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Ultrastructural transformations of nuclei in differentiating *Hyacinthus orientalis* L. pollen grain cells

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Abstract

The ultrastructure of the pollen nuclei was studied during pollen maturation in *Hyacinthus orientalis* L., in which both pollen cells go through full interphase (G_1, S, G_2). The particular stages of interphase, however, do not proceed simultaneously in the vegetative and generative nuclei. The ultrastructural transformations of both pollen nuclei were analysed with reference to the dynamics of variations in the level of RNA and protein synthesis, investigated earlier. A distinction is drawn between the structural changes common for both nuclei, linked immanently with the interphase and the transformations connected with the differentiation of pollen cells.

Key words: Hyacinthus orientalis, ultrastructural differentiation, pollen nuclei, cell cycle

INTRODUCTION

The maturation of the pollen grain in angiosperms includes a sequence of metabolic and structural transformation of both pollen sister cells leading to the development of cells performing different biological functions. This process if often considered a model situation for studies on cellular differentiation. The structure and metabolism of differentiating pollen cells have been studied for a long time (Sanger and Jackson 1971 a, b, c, Echlin 1972, Mascarenhas 1975). However, we still do not know the full sequence of ultrastructural transformations undergone by the nucleus and cytoplasm of the pollen cells from their origin to anthesis. Most studies either do

not cover all the successive maturation phases of pollen cells, or deal with only some cell structures, e.g. plastids (Clauhs and Grun 1977, Schröder 1984) or microtubules (Cresti et al. 1984, Van Lammeren et al. 1985). Also, none of the existing works deal at the same time with the metabolism and structure of both pollen cells during the entire period of pollen grain maturation.

This work presents the structural transformations of the vegetative and the generative nuclei during pollen grain maturation in *Hyacinthus orientalis* with reference to the previously investigated dynamics of variations in the level of RNA and protein synthesis (Bednarska 1984). In *Hyacinthus orientalis*, unlike in other species where only the DNA of the generative nucleus is replicated (see review Mascarenhas 1975, Górska-Brylass et al. 1986), both pollen cells go through full interphase, however, the particular stages of interphase do not proceed simulatneously in both nuclei (Bednarska 1981). A comparison of the structure of the vegetative nucleus in phases G_1, S and G_2 with that of the generative nucleus in the same phases of interphase makes it possible to distinguish the ultrastructural transformations linked with the proceeding differentiation of the pollen cells from those immanently linked with the progress of their interphase.

MATERIAL AND METHODS

The material for study were pollen grains of *Hyacinthus orientalis* of the diploid variety Pink Pearl.

The morphology and ultrastructure of pollen nuclei were studied in seven successive, morphologically defined stages shown schematically in Fig. 1.

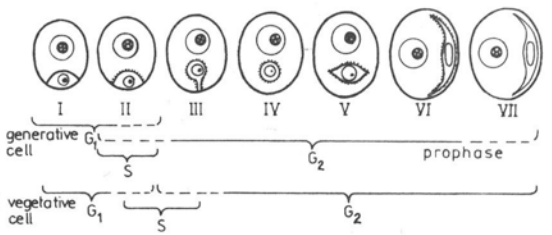

Fig. 1. Development stages of *Hyacinthus orientalis* L. pollen grains, marked interphase periods of pollen cells (after Bednarska 1981). Stage I — parietal generative cell surrounded with cellose wall (callose stage), stage II — parietal generative cell deprived of callose wall (parietal callose-devoid stage), stage III — balloon-shaped generative cell, stage IV — spherical generative cell, stage V — lemon-shaped generative cell, stage VI — spindle-shaped generative cell surrounded by granules, stage VII — spindle-shaped generative cell without wreath of granules

The pollen nuclei's volume was studied on living material placed in 2% isotonic sucrose solution. The volume of spherical nuclei was calculated using the formula for the volume of a sphere, that of elongated nuclei was regarded as the total of the volumes of a clinder and two cones. The

