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Structural and functional polymorphism of plastids in leaves of *Clivia miniata* Rgl. II. Ontogenesis of plastids in mesophyll cells and in cells surrounding vascular bundles

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Abstract

In mesophyll cells and in cells adjoining vascular bundles of leaves in *Clivia miniata* Rgl. there occur chloroplasts differing with respect to their structure and the type of accumulated substances. Chloroplasts of mesophyll cells have a well-developed system of grana and intergrana thylakoids; within the stroma they accumulate solely inclusions of lipid character. Chloroplasts of cells surrounding the bundles are smaller than chloroplasts of mesophyll cells, have a poorly developed system of inner membranes and are able to accumulate only considerable amounts of starch. The third type of chloroplasts occurs in parenchymateous cells of the vascular part of the bundles. These chloroplasts, much smaller than those described above, have a reduced system of inner membranes and are not capable of accumulating either starch or lipid droplets. In stroma, they contain only plastoglobules. It seems probable that morphologically uniform proplastids are the precursors of all the studied types of chloroplasts. Their developmental sequence is determined by the degree of cellular differentiation, the type of cell as well as by the function it performs.

INTRODUCTION

Various type of chloroplasts are found in the mesophyll of leaf blade. The differences among them depend on the sizes of chloroplasts, the intensity of thylakoid development, the presence or the lack of grana, the occurence or the lack of starch as well as on various quantities of accumulated starch (Sarda et al. 1975, Khudairi 1977, Carmi and Shomer 1979). The differences may also occur in the structure of thylakoid membranes. In the leaf blade cells of sunflower, Casadoro and Rascio (1979) describe chloroplasts with normally stained thylakoid membranes and electron-transparent intrathylakoid spaces and chloroplasts with lightly stained membranes and electron-dense intrathylakoid material.

The dimorphism of chloroplasts is well known in leaves of C_4 plants. The adjoining mesophyll cells and vascular-sheath cells contain chloroplasts varying in respect to their morphology, ultrastructure, physiology and biochemistry. The chloroplasts of the sheath cells in C_4 plants are considerably greater than the mesophyll chloroplasts (Laetsch 1968, Laetsch and Price 1969). The former have small grana or none, while the latter are characterized by well developed grana (Hodge et al. 1955, Bisalputra et al. 1969, Laetsch and Price 1969, Kanai and Kashiwagi 1975, Kirchanski 1975, Miyake and Maeda 1978).

The chloroplasts of sheath cells may contain peripheral reticulum, while in chloroplasts of mesophyll cells such a structure is absent or poorly developed (Laetsch 1974, Crookston and Ozbun 1975). Mesophyll chloroplasts of C_4 plants contain phosphoenol pyruvate carboxylase, whereas in sheath cell chloroplasts ribulose diphosphate carboxylase is present (Gunning and Steer 1975). Photosynthesis in chloroplasts of mesophyll takes place according to Hatch-Slack cycle; in bundle-sheath cells with grana-lacking chloroplasts CO_2 is bound during a typical Calvin-Benson cycle (Gunning and Steer 1975, Doohan and Newcomb 1976).

In many plants, bundle-sheath chloroplasts are specialized in the accumulation of large amounts of assimilatory starch (Laetsch et al. 1965, Downton and Tregunna 1968, Bisalputra et al. 1969, Johnson and Brown 1973), whereas mesophyll chloroplasts usually contain smaller amounts of starch or are entirely deprived of it (Laetsch 1968, Bisalputra et al. 1969).

In some C_4 plants there occurs a difference in the rate of chloroplast differentiation in both sheath and mesophyll cells, which is also accompanied by a different degree of metabolic activity of these plastids (Downton et al. 1969).

The chloroplasts of C_3 plants are smaller than the chloroplasts in mesophyll cells (Miyake and Maeda 1976a, 1978). No essential differences in the ultrastructure of these plastids are observed (Miyake and Maeda 1976a). At the early stages of leaf development, in contrast to mesophyll cells, sheath cell plastids accumulate large quantities of starch and they are regarded as amyloplasts. This starch is considered to be storage starch derived from carbohydrates of other organs, but not from photosynthesis (Miyake and Maeda 1976b, 1978).

