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Fine structure ot the protonema in the moss *Ceratodon purpureus* and its response to a cytokinin

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Abstract

Fine structure of the protonema is described, with a special attention to its differentiation depending on the position of cells in the protonemal filament, as well as in response to a cytokinin treatment. Complexes of microfilaments with osmiophilic globules represented structures of particular interest. They appeared temporarily, almost exclusively in apical cells. The cytokinin treatment resulted in the apical cells in an increased number of cytokinetic figures and in structural changes indicating increased metabolic activity. In the intercalary cells, changes in response to the cytokinin were much smaller and mostly concerned an augmented development of the thylakoid system in chloroplasts. After a prolonged (5 days) treatment, degeneration symptoms developed in all cells, particularly in nuclei and chloroplasts, whereas the structure of mitochondria was relatively stable. The results are compared with the observations concerning the cytokinin-induced gametophore buds and with the data of biochemical and physiological investigations of the protonema.

1. INTRODUCTION

Investigations of ultrastructure of protonema cells in mosses were not numerous and usually concerned only some cell components (Sun 1962, Monroe 1968, Zurzycki 1968, Lehmann and Schulz 1969, Schulz and Lehmann 1970, Valanne 1971). A more complete description of the fine structure of protonema was made by Młodzianowski (1970) in *Funaria hygrometrica*, however, without a regard to the differentiation of cells depending on their position in the protonema filament. Therefore, one purpose of this study was to carry out an investigation of cell ultrastructure in the protonema with a special attention to the differences between apical and intercalary cells.

A moss protonema is a suitable model object for investigating the biological activity of cytokinins which specifically induce formation of gametophore buds at some intercalary cells and stimulate the protonemal cell divisions in apical cells (Szweykowska et al. 1971, 1972). The second purpose of this paper was to find out whether changes in ultrastructure of apical and intercalary cells are taking place during incubation of the protonema with a cytokinin.

2. MATERIAL and METHODS

A clone culture of the protonema of *Ceratodon purpureus* (L. ap. Hedw.) Brid. was grown in sterile conditions on cellophane disks placed on surface of a mineral agar medium (Schneider and Szweykowska 1974). Four-week-old protonemata were divided into halves and transferred to the nutrient solution (composition the same as for the stock culture, with the omittance of agar) with and without N^6-(Δ^2-isopentenyl)adenine (IPA) in 1 μM conc., resp. Samples for microscopic examinations were taken after 6, 48, and 120 h of incubation. For electron microscopy the material was fixed in 2% glutaraldehyde in 0.1 M Milloning phosphate buffer of pH 7.4 at 4°C for 24 h and postfixed in 2% OsO_4, in the same buffer and temperature, for 2 h. After washing with the buffer, the material was dehydrated with ethanol, acetone and propylene oxide. Single protonemal cells, the apical and the intercalary ones (located at a distance between 30—40 cells from the apical cell, a position in the filament at which gametophore buds usually arise) were then excised with delicate knives prepared from wolfram wire, and embedded in Epon 812 according to Luft (1961), with the use of a modification for single cells described by Sparvoli et al. (1965). Sections were cut with an LKB ultramicrotome and stained with uranyl acetate and lead citrate (Reynolds 1963, Venable et al. 1965). Observations were made in JEOLCO type 7A electron microscope at a voltage of 80 KV and an objective aperture of 30 μm diameter.

3. RESULTS and DISCUSSION

3.1. Fine structure of the apical and intercalary cells

Cell differentation within a protonema filament as seen in a light microscope is marked by a difference in optical density of cell contents which in the apical cells is considerably higher than in the intercalary ones. The observation in the electron microscope showed that the apical cells have a cytoplasm of distinctly higher electron density and contain

a considerably higher number of cell organelles, the form of which indicates higher metabolic activity. A less active form of all cell structures in the intercalary cells was observed irrespectively of a presence or absence of side branches or gametophore buds at these cells (cfr. Figs. 2 and 14).

Typical longitudinal sections through the apical and intercalary cells, 6 h after transferring the protonema from an agar to a liquid medium, are shown in Figs. 1 and 2. The cytoplasm of the apical cell is rich in ribosomes. Small vacuoles are regularly distributed in the cell, with the exception of its tip end which is deprived of vacuoles. The intercalary cells are highly vacuolized, the cytoplasm shows a low grade of electron density, with a low number of ribosomes. Some concentration of ribosomes was only observed near individual organelles.

In the apical cells, the nucleus was situated in the central part of the cell and had a shape more or less spherical (Fig. 1). The nucleolus, located in the centre of the nucleus, could be classified — according to Busch and Smetana (1970) — to the type of nucleoli with nucleolonema. The fibrillar and granular components were present in approximately equal amounts and were uniformly distributed, without forming separate regions (Fig. 3). Such a well developed form of nucleolus indicates a high metabolic activity of the cell, connected with a high rate of ribosomal RNA and protein syntheses (Brown, 1966; Hyde, 1967; Chapman and Jordan, 1971; Jordan and Chapman, 1971 and 1973).

