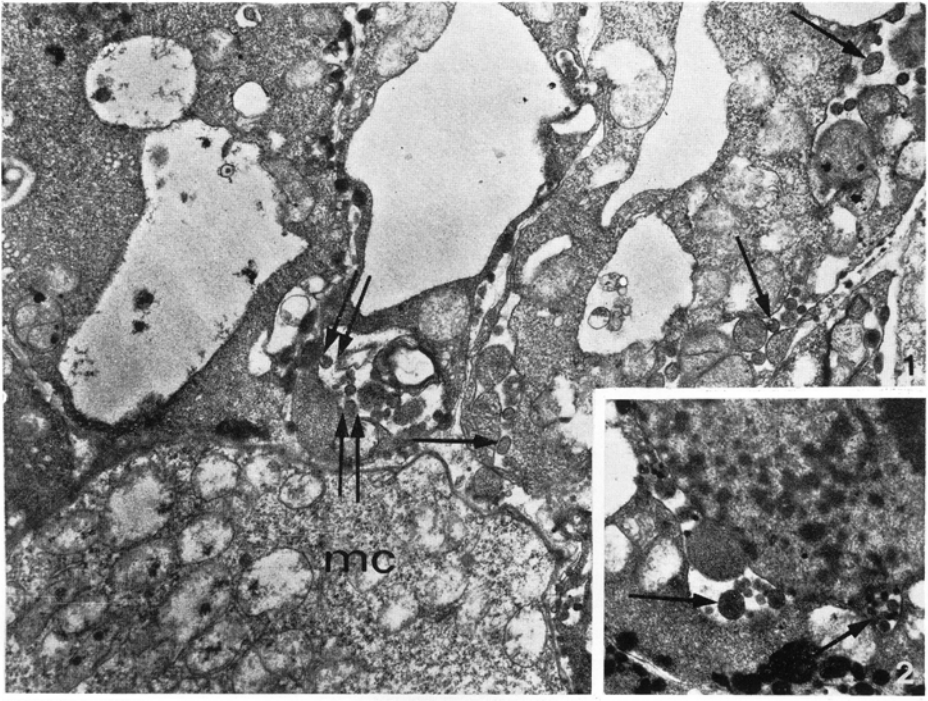
Therefore on the basis of the present evidence we think that the origin of the bodies described here and in *Antirrhinum maius* (LOMBARDO and CARRARO 1976) is mainly cytoplasmic. The high number of these bodies

Fig. 1. — Electron micrograph of a *Kalanchoë* anther. The pollen mother cell (mc) is surrounded by tapetal cells characterized by the presence of spherical bodies (arrows) containing cytoplasmic material, localized in dilations of the ER. Some spherical body is still connected with the membranes of the ER (double-arrows). x 9,500.

Fig. 2. — Nucleus of a tapetal cell of *Kalanchoë obtusa*, showing many spherical bodies in the perinuclear space (arrows). x 11,000.

Fig. 3. — Tapetal cells of *Pelargonium zonale*. Spherical bodies are visible in dilations of the ER; some of them are still connected with the ER membranes (double-arrows). The cytoplasm appears rarefied and vacuolated. The proplastids contain large starch grains. The plasmalemma is sinuous and many electron-dense droplets (arrows) adhere on it. The cell wall (Cw) is still evident. x 12,000.

Fig. 4. — Nucleus of a tapetal cell of *Pelargonium zonale*. Many spherical bodies are localized in the perinuclear space. x 5,500.