The present study ends a series of investigations devoted to differentiation and structure of plastids in leaves of *Clivia miniata*. It deals with the development of structurally and functionally differing types of chloroplasts in mesophyll cells, the cells surrounding vascular bundles and in the parenchymateous cells of the vascular parts of the bundle. The structure of plastids of the sieve tubes and of accompanying cells have also been considered in the observations.

MATERIAL AND METHODS

The material and fixation procedure were as described by Mikulska et al. (1981).

RESULTS

Morphologically identical proplastids occuring in the cells of the basal leaf zone are precursors of chloroplasts in mesophyll and in cells adjoining vascular bundles, as well as of plastids in the vascular tissue of *Clivia miniata* leaves. The first noticeable stage of their differentiation is the appearance of starch grains. Further changes in the development of these proplastids are different in different tissues.

MESOPHYLL CELL CHLOROPLASTS

In proplastids, the precursors of mesophyll chloroplasts, there occur prolamellar bodies of a regular structure of crystalline lattice (Fig. 1). The electron-transparent stroma of proplastids contains fine granulations and a grain of starch. In older cells of the basal leaf zone, the proplastids become greater, while the stroma becomes dense. The prolamellar body is used in the formation of thylakoids. The grain of starch disappears and osmiophilic droplets are to be seen within the stroma (Fig. 2).

An abrupt and intensive development of thylakoids marks the plastids of the middle leaf zone. The appearing stacks of grana thylakoids are arranged in different directions in relation to the longitudinal axis of the chloroplasts. The irregular arrangement of grana is a characteristic feature of mesophyll cell chloroplasts in leaves of *Clivia miniata* (Fig. 3). Fragments of prolamellar bodies persist for a long period of time and may be seen even in mature chloroplasts.

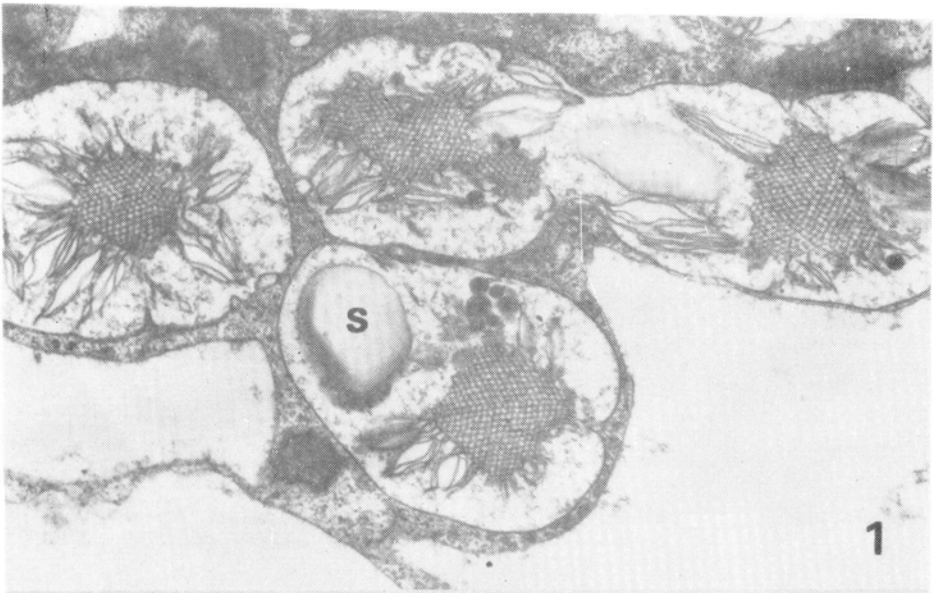
Within the differentiated mesophyll cells of the apical leaf zone, the fully developed chloroplasts contain a rich internal thylakoid membrane system embedded in the reduced stroma (Figs. 4, 5). The grana are numerous, of various heights, composed of several, occasionally even up to 100 thylakoids. These high grana occupy the whole thickness of the chloroplast. At a very early stage, i.e., at the stage of advanced development of proplastids, the plastids of mesophyll cells of *Clivia miniata* leaves lose the ability to accumulate starch; this ability is not restored even after reaching maturity. In the stroma of these plastids there appear osmiophilic droplets, the number and the size of which increases gradually while the chloroplasts develop (Fig. 5). Such inclusions occur already at early stages in the development of plastids (Fig. 2) and they are present throughout the whole process of differentiation and functioning of chloroplasts. The differentiated chloroplasts have sometimes irregular contours. For example, the protrusion caused by the presence of lipid droplets situated below the plastids surface (Fig. 6) or the invagination due to the liberation of the inclusion may be observed. Different sizes of the inclusions may be the evidence of their continuous formation during the differentiation of chloroplast. Occasionally, the membrane surrounding the inclusion is observed (Figs. 8, 9). Sporadically, as it is seen in Fig. 9, the enclosing membrane makes a contact with the thylakoids membrane. The content of the inclusion is homogenous and of different electron density (Figs. 5, 7).

