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The function of the tapetal tissue during microsporogenesis in *Lilium*

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Abstract

The main functional activity of the tapetum in the *Lilium* anther is the synthesis of reserve lipids and carotenoid pigments. The fusion of these substances during tapetum desintegration results in the formation of pollenkitt. Pollenkitt participates in the formation both of the exine and of sporopollenin-containing structures of the tapetal cell (orbicules, tapetal and peritapetal membranes) during the last steps of anther development.

INTRODUCTION

The main topic of this paper is the role of the secretory tapetum of the *Lilium* anther in the synthesis of sporopollenin and pollenkitt-substances participating in pollen wall and coating formation (Heslop-Harrison, 1968a, b; Heslop-Harrison, Dickinson, 1969; Dickinson, 1973). The acetolysis-resistant polymersporopollenin is the major constituent of exine. This substance is also deposited on the surfaces of the tapetal cells of different plants in the form of orbicules and special membranes — tapetal and peritapetal (Banerjee, 1967; Dickinson, 1970; Ogorodnickova, 1976; Reznickova, Willemse, 1980). The pollenkitt, an oily substance composed of lipids and dissolved carotenoids, is considered to be responsible for coherence of pollen grains in masses and for attraction of insects during pollination. Exine formation is believed complete by the time of pollenkitt deposition on the pollen grain surface (Heslop-Harrison, 1968b). For this reason pollenkitt has never been investigated as a possible source of sporopollenin precursor.

In this paper, the late steps of exine genesis and the formation of sporopollenin-containing structures by tapetal cells were followed with special attention paid to pollenkitt participation in these processes.

Plate I

A. Lipid accumulation in the tapetum during the stage of the vacuolate microspore. × 23040

B. Plastid at the stage of the young microspore. × 23040

C. Plastid at the stage of the vacuolate microspore. × 23040

D. Lipid inclusions and carotenoid globules fuse at the stage of the late microspore interphase. × 23040

E. Tapetal plasma membrane breaks just before microspore mitosis. × 23040

F. Pollenkitt is partly applied on the surface of the young pollen grain, a significant amount is still near the anther wall. × 1760

CG — carotene glubules; D — dictyosome; L — lipid inclusions; N — nucleus; O — orbiculae; P — plastid; Pk — pollenkitt; Pm — plasma membrane.

MATERIAL AND METHODS

Anthers of *Lilium hybridum* var. Enchantment were prepared for electron microspory and investigated as described in Willemse and Reznickova (1980).

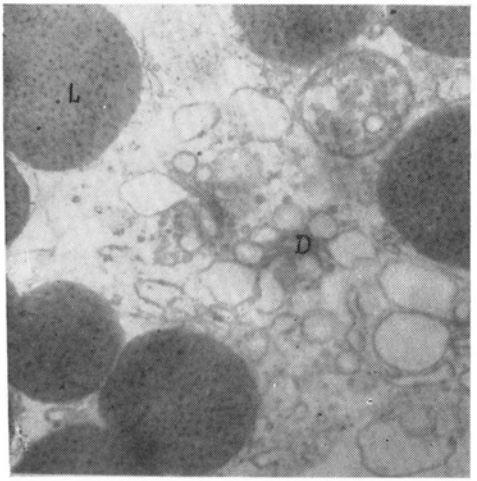
RESULTS AND DISCUSSION

The structure and the succession of events during early post-tetrad stages of pollen wall formation were described elsewhere (Willemse, Reznickova, 1980) and did not differ much from this process in the *Lilium* anther (Heslop-Harrison, 1971; Dickinson, 1976). One additional process is described in this paper — deposition of sporopollenin on the locular surface of the exine in the form of a membrane-like lamella and globules. This process continues during post-mitotic stages of pollen development and is considered a mechanism of pollen wall correction according to the cell volume increase (Wilemse, Reznickova, 1980).

Peritapetal and tapetal membranes have been found in the *Lilium* anther and deposition of sporopollenin has been followed on the orbicules and membranes including the post-mitotic stages of anther development (Reznickova, Willemse, 1980). Thus, contrary to the existing opinion sporopollenin deposition proceeds both on the exine and sporopollenin-containing structures of the tapetal cell after pollen mitosis and tapetum disintegration. The question arises about the source of the immediate sporopollenin precursor at these developmental stages.