In the intercalary cells, the nuclei were smaller, usualy elipsoid, slightly elongated in the direction of the cell length. The nucleolar substructures showed a high degree of dispersion (Fig. 4) which indicated a low metabolic activity of the nucleus. These observations are in agreement with those of Bopp (1955) who using light microscopy described changes in nuclei, from spherical ones with a large nucleolus in the apical cell to very elongated and with very small nucleoli in successive intercalary cells.

In all protonema cells the lens-shaped plastids were arranged parallely to the cell length (Figs. 1 and 2). In the apical cells, they were particularly concentrated near the cell tip (Fig. 1). Their internal membrane system was well developed and consisted of numerous granum and stroma thylakoids (Fig. 5). In the intercalary cells, the plastids contained large amounts of starch and their internal membrane system was poorly developed (Fig. 8). The few granum and stroma thylakoids were situated mainly under the plastid envelope. Deeper in stroma, besides starch grains, some minute plastoglobules were present.

In general, the structure of chloroplasts in *Ceratodon purpureus* was found to be similar to that in another moss species, *Funaria hygrometri-*

PLATE I

Figs. 1—2. Cells of the protonema, after 6 h in the liquid control medium. Fig. 1. The apical cell. × 1 900. Fig. 2. The intercalary cell. × 2 100. Fig. 2a. Fragment of an initial of the protonema branching originating at the intercalary cell. × 1 100. Mt — mitochondria, arrows — endoplasmic reticulum

PLATE II

Figs. 3—11. Fragments of the protonemal cells, after 6 h in the liquid control medium. Fig. 3. Apical cell, fragment of a nucleolus with uniformly distributed fibrillar and granular components. × 30 000. Fig. 4. Intercalary cell, the spindle-shaped nucleus with dispersed nucleolar substructures. × 5 800. Fig. 5. Apical cell, the chloroplasts. × 9 600. Figs. 6—7. The mitochondria from apical (Fig. 6) and intercalary (Fig. 7) cells. × 13 500 (Fig. 6), × 21 000 (Fig. 7). Fig. 8. Intercalary cell, a plastid with a large amount of starch and a small number of thylakoids in the periphery of the organelle. × 12 000. Fig. 9. Apical cell, the osmiophilic globules along the microfilaments. × 21 000. Fig. 10. Apical cell, the Golgi structure. × 24 000. Fig. 11. Intercalary cell, a microbody inserted between plastids. × 13 000. Mb — microbody

PLATE III

Figs. 12—14. After 48 h in the liquid control medium. Fig. 12. An elongated apical cell. × 1 400. Fig. 13. Apical cell, a fragment of the nucleolus with a granular structure. × 30 600. Fig. 14. Intercalary cell with well developed chloroplasts and with an initial of a side branching. × 900. Fig. 15. After 120 h in the liquid control medium, apical cell with numerous osmiophilic globules. × 4 100. Fig. 15a. Osmiophilic globules and canals of the endoplasmic reticulum, the largest globule surrounded by ER. × 28 600