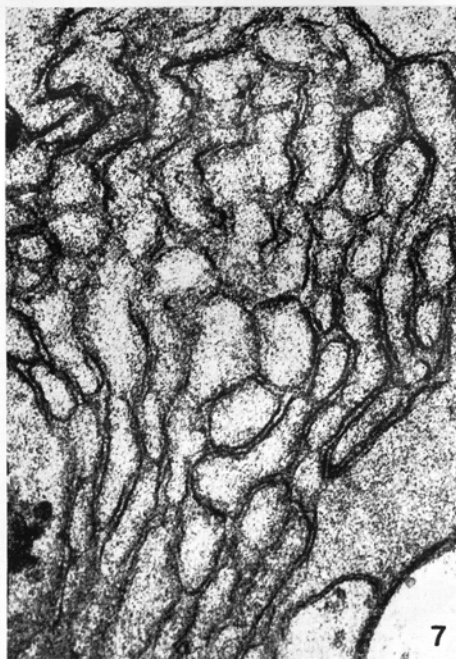
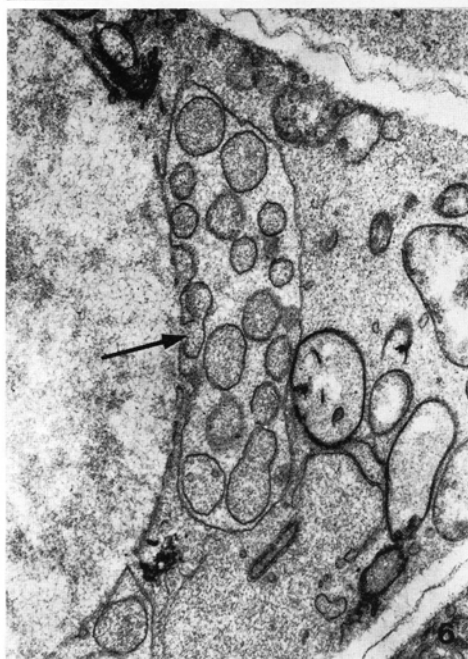
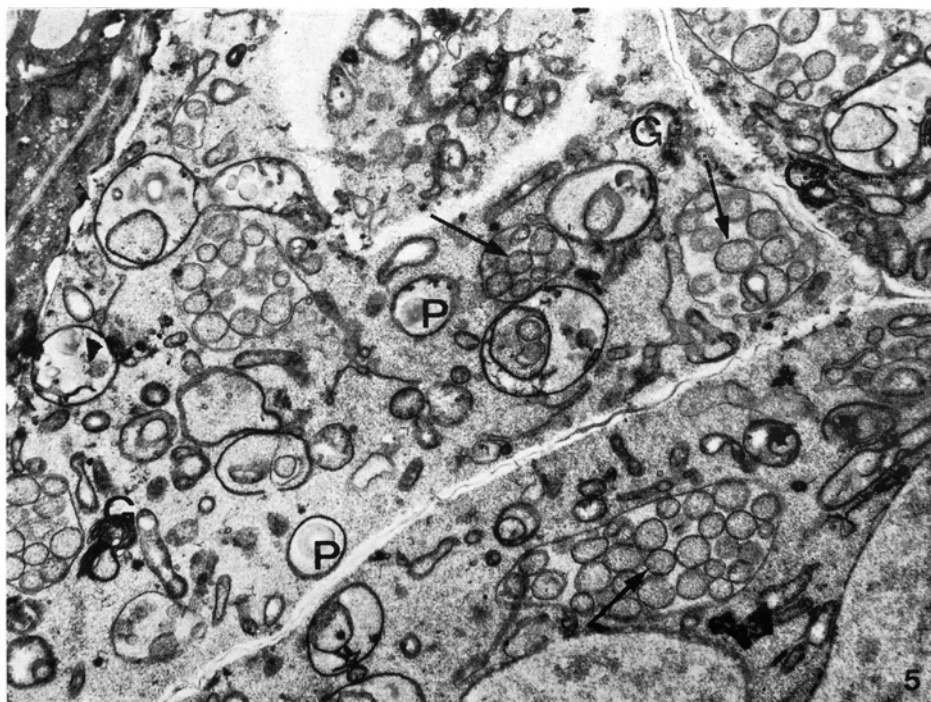


Fig. 5. — Tapetal cells of *Pelargonium zonale* after permanganate fixation. The spherical bodies are clearly visible in the cytoplasm and perinuclear space (arrows). Starch-containing proplastids (P) and Golgi bodies (G) are also present. x 8,000.

Fig. 6. — Nucleus of a tapetal cell of *Pelargonium zonale* after permanganate fixation. Note many spherical bodies in the perinuclear space, most of which are in direct contact with the nuclear content (arrow). x 16,500.

Fig. 7. — Tapetal cell of *Antirrhinum maius* after permanganate fixation: characteristic trabecular disposition of the ER. x 30,000.



Fig. 8. — Section through an anther of *Pelargonium zonale* in a later stage of development. The tapetal cells contain many grey bodies, proplastids, and mitochondria with clear matrix. The ER runs parallel to the anther cavity. The cell boundaries are not visible, while the plasmalemma is sinuous and delimits cytoplasmic papillae projecting between the bacula of the pollen grain. $\times 8,000$.

suggests a high activity of the tapetal cells in a stage when the pollen grains are still immature.

In a later stage the cell wall of the tapetal cells disappears and the plasma membrane forms long papillae projecting between the bacula of the pollen grain wall. This phenomenon is here more evident than in *Antirrhinum maius* (LOMBARDO and CARRARO 1976). Still later the cytoplasm of the tapetal cells contains mitochondria with clear matrix and remnants of cristae and many grey bodies, which will contribute to the Pollenkitt formation (Fig. 8).

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SUMMARY

The ultrastructure of the tapetal cells was studied in *Kalanchoë obtusa* and *Pelargonium zonale*. In an early stage of development the most characteristic feature was the presence of many spherical bodies bounded by a single membrane and containing cytoplasmic material. These bodies were localized in dilations of the ER and in the perinuclear space. In later stages, when the pollen was mature, the tapetal cells of *Pelargonium* contained many «grey» bodies and their plasmalemma was in close connection with the sculptures of the pollen grains.

RIASSUNTO

E' stata studiata al microscopio elettronico l'ultrastruttura delle cellule del tappeto di *Pelargonium zonale* e *Kalanchoë obtusa*. In stadi precoci di sviluppo esse presentano numerosi «bodies» sferoidali delimitati da una membrana semplice e contenenti materiale citoplasmatico. Questi «bodies» sono localizzati in dilatazioni dell'ER e nello spazio perinucleare. In stadi successivi di maturazione del polline le cellule del tappeto di *Pelargonium* contengono numerosi «grey bodies» sono per lo più prive di parete cellulosa e il loro plasmalemma è in stretta connessione con le sculture del polline.