CHLOROPLASTS OF PARENCHYMATEOUS CELLS ADJOINING VASCULAR BUNDLES

In the older part of the basal leaf zone of the cells adjoining vascular bundles, proplastids become greater; within the lucent and electron--transparent stroma there occurs a prolamellar body composed of vesicles. In the central part of plastids, large starch grains are localized (Fig. 10). Successive phase of the differentiation of these plastids leads to the formation of grana and stroma thylakoids, situated in the peripheral parts of plastids surrounding one or several grains of starch (Fig. 11). Developed chloroplasts of the cells surrounding vascular bundles are characterized by the presence of well-distinguished grana and stroma thylakoids. The height of grana is even; they are generally formed of a dozen or so thylakoids (Fig. 12). In the vicinity of the surrounding membrane, the vesicles filled with electron-transparent content are observed (Figs. 11, 12). These chloroplasts throughout the whole ontogenetic development retain the ability to accumulate starch. In the chloroplasts, the osmiophilic inclusions, so characteristic of the mesophyll cell chloroplasts, do not appear.

PLASTIDS OF VASCULAR TISSUE

Small parenchymateous cells occuring in the vascular parts of the bundles and adjoining them also contain chloroplasts which differ from



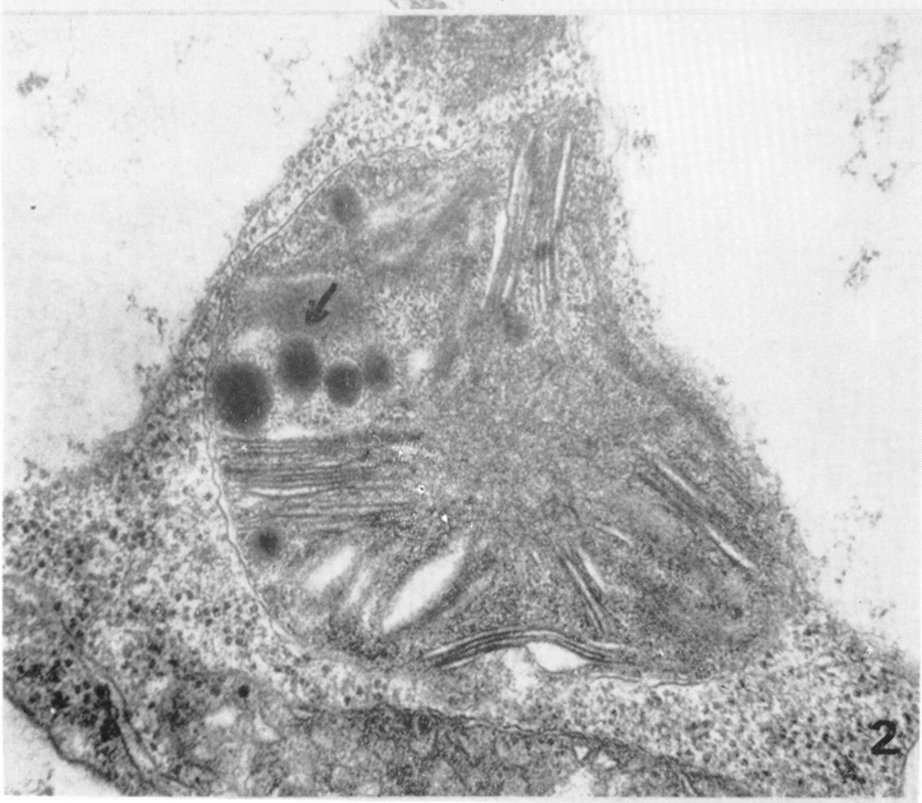


Fig. 1. Plastids in mesophyll of the basal zone of *Clivia miniata* leaves, showing crystalline prolamellar bodies and starch grains (s). × 17 600; Fig. 2. Plastid of an older mesophyll of the basal zone of *Clivia miniata* leaves. Prolamellar body after dispersion, visible lipid inclusions — arrow. × 35 000