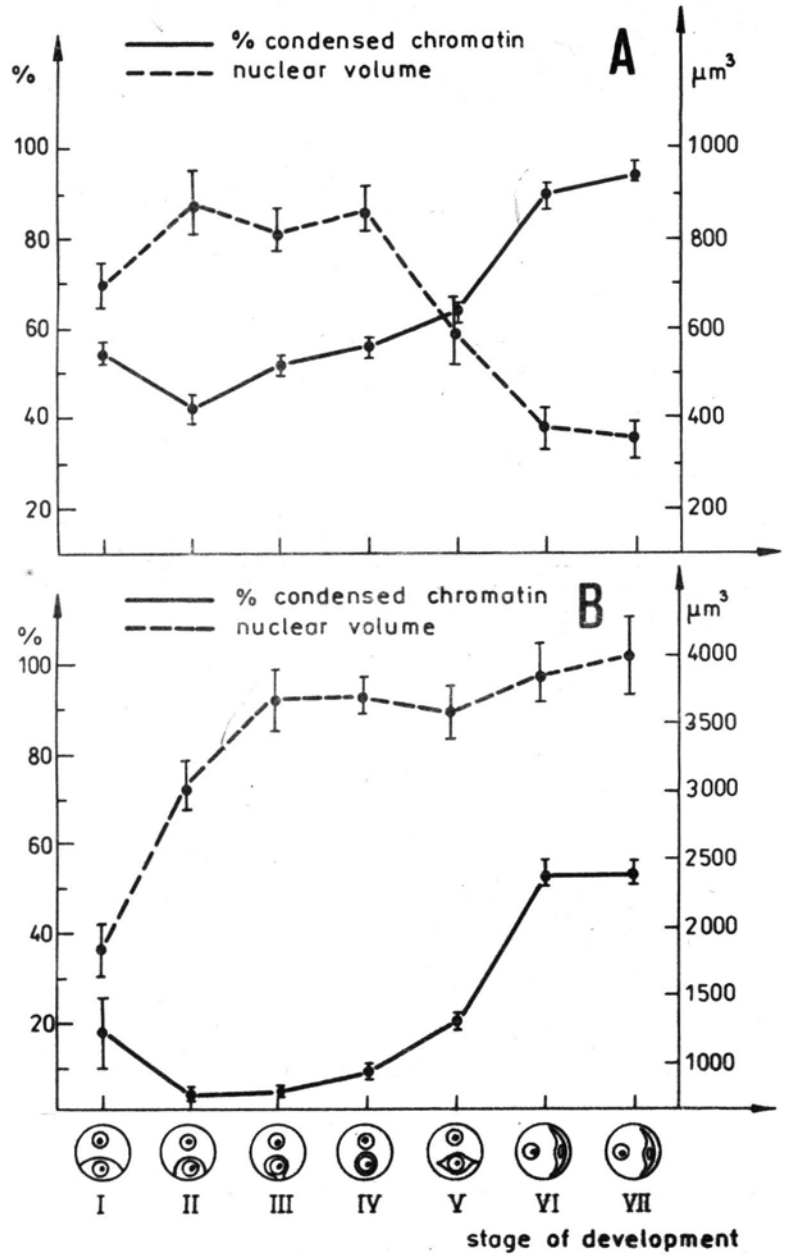

Fig. 2. Changes in the degree of chromatin condensation in pollen nuclei in conjunction with the changes in their volumes. A — generative nucleus, B — vegetative nucleus

presence of nuclei acids was assayed on semithin sections stained by Feulgen's method and with a mixture of methyl green and pyronine after Brachet (1953).

The anthers for ultrastructural studies were fixed in 2.5% glutaraldehyde in Na-cacodylate buffer at pH 7.2, temp. +4°C for 18 h. then post-fixed with OsO_4 and embeded in Epon 812. The sections were contrasted with an aqueous solution of uranyl acetate and lead citrate. The preparations were viewed in a Tesla BS-500 electron microscope.

The percentage of condensed chromatin in pollen nuclei was determined by the gravimetric method after Dardick and Setterfield (1976). The RNP structures were identified by the EDTA technique after Bernhard (1969).

RESULTS

THE MORPHOLOGY OF POLLEN NUCLEI

The volumes of the pollen nuclei, already differing at the moment of individualization of the pollen cells, underwent further changes during maturation of the pollen grain. The changes in volume of these nuclei, however, took a different course in each of the two cells (Fig. 2). In both cells the nuclei increased volume in the period G_1-S (stage I-II in the generative cell, and I-III in the vegetative one). In phase G_2 the volume of the vegetative nucleus remained unchanged (stages III-VII), while the volume of the generative nucleus became rapidly reduced towards the end of that phase (stages V-VI).

In the course of differentiation of the pollen grain, both the generative and the vegetative nucleus underwent the lobing process in phase G_2; this process did not occur simultaneously in both of them. In the generative nucleus, lobing already started in early G_2 phase i.e. in stage III, and reached its peak in stage IV (Fig. 3C, D). The generative nucleus remained lobed in the succeeding development phases until the anthesis of the pollen grain (Fig. 3F, G). The vegetative nucleus, while maintaining its spherical outline throughout pollen grain maturation, became intensely lobed in late G_2 phase (stage VI) and remained so until anthesis (Fig. 3F, C).

ULTRASTRUCTURAL ORGANIZATION OF POLLEN NUCLEI

Changes in the degree of condensation of chromatin

In both pollen nuclei changes occurred in the degree of chromatin condensation (Fig. 3). In the period G_1-S, chromatin decondensed, in phase G_2 it recondensed (Fig. 2).