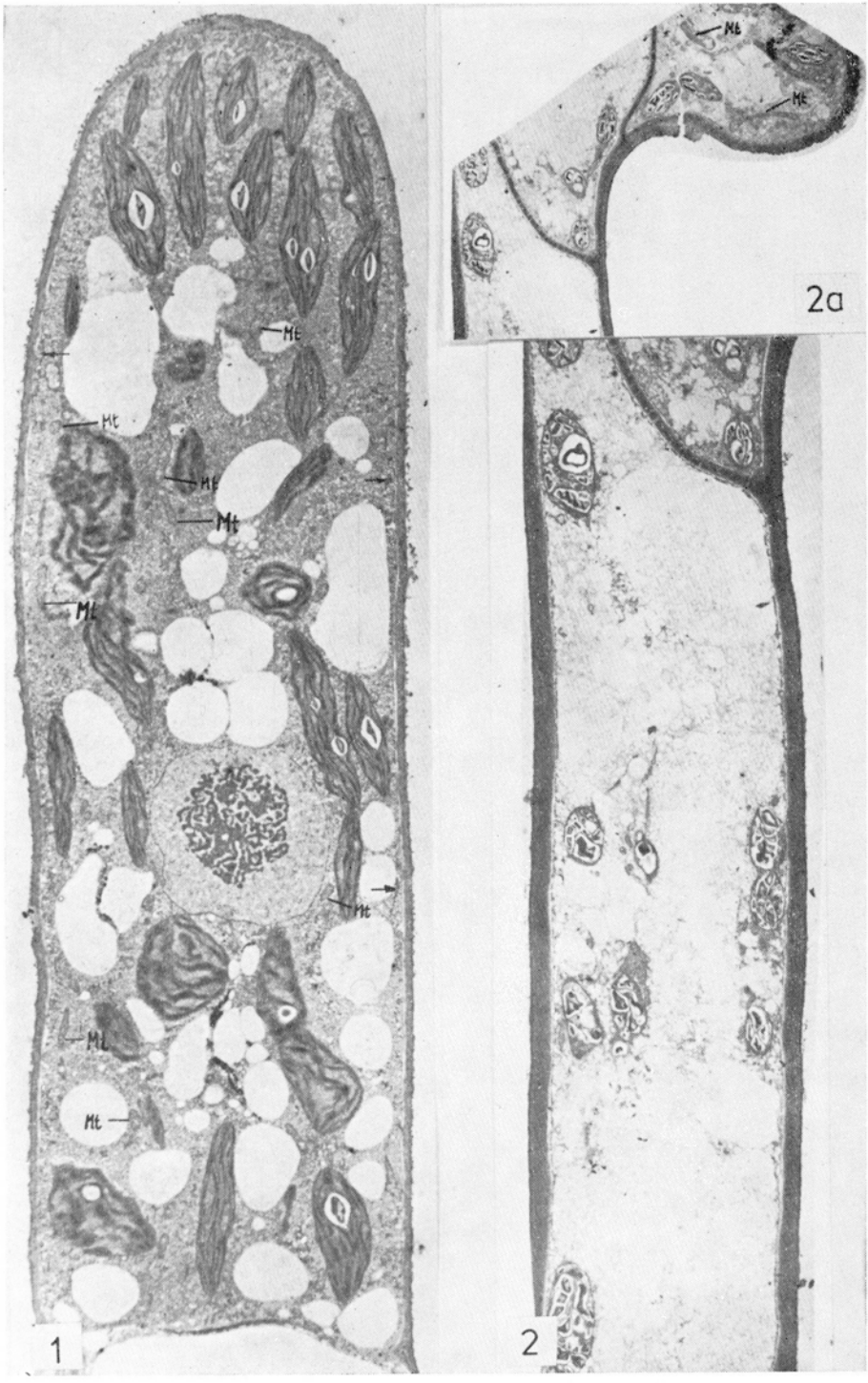
PLATE IV

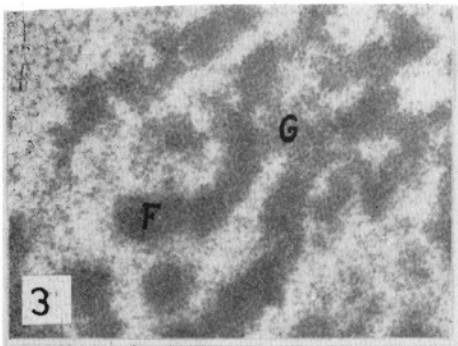
Figs. 16—20. After 6 h of the cytokinin treatment, apical cells. Fig. 16. A cell shortly after division. Numerous mitochondria visible near the developing cell wall, and aggregations of microfilaments with osmiophilic globules in the centre of the cell. × 1 900. Arrows — the new cell wall. Fig. 17. An early stage of the cytokinesis, with a phragmoplast, aggregations of vesicles and of an electron dense material in the future cell plate. × 4 000. Fig. 18. An active form of a mitochondrion. × 15 400. Fig. 19. The tip end of a cell with Golgi structures and numerous Golgi vesicles. × 16 800. Fig. 20. Polyribosomal configurations in the cytoplasm. × 30 000. Fig. 21—22. After 48 h of the cytokinin-treatment, apical cells. Fig. 21. A longitudinal section of an elongated and active cell. × 1 200. Fig. 22. A nucleolus with well developed granular component of the nucleolonema. × 8 000

PLATE V

Fig. 23. After 120 h of the cytokinin treatment, a degenerating apical cell, with disintegrating nuclear and plastidic envelopes. × 2 700. Fig. 23a. Fragment of a chloroplast, deprived of envelope and with an osmiophilic ring surrounding an electron light area. × 31 200. Mt — Mitochondria, arrows — osmiophilic globules. Figs. 24—25. After 48 h of the cytokinin treatment, intercalary cells. Fig. 24. Fragment of a longitudinal section with numerous chloroplasts showing well developed thylakoid systems. × 1 500. Fig. 25. Chloroplasts with highly developed grana × 4 000. Fig. 26. After 120 h of the cytokinin treatment, fragment of an intercalary cell with a degenerating chloroplast. × 12 000