For this source we looked at the tapetum. The bulk of lipids and carotenoid pigments accumulated there undergo hydrolysis during late microspore interphase and probably provide young pollen grains with

PLATE I



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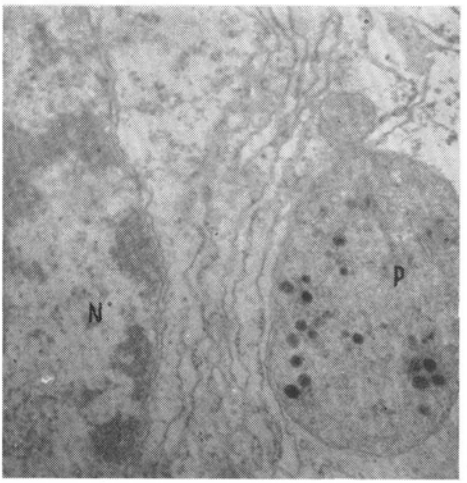

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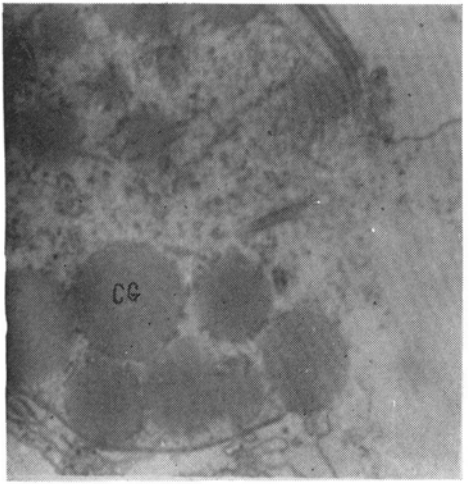

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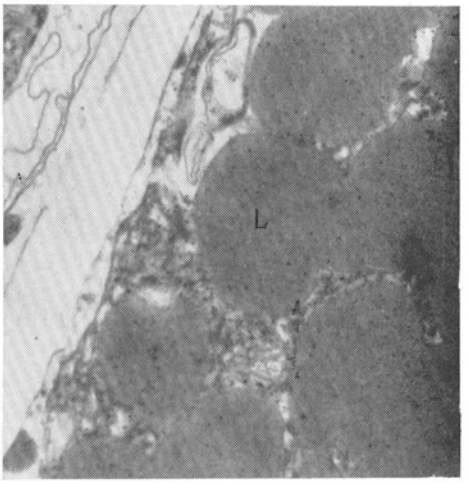

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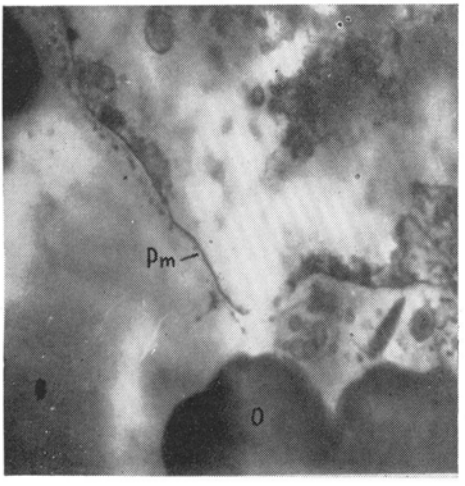

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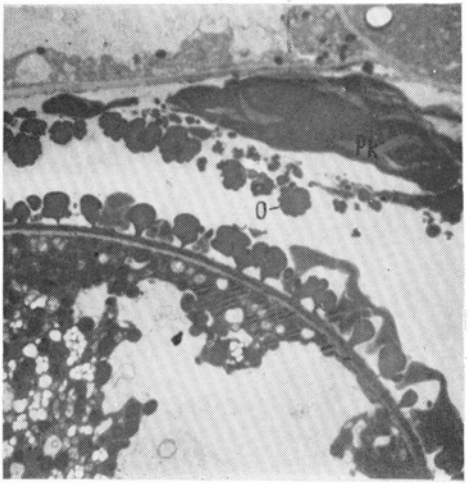