PLATE I

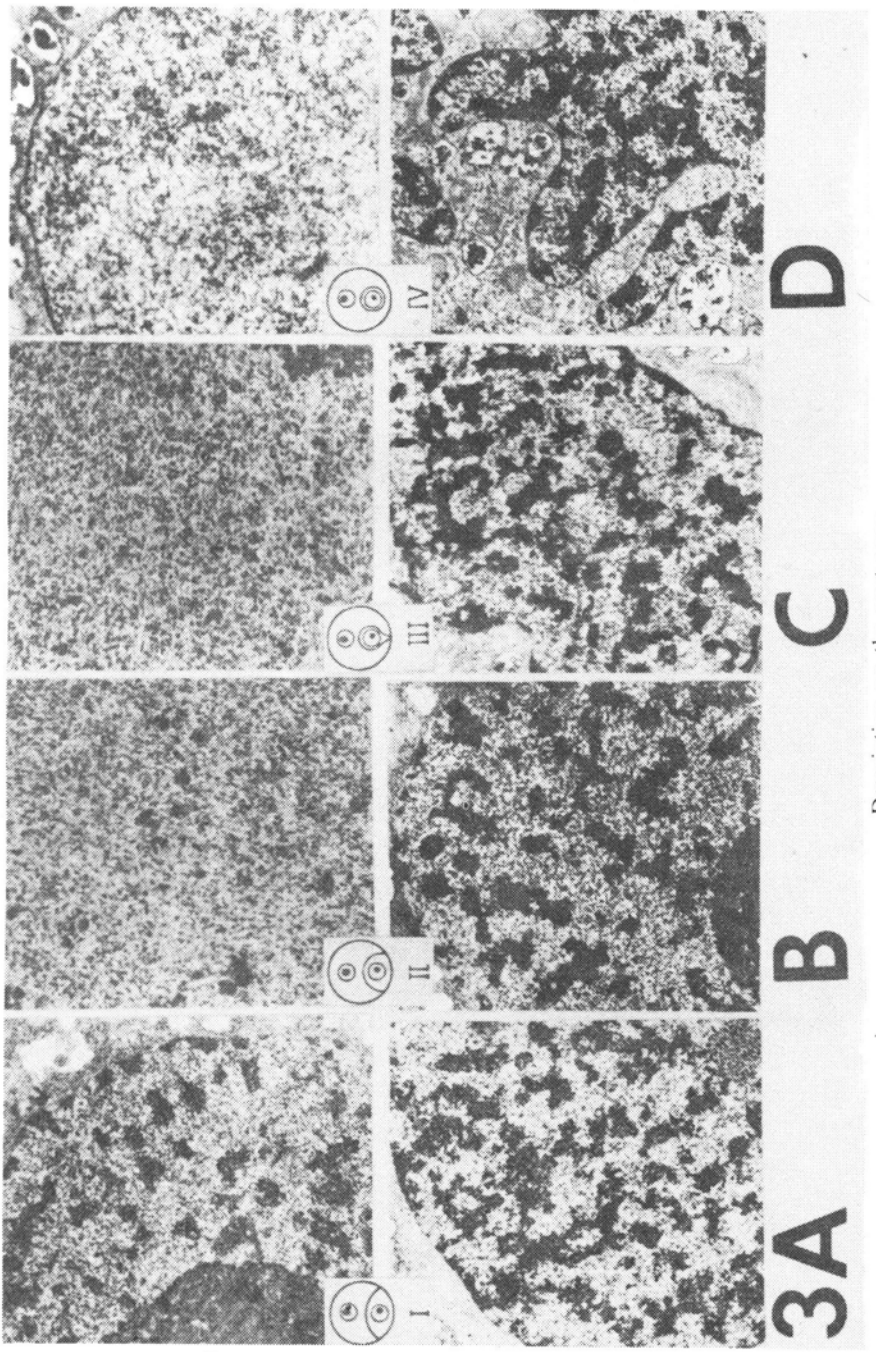

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PLATE II

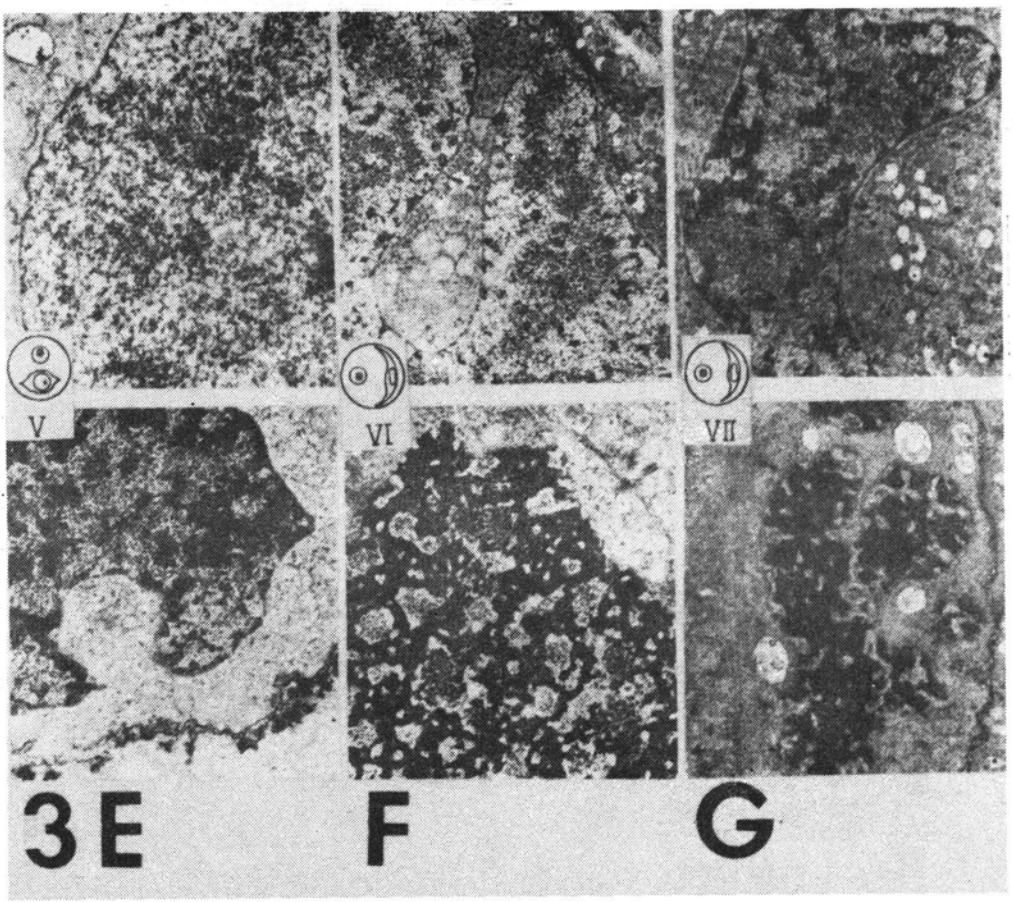

Fig. 3. The organization of chromatin of pollen nuclei in successive stages of differentiation of the pollen grain. × 10 000