Plate I

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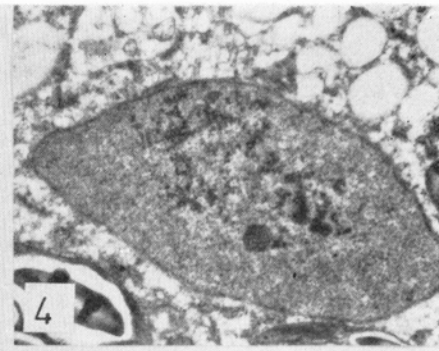
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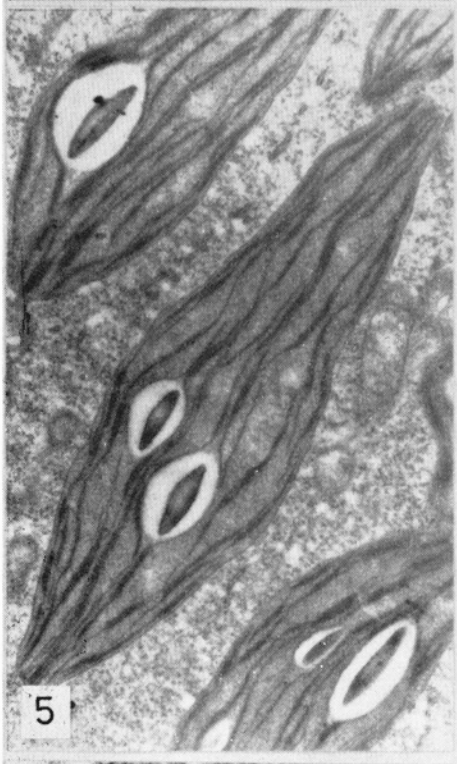
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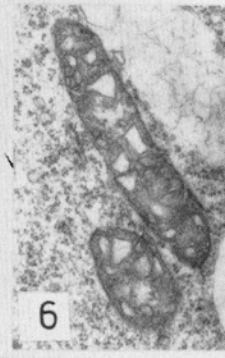
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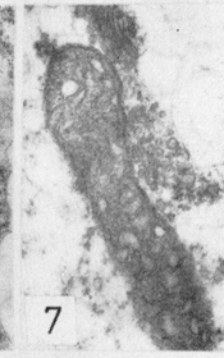
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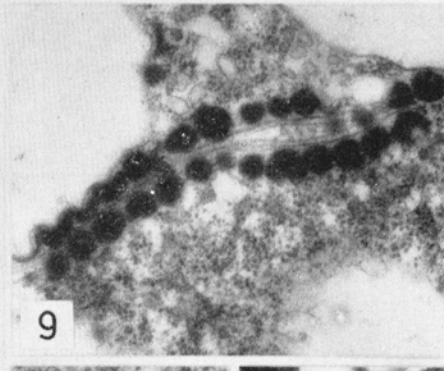
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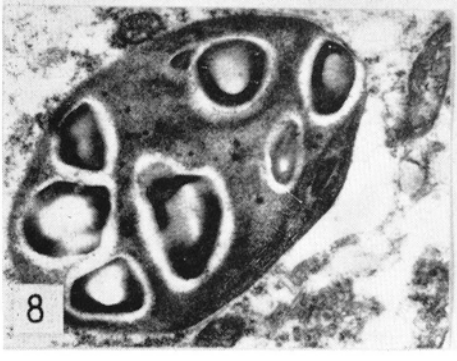