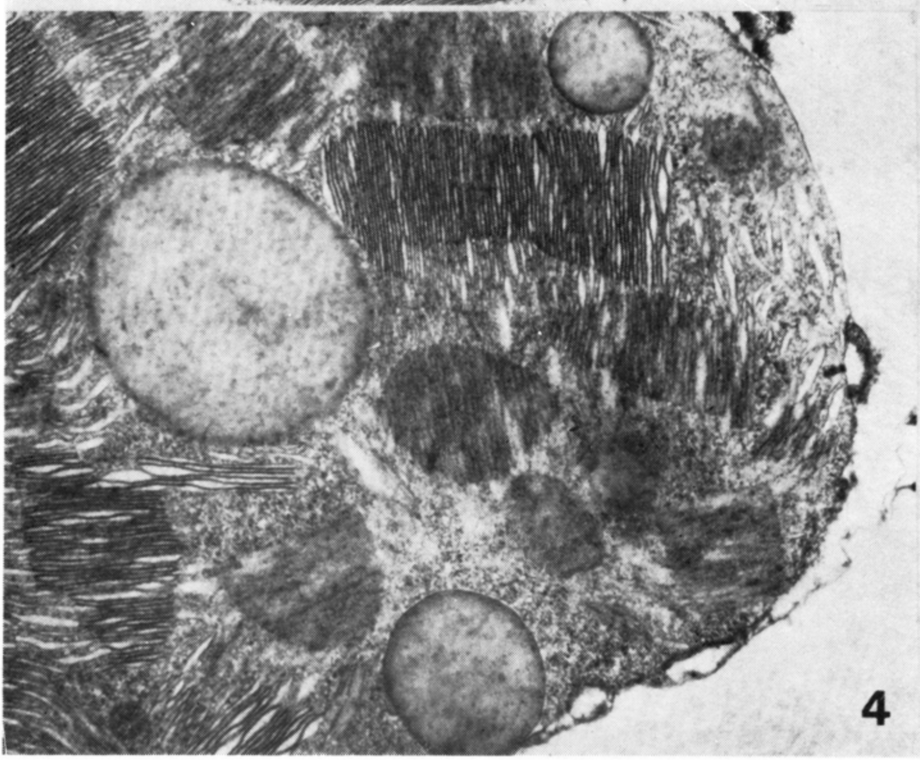
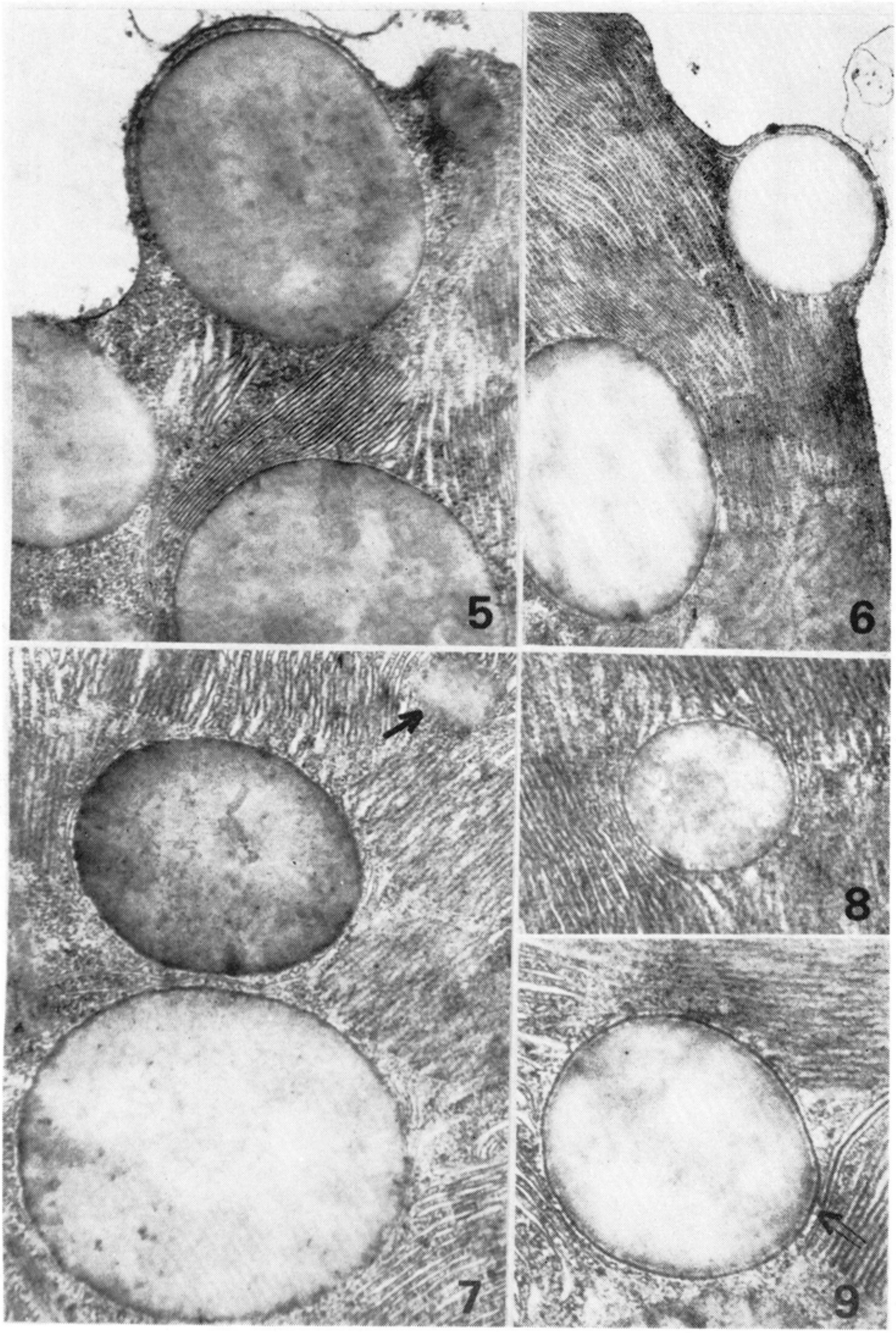