PLATE III

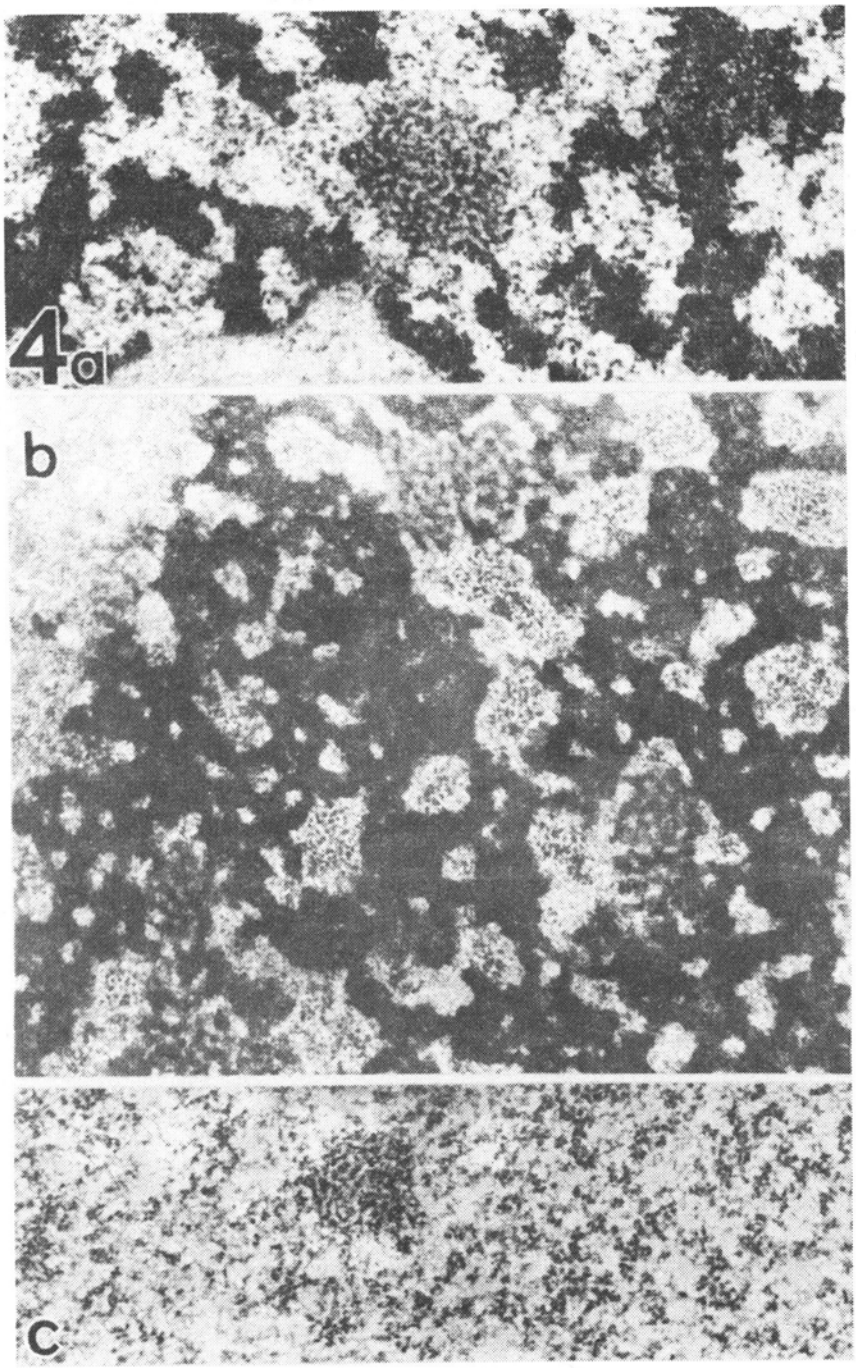

Fig. 4. Puff-like structures in the nuclei of pollen cells. a — nucleus of the spherical generative cell, b — nucleus of the spindle-shaped generative cell, c — vegetative nucleus. ×25000

PLATE IV

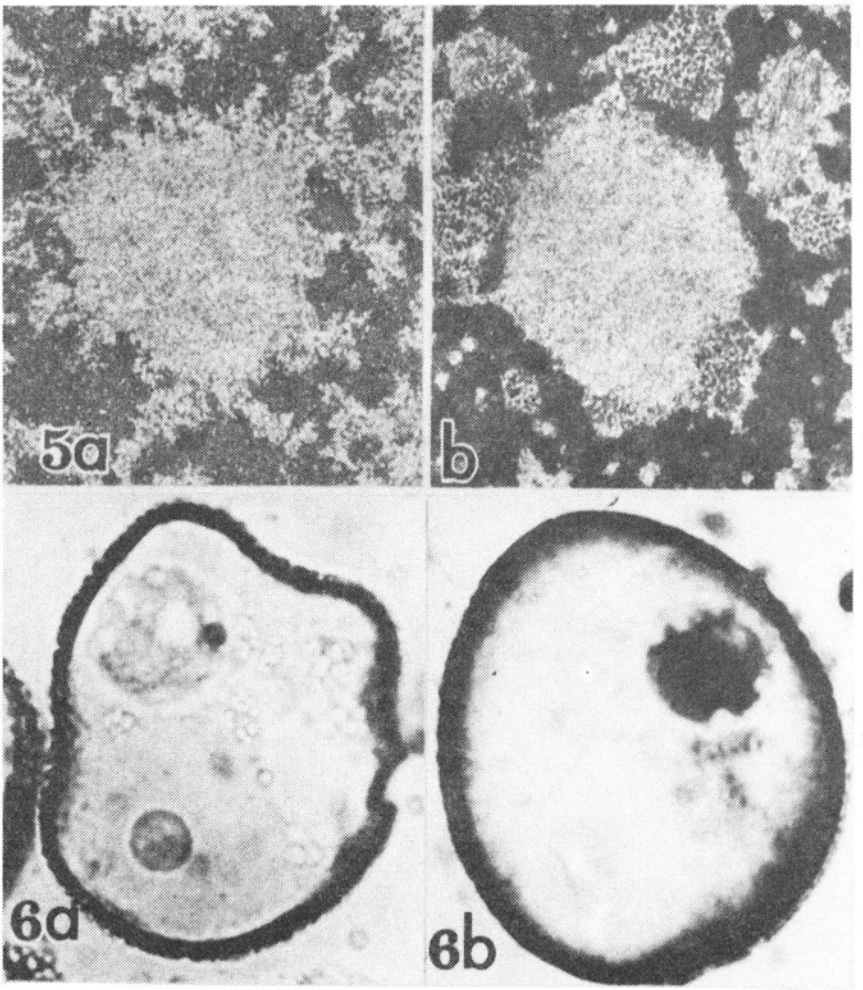

Fig. 5. Electron-transparent spaces in the nucleus of the generative cell. a — stage of spherical generative cell. b — stage of spindle-shaped generative cell. ×25000

Fig. 6. Light spaces in the generative nucleus which do not stain with stains for nucleic acids. ×1250. a — light spaces completely surrounded by nuclear chromatin (stage IV), b — light spaces localized on the border between the nucleus and cytoplasm (stage V)