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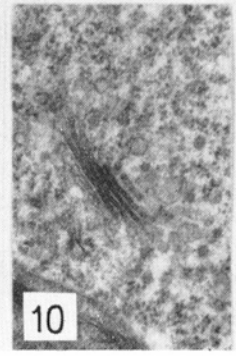
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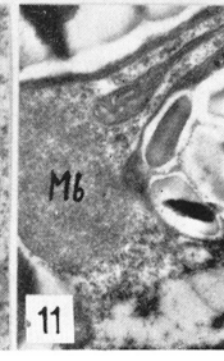
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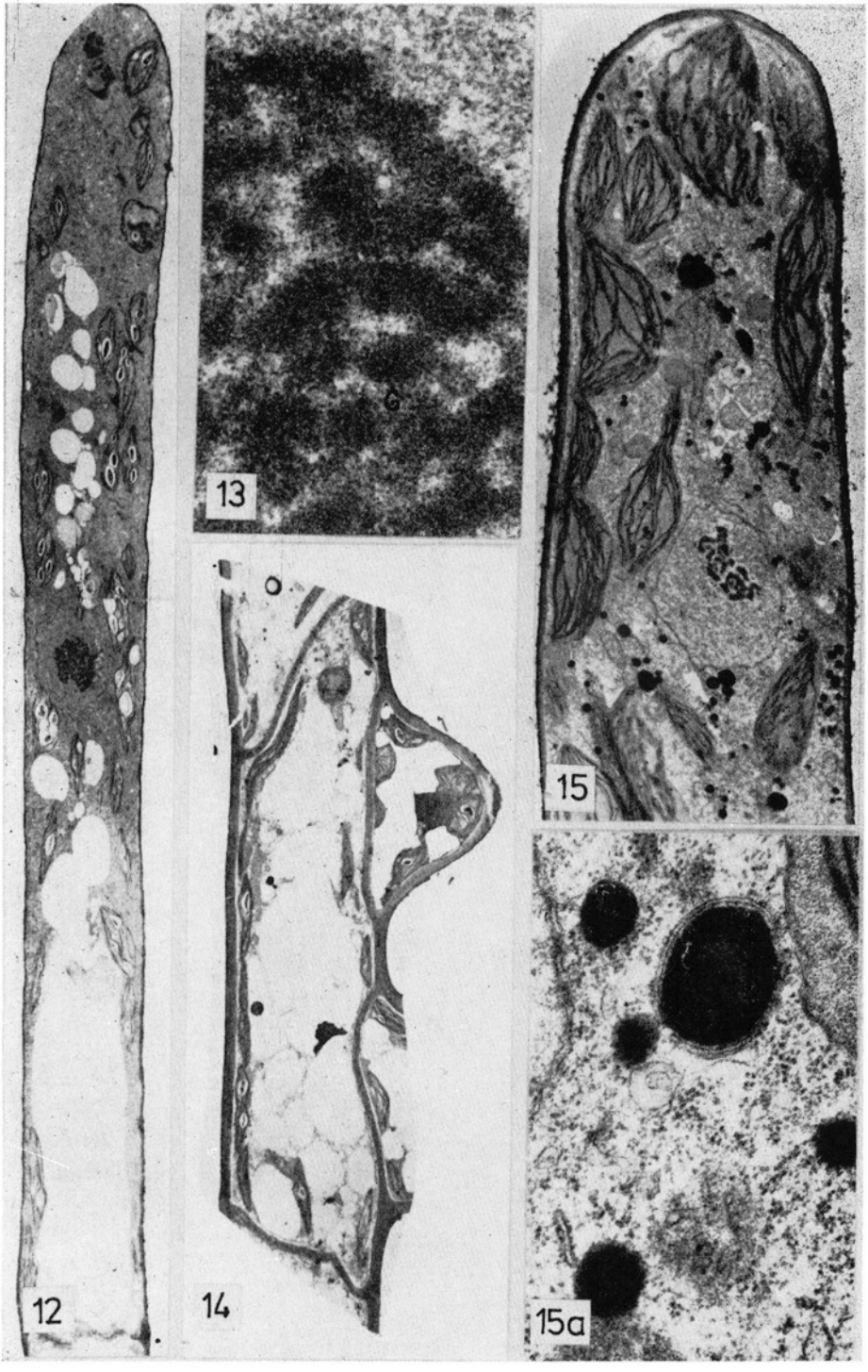
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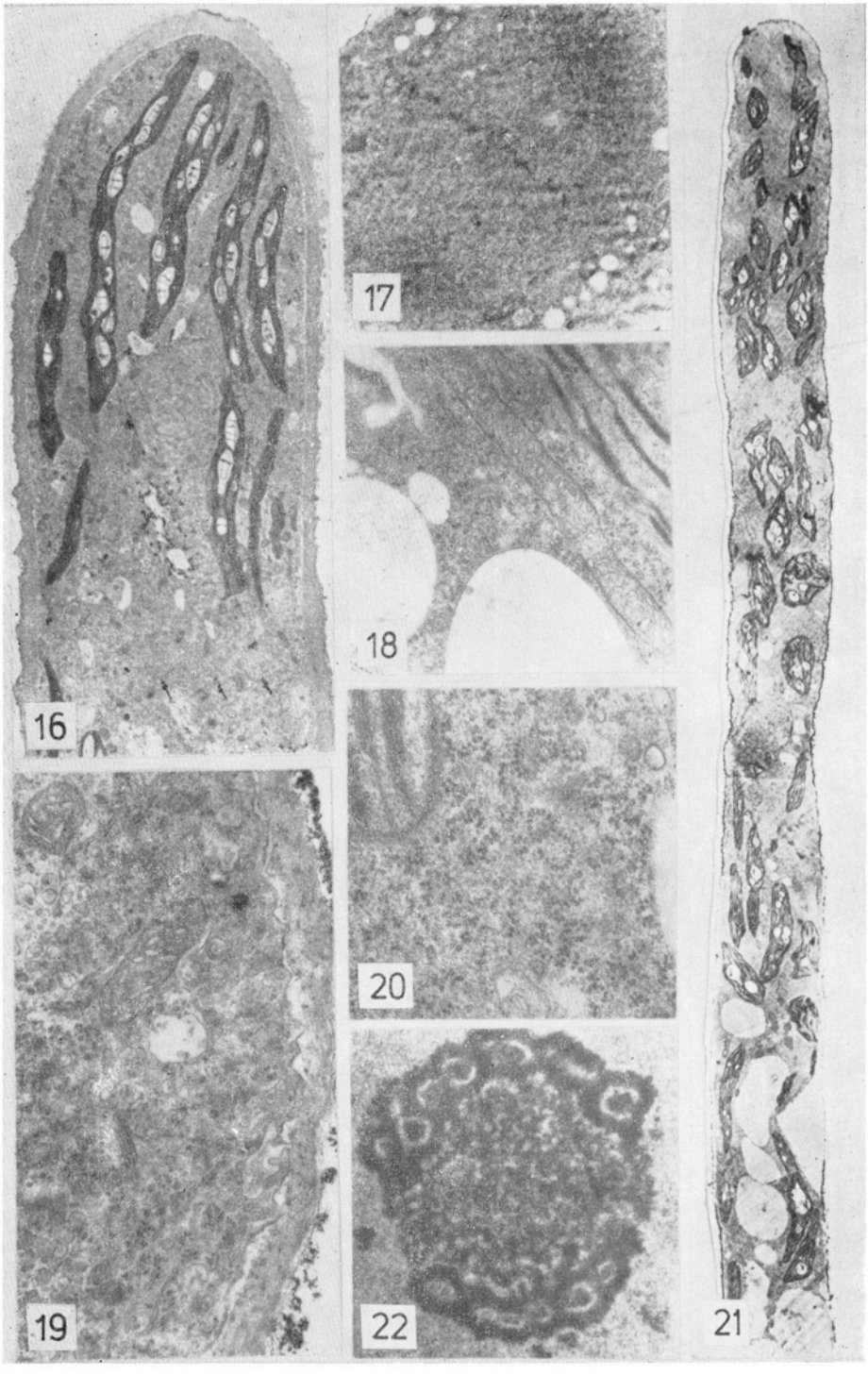
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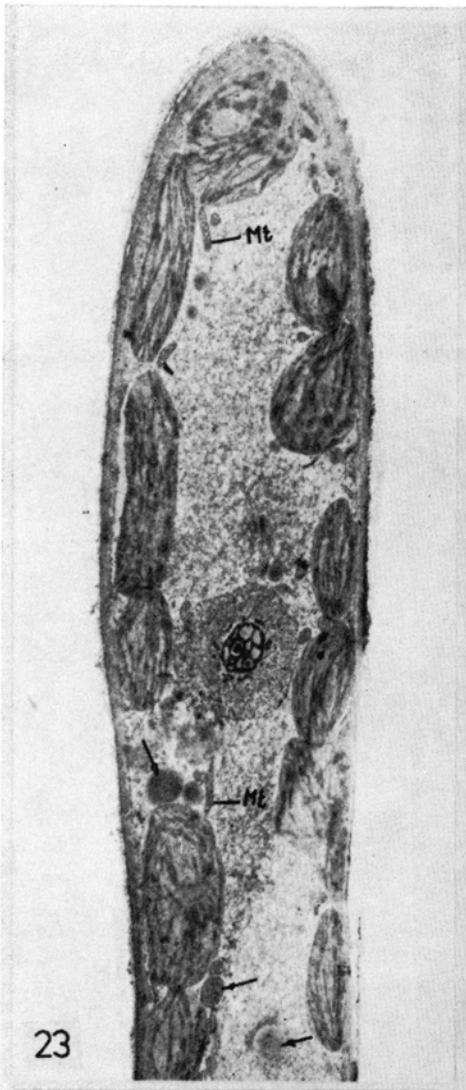
Plate V