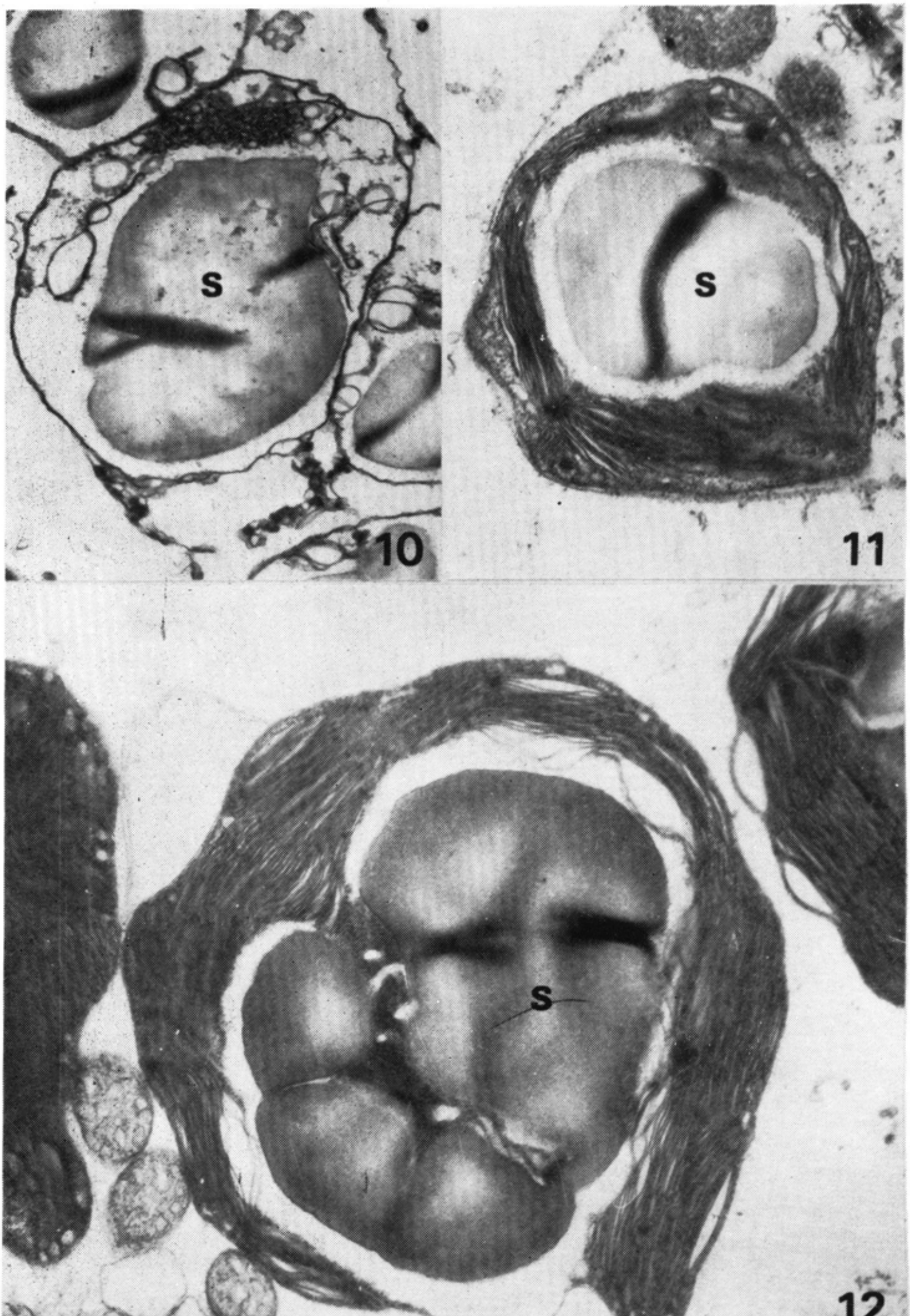