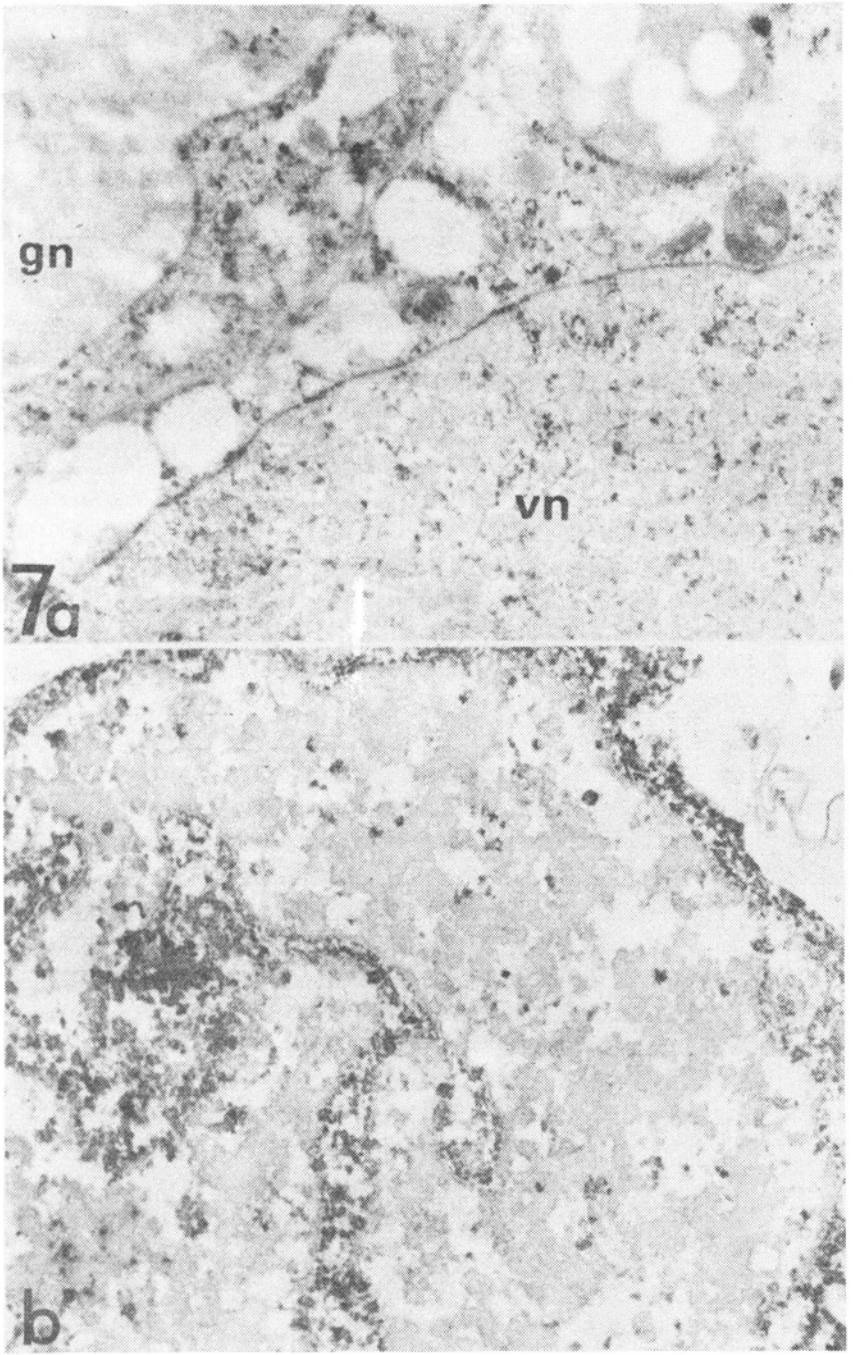

Fig. 7a. Pollen nuclei in the spherical generative cell stage (EDTA technique). The vegetative nucleus rich in RNP structures, the generative nucleus nearly completely devoid of these structures. ×12 500. gn — generative nucleus, vn — vegetative nucleus. Fig. 7b. The vegetative nucleus shortly before anthesis (EDTA technique). RNP structures in the form of aggregations are localized mainly around bleached aggregations of condensed chromatin. ×12 500

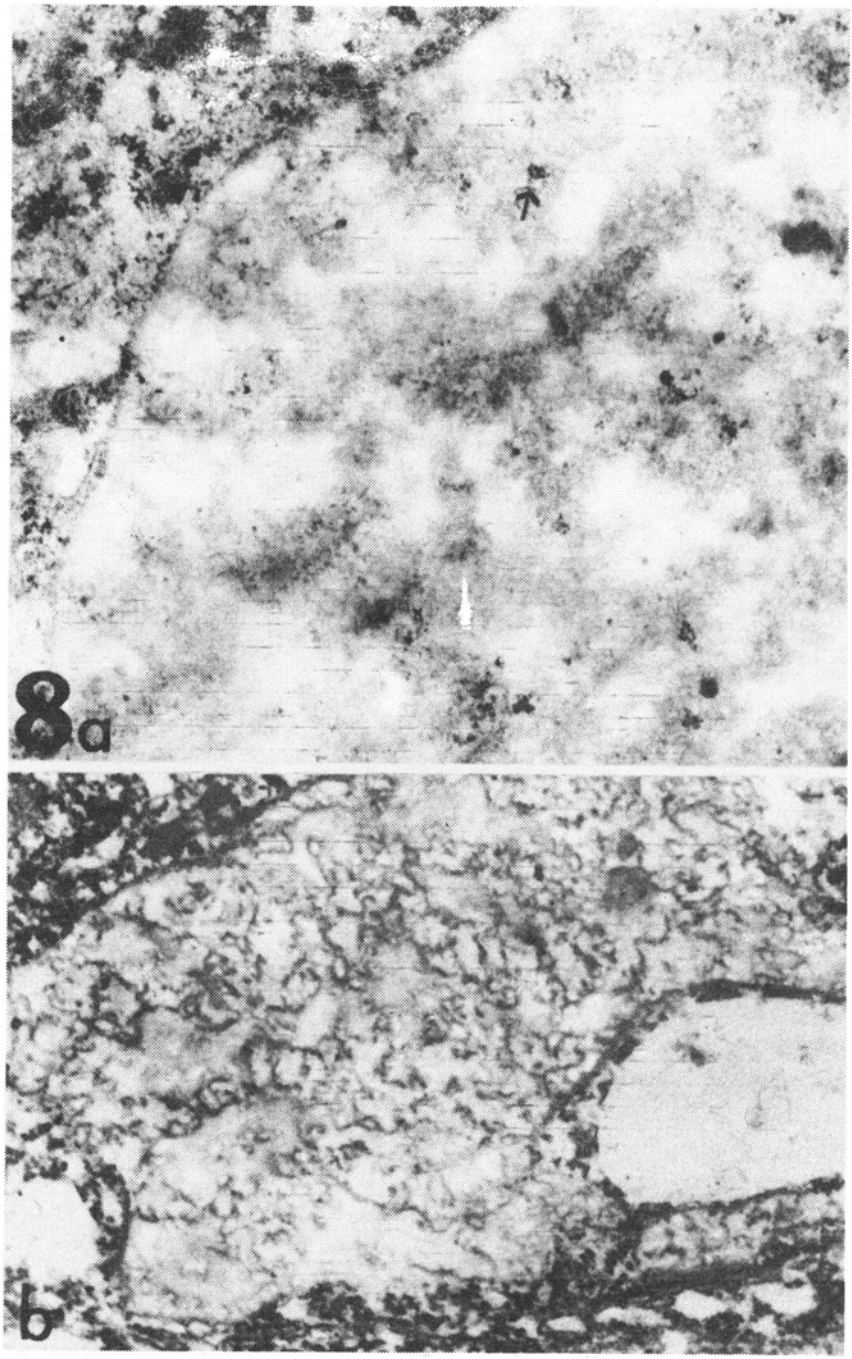

Fig. 8a. Nucleus of generative cell in the parietal stage (st. II), after using the EDTA technique. RNP structures in the form of small granules localized mainly in spaces between condensed chromatin aggregations (arrow). ×25000. Fig. 8b. Nucleus of spindle-shaped generative cell during anthesis (EDTA technique). Bleached aggregations of condensed chromatin are surrounded by a continuous RNP layer. ×13500