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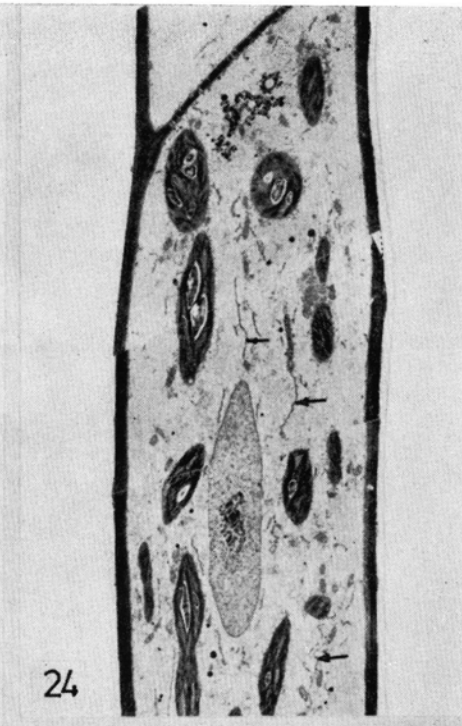

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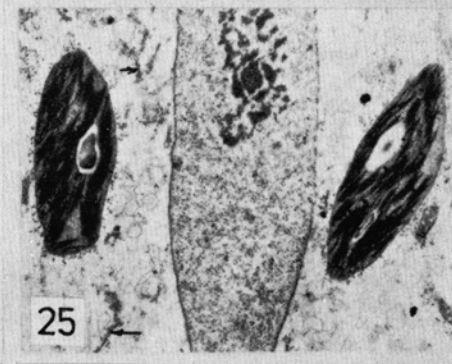

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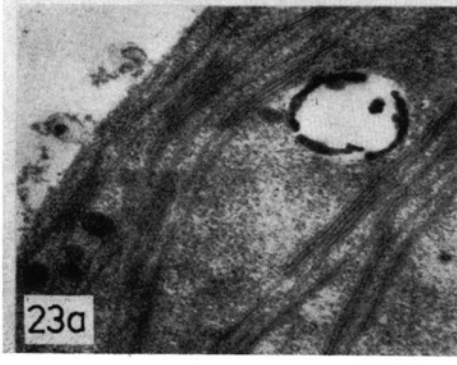

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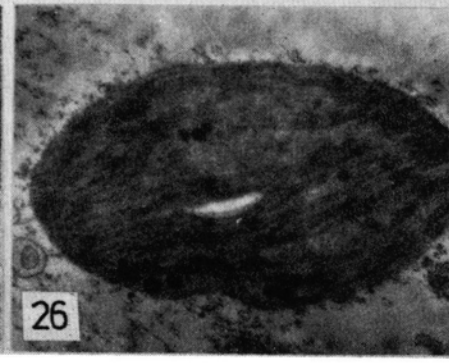

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ca (Sun 1962, Zurzycki 1968, Młodzianowski 1970), and somewhat more primitive than in vascular plants.