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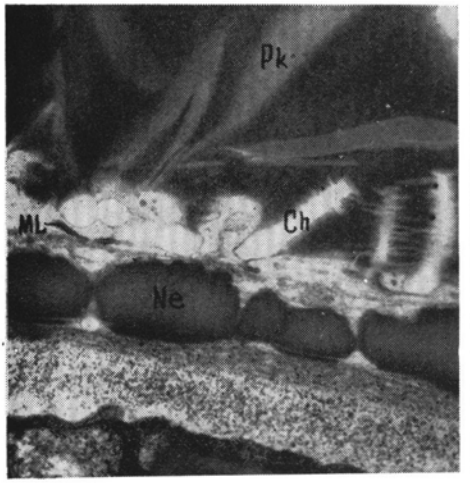

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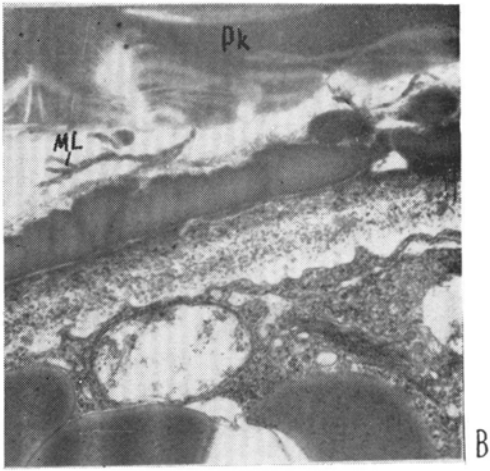

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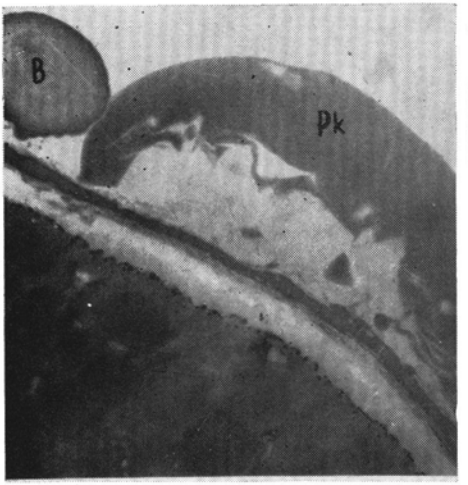

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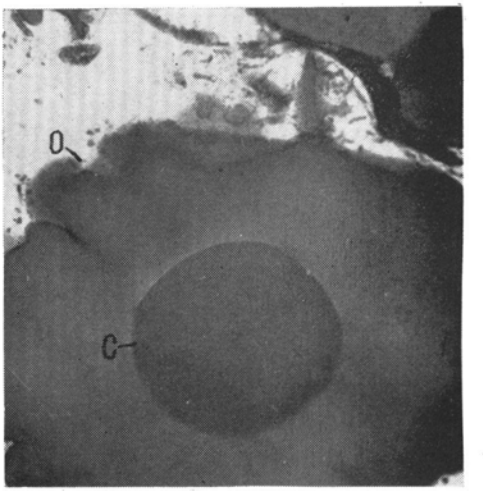

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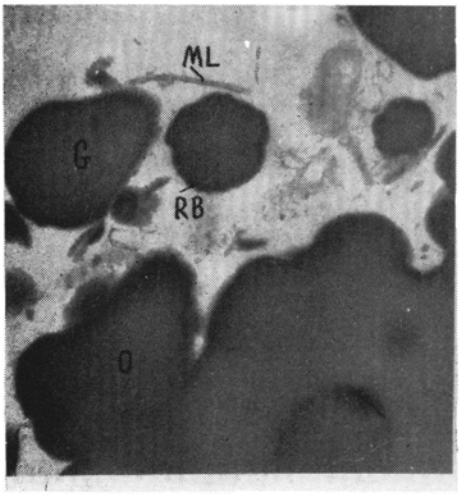

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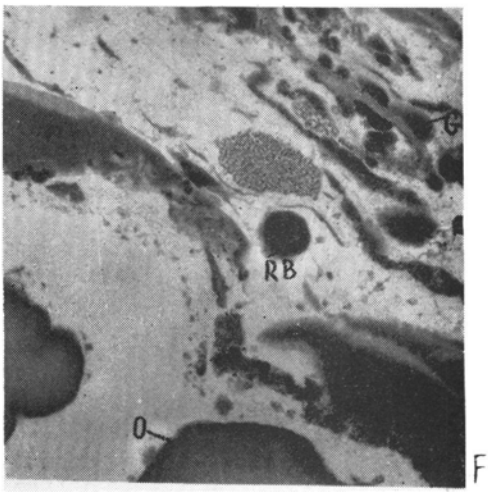