Fig. 3. Young chloroplast in the mesophyll of the middle leaf zone in *Clivia miniata* showing an irregular arrangement of grana. × 16 200; Fig. 4. Fragment of mature mesophyll chloroplast of *Clivia miniata* leaves with osmiophilic droplets. × 20 500



Figs. 5-9. Fragments of mature mesophyll chloroplasts of *Clivia miniata* with numerous osmiophilic inclusions. Visible protrusions of stroma are caused by the presence of lipid droplets (Fig. 5 — × 20 500; Fig. 6 — × 16 000) and newly formed lipid inclusions (Fig. 7 — single arrow, × 20 000); lipid droplets with a surrounding membrane (Fig. 8 — × 20 000; Fig. 9 — × 40 000). The connection of surrounding membrane with thylakoid membrane (double arrow)



Figs. 10-12. Plastids of cells surrounding vascular bundles in *Clivia miniata* leaves; s — starch grains. Fig. 10 — early stage of differentiation; plastid with vesicular prolamellar body, $\times$ 14 000. Fig. 11 — young chloroplast with appearing grana, $\times$ 14 000. Fig. 12 — mature chloroplast with numerous grana and starch grains, $\times$ 16 000

both mesophyll chloroplasts and the chloroplasts of the cells adjoining the bundles. These chloroplasts, considerably smaller than the chloroplasts described above, are lens-shaped and sometimes elongated. Some of them separate parts of plastids at one end (Fig. 16). It has not been possible to further trace these fragments. The chloroplasts are arranged with their long axes parallel to the long axis of the cell. The stroma is faintly granular and moderately electron dense. The system of inner membranes occupies the interior of plastids. The layer of stroma devoid of membranes is situated between the surrounding membranes and the thylakoids. Some thylakoids are swollen. These plastids do not accumulate either starch or osmiophilic inclusions and contain typical plastoglobules (Fig. 17). The ultrastructural features of these organelles suggest, that they are inhibited in the development.