In the apical cells, the mitochondria were numerous and distributed throughout the whole cell (Fig. 1). In intercalary cells they occurred in the neighbourhood of other cell structures (most often plastids). In both cell types the profiles of mitochondria were oval or elongated in the direction of cell length. The internal membrane system was of the sacculi type (Figs. 6 and 7) and in the fine granular matrix, which was more electron dense than the cytoplasm, ribosomes and electron light areas with macromolecules of mitochondrial DNA were visible (Fig. 6).

On sections of the apical cells, endoplasmic reticulum was observed in form of short fragments scattered throughout the whole cell, with particular concentration near the cell walls (Fig. 1, arrows) and microbodies. It was always of the granular type, densely covered with ribosomes.

In the intercalary cells, the endoplasmic reticulum was observed only occasionally.

The microbodies containing fine granular, homogenous matrix were observed in both the apical and intercalary cells, mainly near plastids, often inserted between plastid ends (Fig. 11). Very often they were also found in a close contact with the endoplasmic reticulum.

In both the apical and intercalary cells, Golgi structures were found infrequently, mainly near nucleus or partition walls between two neighbour cells. Their dictyosomes were filled with an electron dense content (Fig. 10).

To the most interesting structures observed in the apical cells belonged complexes of small strongly osmiophilic globules, arranged in rows along microfilaments (Fig. 9). They occurred in the cytoplasm, most frequently near the vacuoles, and were never bound with any other cell structures, contrary to similar complexes described by Valanne (1971) who observed their close relation to the Golgi structures. In intercalary cells they were observed very seldom.

3.2. Changes in the protonema ultrastructure following incubation in a liquid medium

Small changes in the cell structure were observed as the protonema was incubated in the control solution. They may represent one of the aspects of a "transfer effect" from a solid (agar) to a liquid medium. The length of the apical cells increased from about 100 μm after 6 h to about 130 μm after 48 h, and the thickness of their walls decreased from 0.69 ± 0.05 μm after 6 h to 0.21 ± 0.01 after 48 h (Fig. 12). In the nucleolonema, the granular component predominated (Fig. 13). In chloroplasts, the size of grana was somewhat larger, the number of compart-

ments per granum amounting up to 15 after 48 h (up to 12 after 6 h). In the intercalary cells, a disappearance of starch was observed, accompanied by a development of the thylakoid system (Fig. 14).

After 120 h, some changes were observed indicating lowering of metabolic processes, resembling those occurring in ageing cells (Fig. 15). In apical cells, they were represented e.g. by a presence of numerous osmiophilic globules in the cytoplasm and by an increase in the number of plastoglobules per chloroplast section from 3.0 ± 0.4 after 48 h of incubation in the liquid medium to 14.8 ± 2.2 after 120 h. The cytoplasmic globules were often accompanied or even surrounded by the endoplasmic reticulum (Fig. 15a).

3.3. The effect of the cytokinin treatment

The effect of cytokinins on the fine structure of cells was hitherto investigated mostly in connection with the stimulation of cell divisions (Hayat and Salama 1966, Nitsch 1967, Neumann, Cireli and Cireli 1969) and with the retardation by these substances of ageing processes in detached leaves (Shaw and Manocha 1965, Sveshnikova et al. 1966, Mittelheuser and van Steveninck 1971, Młodzianowski and Ponitka 1973, Młodzianowski and Kwintkiewicz 1973).

The effect of kinetin on the ultrastructure of protonemal cells in *Funaria hygryometrica* was studied by Młodzianowski and Szweykowska (1971), however, the observations were made after a rather prolonged, 6-day-treatment. Some symptoms of destruction and ageing were only found. On the other hand, it has been shown that shortly after the addition of a cytokinin to the incubation medium, the protein and RNA levels increase in the protonema, the activities of hydrolytic enzymes decrease, cell divisions are enhanced and gametophore buds are induced (Brandes 1967, Szweykowska et al. 1971, 1972, Ratajczak and Szweykowska 1973, Schneider and Szweykowska 1974). An incubation for more than about 48 h results in a lowering of the RNA and protein contents and in an increase in the activities of hydrolytic and oxidative enzymes. These two phases of the cytokinin action are reflected in the fine structure of the cytokinin-induced gametophore buds (Idzikowska and Szweykowska, 1978). Observations presented in this paper show that they concern as well the cells of the protonema.