F

Plate II

A. Channel-like structures in the pollenkitt on the surface of the young pollen grain. × 23040

B. Membrane-like lamellae on the surface of the young pollen grain. × 23040

C. Pollenkitt is partly destroyed from the inside by the time of anthesis. × 8320

D. Sporopollenin deposition on the orbiculae at the stage of the late microspore interphase. × 23040

E. Sporopollenin deposition in form of globules and round bodies at the post-mitotic stages of anther development. × 23040

F. A complicated membrane linning the locules before anthesis. × 23040

B — baculae; C — core; Cl — clusters; Ch — chanel-like structures; G — sporopollenin globules; ML — membrane-like lamellae; Ne — nexine; RB — round bodies. The rest as at Plate I.

the precursors for rapid starch and lipid accumulation (Reznickova, 1979).

Tapetal cells enter the phase of lipid and carotenoid accumulation at the beginning of the stage of the vacuolate microspore. During subsequent development lipid inclusions become abundant in the cytoplasm (Plate IA). By this time plastids are differentiated into chromoplasts. A substance with a smaller electron density than lipids accumulates in globules about 0.5 μm within the plastids. Accumulation of this substance is accompanied by development of the inner membrane system of the plastid (Plate IB, C).

Tapetal cell autolysis is completed at the stage of late microspore interphase. Both the inner membrane system and outer envelope of the plastids are lost by this time. Consequently, lipid inclusions localized in the cytoplasm fuse with globules from the chromoplasts. These processes result in formation of pollenkitt which is held near the anther wall by the tapetal plasma membrane (Plate ID, E). The plasma membrane breaks just before microspore mitosis and the major part of the pollenkitt passes through the tapetal membrane and becomes applied to the pollen grain surface. A considerable amount of the pollenkitt is left near the anther wall though.

The pollenkitt is deposited over the entire surface of the pollen grain but contact is closer between the bacula (Plate IF). In places of direct contact between pollenkitt and nexine, channel-like structures arise in the pollenkitt which may indicate enzymatic digestion (Plate IIA). The membrane-like lamellae lavishly covered with sporopollenin can be seen either joining nexine or confacting the globules on the surface of the nexine. Their lenght is greater than at previous stages. Sometimes they appear branched (Plate IIB). The membrane-like lamellae are also present at the following stages of pollen development, but the process becomes less active. By the time of anthesis the pollenkitt globules are nearly destroyed from the inside (Plate IIC). At the stage

of late microspore interphase sporopollenin is heavily deposited on the orbicules in the form of clusters and ribbons of electron dense material (Plate IID). Further increase in the diameter of the orbicules on the sections and more complicated outlines indicate continuous deposition of sporopollenin during the post-mitotic anther development. A number of globules of different shape as well as the dark round bodies are present at the base of the orbicules and probably join them (Plate IIE). The electron dense round bodies frequently fuse which results in the formation of complicated structures resembling oribicules but without a core. These round bodies and globules are formed amidst pollenkitt remnants near the anther wall. Sporopollenin condenses on membrane-like lamellae or simply on the remnants of the pollenkitt. Sporopollenin synthesis proceeds here untill anthesis.

By anthesis the locular surface of the anther is lined with a compound membrane consisting of the peritapetal membrane and the tapetal membrane with attached orbicules. Numerous sporopollenin globules and round bodies are sandwiched between them with the rests of the pollenkitt (Plate IIF).

Thus, the investigation showed that the late steps of sporopollenin deposition on the exine and the structures formed by the tapetal cell can be connected with the mobilization of the lipid-carotenoid complex — the pollenkitt after tapetum disintegration. Our previous work has demonstrated that starch and lipid accumulation occur simultaneously in the vast mass of young pollen grains just after microspore mitosis. This process requires large amounts of precursors (Reznickova, 1979). Pollenkitt seems to represent a source of precursors for such a process. Pollenkitt digestion (apparently enzymatic) and its transfer to the surface of the pollen grains precedes starch and lipid accumulation in the pollen cytoplasm.

The precursor for sporopollenin synthesis may be liberated as a result of lipid hydrolysis. It polymerizes both on the surface of the pollen grains and near the anther wall, contributing to the nexine and to the complicated membrane linning the loculus. Sporopollenin synthesis is closely related to nutrient substance metabolism in the developing anther and to the trophical function of the tapetum.

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