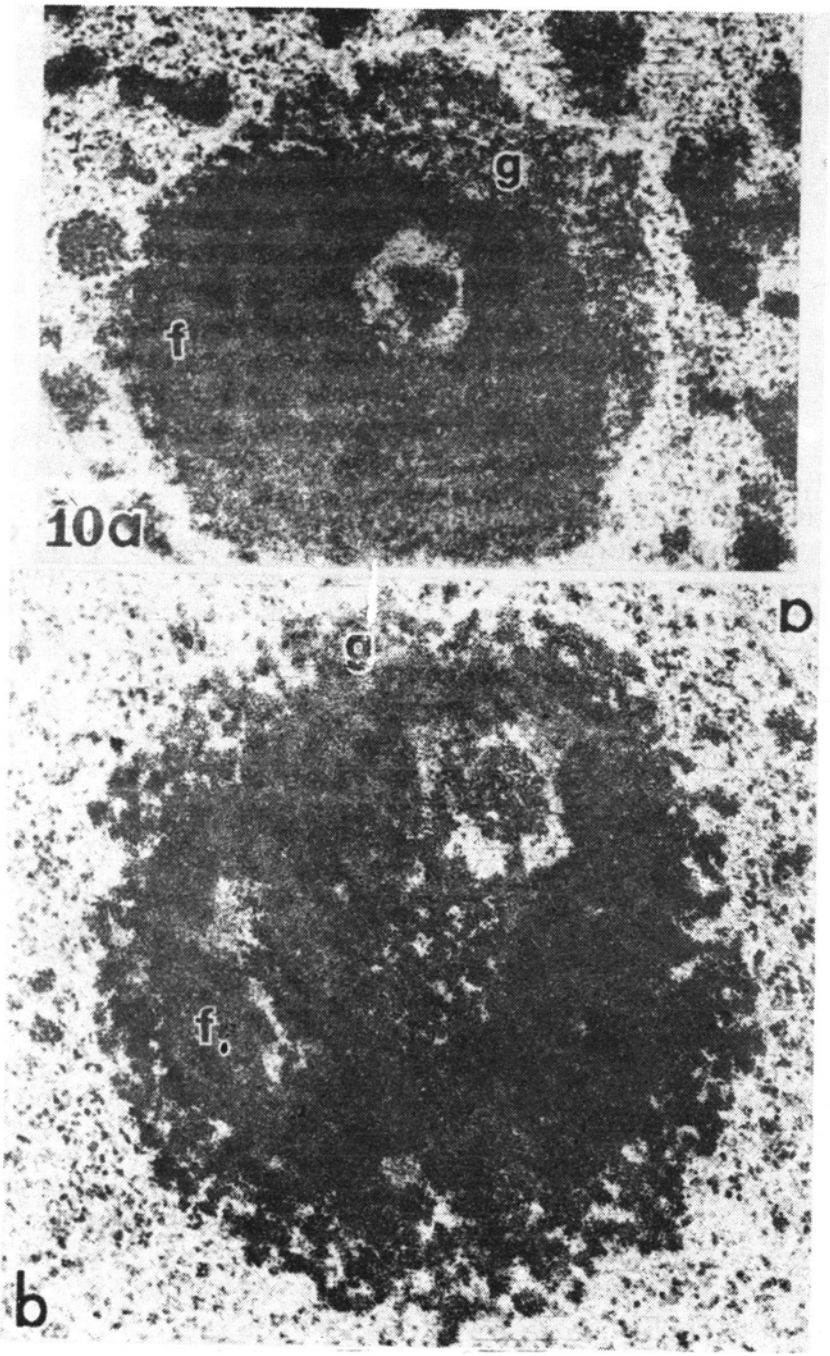

Fig. 10a. Segregated nucleolus of the generative cell in the parietal, callose-devoid stage, ×25000. g — granular part, f — fibrillar part. Fig. 10b. Nucleolus of the vegetative cell. The granular part almost evenly surrounds the fibrillar part. ×25000. g — granular part, f — fibrillar part

Considering the fact that the changes in the degree of condensation of chromatin in both pollen nuclei of *Hyacinthus orientalis* proceeded while their volumes also changed (Fig. 2), it was necessary to use three terms in this paper: decondensation — transition from condensed into decondensed chromatin seen as a reduction in the size of chromatin aggregations, independent from changes in nucleus size, active condensation — transition of decondensed into condensed chromatin reflected in an increasing amount of condensed chromatin in the nucleus while its volume remained either unchanged or increased, passive condensation — increase in the amount of condensed chromatin in the nucleus under conditions of rapid reduction of its volume. Passive condensation does not rule out simultaneous active condensation.

Just after the formation of pollen cells (phase G_1), the generative nucleus was characterized by higher degree of chromatin condensation than the vegetative nucleus (Fig. 3A). This was due in the first place to the fact that in the smaller generative nucleus, the condensed chromatin aggregations lay closer together than in the larger vegetative nucleus. In the generative nucleus, the process of chromatin decondensation in the period G_1-S (stages I-II) was reflected by a reduction in the size of chromatin aggregations (Fig. 3A, B).

A structural reflection of the start of active condensation of chromatin was seen in the generative nucleus in early phase G_2 (stages II-IV) as a slight increase in the amount of condensed chromatin in the cross-sectional area of the nucleus while its volume remained constant (Fig. 2). In late phase G_2 (stages IV-VI) the rapid reduction of the volume of the generative nucleus was associated with a pronounced increase in the proportion of condensed chromatin in the its cross-section area and with an increase in the size of the chromatin aggregations (Figs. 2, 3D-G). This then is passive condensation, which of course does not rule out simultaneous occurrence of active condensation. In the terminal period of pollen grain maturation the process of condensation of the generative nucleus chromatin led to the formation of prophase chromosomes. These chromosomes, ca 1.2 μm in diameter, were clearly visible in a light microscope.