3.3.1. The apical cells

In the presence of the cytokinin an increased rate of cell divisions in apical cells after 6 h of IPA treatment was indicated by frequently observed cytokinetic figures (Fig. 17). The mitochondria, when compared

with the control, seemed to be activated, with more numerous, small sacculi, ribosomes, minute osmiophilic grains and light regions with DNA fibrils (Fig. 18). A particular concentration of mitochondria, as well as of active forms of Golgi structures, was observed near the newly forming cell walls (Fig. 16). The active Golgi structures and very numerous Golgi vesicles concentrated also near the cell tip where they probably took part in growth of the plasmalemma and of the cell wall, occurring in this cell region (Fig. 19). A stronger development of granular endoplasmic reticulum and of polyribosomes (Fig. 20) and larger aggregations of osmiophilic globules accompanied by microfilaments (Fig. 16) were also observed.

After 48 h of the cytokinin treatment, figures indicating cell divisions were not observed. As in the control, the length of cells greatly increased from about 70 μm after 6 h to about 150 μm after 48 h of the IPA treatment, and the thickness of their walls decreased from $0.63 \pm \pm 0.08$ to 0.23 ± 0.02 μm, but the protoplasts maintained a structure indicating a high metabolic activity (Fig. 21). The electron density of cytoplasm was very high due to an enormous number of mono- and polyribosomes. The nucleoli were very large, with highly developed granular component of the nucleolonema (Fig. 22), and the nuclear envelopes were frequently provided with ribosomes attached to their outer surfaces. Among the numerous cell organelles, the chloroplasts were most abundantly represented. Tens of them could be found on one cell section (Fig. 21). It is interesting that they were differentiated into shorter, lens--shaped forms of about 6 μm length, occurring near the cell tip, and into elongated forms, the length of which increased as they were situated more towards the basal end of the cell, amounting up to 14-20 μm (Fig. 21).

The Golgi structures were not numerous, and the aggregations of osmiophilic globules with microfilaments were not observed.

After 120 h of an incubation with the cytokinin, degeneration processes were observed, much more pronounced than "ageing" found in the control protonema (Fig. 23). The nuclear envelopes were mostly disintegrated and only their fragments remained, the nucleoli were small and showed large and numerous electron light areas ("vacuolization"). The chloroplasts were shorter, in some of them the plastidal envelopes disappeared and large, strongly osmiophilic plastoglobules as well as electron light areas surrounded by an osmiophilic ring (Fig. 23a) appeared in the stroma. Spherical osmiophilic bodies of a various size and of an uneven grade of electron density appeared in the cytoplasm (Fig. 23, arrows). Structures of relatively high stability were represented by the mitochondria. They maintained their envelopes even in cells with advanced degradation symptoms. Only their internal membrane system was poorly developed.

3.3.2. The intercalary cells

The 6 h treatment of the protonema with the cytokinin showed little effect on the structure of intercalary cells. No differences could also be found between the cells from which gametophore buds developed and the cells without buds. Though all cell organelles were present in these cells, their form and appearance indicated a low activity.

After 48 h, the development of the thylakoid system in chloroplasts was much promoted (Figs. 24 and 25). In some plastids the number of thylakoids per granum came up to 20, whereas in the control variant to 12 only. The endoplasmic reticulum was also represented in a somewhat grater amount, and the number of ribosomes attached to its membranes appeared to be larger (Figs. 24 and 25, arrows).

After 120 h, degeneration symptoms were observed similar to those found in the apical cells. They mainly concerned nuclei and chloroplasts (Fig. 26).

The results obtained in this study show that the induction of gametophore buds and structural changes in their cells are not the only effects of the cytokinins on the moss protonema, and that structural changes appear also in the protonemal cells. The apical cells of the protonema are particularly sensitive, whereas changes in the intercalary cells — though they exactly give rise to the gametophore buds — are much smaller. The observations also confirmed the previous conclusion (Idzikowska and Szweykowska 1978) that the early period of the cytokinin treatment, up to 48 h, is of most importance in various kinds of investigations, because longer treatments result in degeneration symptoms in structure of the protonema.

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Ultrastruktura splątka mchu Ceratodon purpureus i jej zmiany pod wpływem cytokininy

Streszczenie

Ultrastruktura splątka została opisana ze szczególnym uwzględnieniem zróżnicowania komórek w zależności od ich położenia w nici protonemalnej oraz zmian wywołanych działaniem cytokininy. Do struktur szczególnie interesujących należą zespoły złożone z osmofilnych globul i mikrofilamentów, które pojawiały się okresowo i występowały niemal wyłącznie w komórkach szczytowych. Pod wpływem cytokininy zwiększała się częstość występowania figur cytokinetycznych w komórkach szczytowych, zaś struktura tych komórek wskazywała na ich zwiększoną aktywność metaboliczną. W komórkach interkalarnych zmiany wywołane cytokininą były znacznie mniejsze i głównie dotyczyły silniejszego rozwoju systemu tylakoidalnego w chloroplastach. Po dłuższym czasie działania cytokininy (5 dni) we wszystkich komórkach obserwowano objawy degeneracji, która dotyczyła zwłaszcza jąder i chloroplastów, podczas gdy struktura mitochondriów była prawie nie zmieniona. Wyniki pracy zostały porównane z obserwacjami dotyczącymi pąków gametoforowych indukowanych przez cytokininę oraz z rezultatami badań biochemicznych i fizjologicznych splątka.