The plastids in sieve tubes are spherical, ovoid or amoeboid. Plastids in very young sieve tubes have a moderately electron dense matrix (Fig. 12). As the sieve tube differentiation progresses, the matrix of the plastids becomes more electron lucent (Fig. 13). The plastids in sieve tubes of *Clivia miniata* leaves are of the P-type containing cuneate crystaloids (Figs. 12, 13). These cuneate inclusions have no surrounding membrane. Within the accompanying cells adjoining the sieve tubes, there occur plastids of different structure. They are oval and elongated. The stroma is lucent, electron-transparent and contains numerous vesicles and, occasionally, membraneous fragments and simple grains of starch (Fig. 15).

DISCUSSION

Similarly as in leaves of *Atropa belladonna* L. (Casadoro and Rascio 1977) and of *Helianthus annuus* L. (Casadoro and Rascio 1979), in *Clivia miniata* a gradient of cellular differentiation is observed from the basal to the apical part of the leaf, accompanied by the gradient of plastid differentiation. In each zone along the leaf axis, the degree of plastid differentiation in a particular tissue is very similar. In the apical leaf zone, the plastids reach the final stage of their inner organization. The cross section of leaf blade shows: the upper and lower epidermis, mesophyll and vascular bundles which contain different types of plastids characteristic of these tissues. In the upper and lower epidermis of the differentiated leaf zone, there occur proteoplasts (Mikulska et al. 1981) and in mesophyll — dimorphic chloroplasts and other types of plastids typical for the vascular tissue. Chloroplasts of mesophyll cells and of the cells adjoining vascular bundles differ in the ultrastructure and type of accumulated inclusions. These differences exist not only in the stage of mature chloroplasts but are evident already at the beginning of ontogenesis. Prolamellar body in the plastids of mesophyll cells constitutes a regular paracrystalline structure, whereas the prolamellar body of plastids in the cells adjoining the bundle is of vesicular character. Similar differences in the structure of prolamellar body were observed by Klein et al. (1975) in etioplasts of mesophyll and bundle sheath cells in *Zea mays*.

Prolamellar bodies of the plastids in the mesophyll of *Clivia miniata* leaves often persist even in differentiated chloroplasts. This phenomenon indicates that the presence of such a structure is not caused by the light factor but is a normal stage of chloroplast ontogenesis. This has already been postulated in our previous papers (Mikulska 1964, Damsz 1978). Rascio et al. (1976) claim that "prolamellar body formation and dispersal seems therefore to be under the direct regulation by the metabolic status of the cytoplasm" as well as that the presence of prolamellar body is related to cell age (Rascio et al. 1980).

The development of grana and intergrana thylakoids in chloroplasts of *Clivia miniata* mesophyll is very intensive and takes place mainly in the middle part of the long axis of the leaf. The stacks of grana thylakoids are arranged very irregularly and the height of grana is considerably differentiated. Chloroplasts of cells adjoining vascular bundles contain lower grana with their heigths less differentiated and they are arranged more regularly as compared to chloroplasts of mesophyll cells. Numerous authors report ultrastructurally differing chloroplasts of mesophyll and of the sheath cells of C_4 plants (Hodge et al. 1955, Bisalputra et al. 1969, Laetsch and Price 1969, Laetsch 1974, Kanai and Kashiwagi 1975, Miyake and Maeda 1978). Whatley (1979) points out the differences in structures of chloroplasts in various cells of primary leaves in *Phaseolus vulgaris*. The differentiating chloroplasts of mesophyll in *Clivia* leaves lose starch grains at early developmental stages and do not resume the ability to accumulate starch during later periods of ontogenesis. On the other hand, chloroplasts of the cells surrounding vascular bundle accumulate exclusively grains of starch. Sarda et al. (1975) describe the polymorphism of chloroplasts in *Bryophyllum* leaves, manifesting itself in different amounts of accumulated starch and its varying resistance to darkness. Khudairi (1977) distinguishes three types of chloroplasts in leaves on the basis of different contents of starch. Shomer-Ilan et al. (1975) indicate different number of starch grains in chloroplasts of *Suaeda* leaf mesophyll. Carmi and Shomer (1979) emphasizes that the accumulation of starch is greater in chloroplasts of spongeous cells than in chloroplasts palisade cells of *Phaseolus vulgaris* primary leaves.