In the vegetative cell, the process of chromatin decondensation, which occurred in the period G_1-S (stages I-II), proceeded with a much greater intensity than in the generative nucleus (Fig. 3A, B). It was associated with an increase in the volume of the nucleus to nearly double the original size and with a reduction in size of the chromatin aggregations (Fig. 2). The process of active chromatin condensation in phase G_2 lasted from stage III to VI, when the volume of the nucleus remained constant, while the number and size of condensed chromatin aggregations increased (Figs. 2, 3D-G).

Puff-like structures

In both pollen nuclei, circular fibrillar spaces differing from the surrounding chromatin by the thickness of the fibres and their organization (Fig. 4), occured among the chromatin fibres. These structures are defined in literature as puff-like structures (Lafontaine 1979). In the generative cell, puff-like structures occurred throughout the interphase period, i.e. from stage I to VI. In anthesis they were no longer visible. During the development of the pollen grain, the puff-like structures changed in number, size and ultrastructure. They were the most numerous in development stages II and VI. In those periods they were also the smallest in size (0.8-1.0 μm). A decrease in the number of puff-like structures in stages III to V was associated with an increase in their size to ca 1.4 μm in diameter. The ultrastructural changes in the puff-like structures were reflected in the first place in an increase in the thickness of the fibres making up the puff, from 20-40 nm in the initial period of pollen grain development to 60-80 nm in stage VI (Fig. 4A, B).

In the vegetative nucleus, puff-like structures were much less frequent. They ranged from 0.6 to 0.9 μm in diameter. The increase in thickness of the fibres making up the puff-like structure during pollen grain maturation was only slight: from 20-30 nm just after microspore division to 30-40 nm shortly before anthesis.

Intranuclear electron-transparent spaces

A characteristic feature of the generative nucleus, distinguishing it from the vegetative nucleus, was the periodical occurrence in it of electron--transparent spaces devoid of membrane, filled with delicate, 8-16 nm thick fibres (Fig. 5). They occurred in development stages III to VI. i.e. in phase G_2.

The circular light spaces were clearly visible in a light microscope. They did not strain with nucleic acid stains and were ca 2 μm in diameter. They were completely surrounded by chromatin (Fig. 6A), or lay on the borderline between the nucleus and cytoplasm (Fig. 6B). The light spaces varied in number in the course of pollen grain maturation. They were most numerous in the spherical generative cell, i.e. in the period preceding the rapid reduction in the nuclear volume.

Extranucleolar RNP structures accompanying chromatin

The extranucleolar RNP structures, resistant to bleaching by Bernhard's technique (1969), irrespective of their morphology, were divided into perichromatin structures, i.e. those revealed in the marginal condensed chromatin

zone, and interchromatin structures, i.e. those revealed in spaces among condensed chromatin aggregations.

In the vegetative nucleus, the extranucleolar RNP structures associated with chromatin occurred nearly throughout the entire interphase (stages I-VI), mainly in the perichromatin zone. In the initial development stages they formed chains around the bleached chromatin (Fig. 7A). Later (stage VI), they occurred almost exclusively in the form of lumps (Fig. 7B), which disappeared just before anthesis.

The number of extranucleolar RNP structures was much smaller in the generative nucleus. As a rule, they were interchromatin structures forming small aggregations (Fig. 8B). They were noted only in the initial development stages. In stage IV the RNP structures disappeared nearly completely. They reappeared in the spindle-shaped generative cell at the time when the nucleolus disappeared. They formed a continuous narrow zone of electron--dense material surrounding the bleached condensed chromatin (Fig. 8B).

The nucleolus

The nucleoli of the pollen cells differed in size, ultrastructure and the duration of their occurrence.

The volume of the nucleolus of the generative cell was gradually reduced from stage I to V (Fig. 9). No nucleolus was observed in the mature generative cell. In the vegetative cell, the nucleolus was present throughout

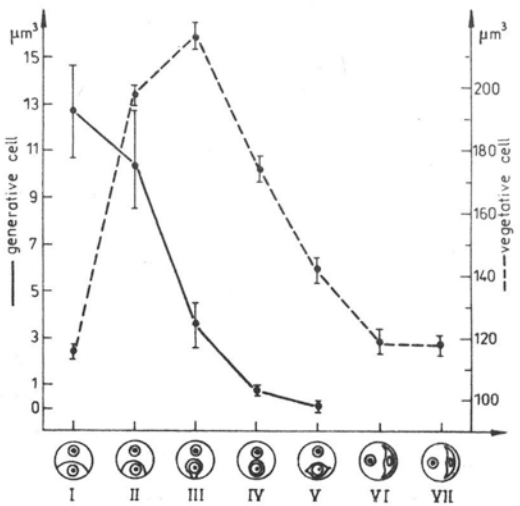

Fig. 9. Volumes of the nucleoli of the generative and vegetative cell in successive stages of differentiation of the pollen grain

the maturation period of the pollen grain. In the period G_1-S the nucleolus grew in size (stages I-III), then in phase G_2 (stages IV-VII) it decreased in volume.

In the generative cell, already as soon as the period of its parietal position (stage II) the nucleolus exhibited typical segregation into granular and fibrillar zones (Fig. 10A). This type of nucleolus peristed until stage IV. During the period of generative cell elongation a residual nucleolus devoid of its granular part formed a dense compact mass.

In the vegetative cell, in the initial development period the nucleolus was made up of a central fibrillar zone surrounded by a granular zone containing numerous light areas (Fig. 10B). Towards the end of pollen grain maturation the number of light areas markedly decreased.

DISCUSSION

The changes observed in the structure of the pollen nuclei of *Hyacinthus orientalis* in the course of the successive stages of pollen maturation are linked in the first place with the process of differentiation of the two pollen cells resulting in their performing different functions. The differentiation takes place during interphase, which in both pollen cells of *Hyacinthus orientalis* includes G_1, S and G_2. The particular stages of interphase, however, do not proceed simultaneously in the vegetative and the generative nuclei (Bednarska 1981). A comparison of the successive phases, G_1, S and G_2 in the generative with those in the vegetative cell makes it possible to distinguish the transformations characteristic of interphase and common to both nuclei from those related to the proceeding differentiation of those nuclei. The following are transformations characterizing both pollen nuclei: a) increase in nuclear volume in period G_1-S, b) chromatin decondensation in period G_1-S, c) chromatin condensation in phase G_2, d) nuclear lobing in phase G_2, e) occurrence of puff-like structures throughout the entire interphase.

The increase in volume of the pollen nuclei in *Hyacinthus orientalis* coincides with the period of maximum RNA and nuclear and cytoplasmic protein synthesis (Bednarska 1981, 1984). An increase in nuclear volume in period G_1-S and changes in the degree of chromatin condensation, viz. decondensation in period G_1-S and condensation in phase G_2, have been found in many other cell types (Lord and Lafontaine 1976, Nagl 1977, Kwiatkowska and Maszewski 1978). It can therefore be assumed that those are common processes, characteristic of the successive stages of interphase.

In both types of *Hyacinthus orientalis* pollen cells the puff-like structures are also subject to the process of condensation during interphase. This

feature of puff-like structures seems to indicate that they correspond with centromeres (Lafontaine et al. 1979, Lafontaine and Luck 1980).

The process of nuclear lobing does not occur in each cellular interphase, through it seems common in the vegetative, and frequent in the generative pollen cell (Sanger and Jackson 1971c, Echlin 1972). In *Hyacinthus orientalis*, the lobing of pollen nuclei coincides with the disappearance of the extranucleolar RNP structures and with a pronounced lowering in RNA and protein synthesis (Bednarska 1984). A similar correlation between the drop in RNA synthesis and growth in nuclear surface through lobing was found by De la Torre et al. (1973) in meristematic *Allium cepa* cells. It therefore seems that the considerable increase of pollen nuclei surface through lobing may be connected with RNP transport to the cytoplasm.

The following morphological and ultrastructural transformations of pollen nuclei in *Hyacinthus orientalis* seem to reflect the process of differentiation of the pollen cells: a) different trends in size changes in nuclei in phase G_2, b) different degrees, and probably different mechanisms, of chromatin condensation throughout the entire period of pollen grain maturation, c) different numbers and localizations of RNP structures, d) different structural transformations of nucleoli, e) the occurrence of electron-transparent spaces only in the generative nucleus.

A comparison of the degree of chromatin condensation with the variations in the size of the pollen nucleus in *Hyacinthus* reveals slightly different mechanisms of the process of chromatin condensation in the vegetative and the generative nucleus. In the vegetative nucleus we probably have to do with the process of active condensation, which is indicated by the increase in the amount of condensed chromatin at constant nuclear volume. In the generative nucleus, an initial period of active condensation is followed by passive condensation associated with a rapid reduction in nuclear volume. The mechanism of rapid reduction of the generative nucleus volume in *Hyacinthus orientalis* seems to be linked with the disappearance of the electron-transparent spaces observed before in that nucleus; their contents, as it seems, are expelled from the nucleus to the cytoplasm. This is suggested by the pictures from the light microscope, which reveal the varying and frequently marginal localization of these spaces (Fig. 6B).

The degree of chromatin condensation and the number of extranucleolar RNP structures are correlated with the level of RNA synthesis in the pollen cells. The generative nucleus with a more condensed chromatin is characterized by a lower level of RNA synthesis than the vegetative nucleus throughout the entire differentiation period of the pollen grain. Moreover, in both pollen nuclei the process of chromatin decondensation is associated with a rise in the RNA synthesis level, whereas the condensation process is linked with a drop in this level (Bednarska 1984).

The chromatin-accompanying extranucleolar RNP structures, which in the studied cells correspond to perichromatin fibrils and granules and to interchromatin granules, are generally regarded as a structural reflection of the cumulation and transport of the transcription product (Bernhard 1969, Fakan and Bernhard 1971, Puvion and Moyne 1978, Puvion and Lange 1980). In the pollen cells of *Hyacinthus orientalis* the appearance of the extranucleolar RNP structures coincides with the period of intensive RNA synthesis. In the generative nucleus, with its strongly condensed chromatin and lower level of RNA synthesis the number of extranucleolar RNP structures is considerably smaller than in the vegetative nucleus with more dispersed chromatin and higher level of RNA synthesis. These structures disappear in both nuclei during the period of low RNA synthesis (Bednarska 1984), associated with increased chromatin condensation. The progress of chromatin condensation in the pollen nuclei of *Hyacinthus orientalis* considered in conjunction with the level of RNA synthesis supports the opinion, based on studies of other types of cells, that chromatin condensation limits its transcriptive activity (Kwiatkowska and Maszewski 1979, Nagl 1979, 1985).

The differences in the level of RNA synthesis in *Hyacinthus orientalis* pollen cells are also reflected in different transformations of the nucleoli of the vegetative and the generative cell. The vegetative nucleolus is characterized by an ultrastructure typical of the active nucleolus, whereas the generative nucleolus undergoes early segregation, which is generally considered to be a sign of its inactivation (Gimenez-Martin et al. 1977). This supports earlier autoradiographic studies, which have revealed a high level of incorporation of ^{3}H-uridine into the vegetative nucleolus, and practically no incorporation at all into the generative nucleolus (Bednarska 1984).

The results obtained in this work show the process of deepening differentiation of the pollen cells in the course of the full interphase of these cells. It seems that the non-concurrence of the progress of interphase is not only a reflection of the already existing differentiation of the pollen cells, but also a factor which enhances their differentiation. Cells in different phases of their life cycle are characterized by different competences and respond differently to identical physiological stimuli (e.g. hormones), which leads to their further differentiation. This differentiation is reflected not only in the structure of the pollen nuclei, but is particularly pronounced in the cytoplasm of pollen cells, which is the subject of the next part of this study.

Acknowledgment

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Ultrastrukturalne transformacje jądra w różnicujących się komórkach pyłkowych Hyacinthus orientalis L.

Streszczenie

Badano ultrastrukturę jąder pyłkowych podczas dojrzewania pyłku *Hyacinthus orientalis* L. — gatunku, u którego obydwie komórki pyłkowe przechodzą pełną interfazę (G_1, S, G_2). Przemiany ultrastrukturalne obydwu jąder pyłkowych analizowano na tle poznanej wcześniej dynamiki zmian w poziomie syntezy RNA i białek. Porównano strukturę jądra wegetatywnego w fazie G_1, S i G_2 ze strukturą jądra generatywnego w analogicznych fazach interfazy. Wyróżniono zmiany strukturalne wspólne dla obydwu jąder, związane immanentnie z interfazą oraz przemiany związane z różnicowaniem komórek pyłkowych.