The chloropiasts of *Clivia miniata* mesophyll accumulate osmiophilic inclusions from the very early developmental stages. Previous investigations (Mikulska 1960) prove that in the early stages of plastid development, these inclusions contain neutral lipids and in older chloroplasts the inclusions indicate also positive reactions for neutral lipids, fatty acids and phospholipids. Tritiated palmitic acid incorporation indicates that the synthesis of this material takes place within the chloroplasts (Olszewska and Mikulska 1967). These inclusions are always localized in the stroma in the vicinity of areas containing DNA (Mikulska et al. 1974). A single membranes is to be seen around some inclusions. Simola (1973) and Toyama (1980) describe the presence of a single membrane limiting osmiophilic plastoglobules. The appearance and the development of lipid droplets within chloroplasts of *Clivia miniata* leaves is not accompanied by the degeneration of thylakoids. The opinion prevails in literature that the development of plastoglobules is indicative of the degeneration or senescence of chloroplasts. It is accepted that the formation of a greater number of plastoglobules is accompanied by a destruction of thylakoid membranes (Lichtenthaler and Sprey 1966, Lichtenthaler 1969, Toyama 1980).

Damsz (1978) observed the appearance of lipid droplets in the chloroplasts of leaves of some orchids occurring usually after the disappearance of starch grains. According to this author, the phenomenon may indicate the functional polymorphism of chloroplasts. Simpson and Lee (1976), however, observed simultaneous occurence of starch grains and lipid inclusions in chloroplasts.

Another type of chloroplasts in *Clivia miniata* leaves occurs in small parenchymateous cells of the vascular part of the bundle. These chloroplasts are smaller than mesophyll chloroplasts and the chloroplasts of the cells surrounding bundles, show a poorely developed system of thylakoids. They are not able to accumulate either starch grains or lipid droplets. Typical plastoglobules are found within the stroma of these chloroplasts. Similar plastids with reduced or residual lamellae have been observed by Miyake and Maeda (1976a) in the xylem parenchyma of rice leaves.

The sieve tube members in leaves of *Clivia miniata* contain plastids with cuneate crystalline inclusions. Basing upon the studies of Behnke (1975), these plastids have been included in the P-type category. The presence of cuneate crystalline inclusions in the sieve tube plastids is characteristic of monocotyledonous plants (Behnke 1969, 1973). Cells adjoining the sieve tubes, which due to the dense cytoplasm are considered to be the accompanying cells, contain plastids devoid of thylakoids but containing starch grains. According to Esau (1978), a criterion for the differentiation of accompanying cells is the lack of starch in plastids. The author claims that "the cells however are capable of forming starch and do so under some conditions".

On the basis of the present observations it may be supposed that developmental sequence of plastids and the type of plastids in leaves is dependent upon the degree of cellular differentiation, the type of cell, the function it performs and the localization of the cell in leaf blade. The precursors of these different types of plastids, being sometimes very complex in their structure, and performing various functions, are morphologically similar proplastids characterized by a very simple structure. Laetsch and Price (1969) and Brangeon (1973) claim that mesophyll plastids and the plastids of the bundle-sheath cells originate probably from the same proplastid population and that they represent different phenotypic expressions of a common genotype.

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Polimorfizm strukturalny i funkcjonalny plastydów liści Clivia miniata Rgl. II. Ontogeneza plastydów komórek mezofilu i plastydów komórek otaczających wiązki waskularne

Streszczenie

W komórkach mezofilu i w komórkach przywiązkowych liści *Clivia miniata* Rgl. znajdują się różne, pod względem struktury i rodzaju akumulowanych substancji, chloroplasty. Chloroplasty komórek mezofilu posiadają bardzo dobrze rozwinięty system tylakoidów granowych i międzygranowych; w stromie gromadzą wyłącznie inkluzje o charakterze lipidowym. Chloroplasty komórek mezofilu, ze słabiej rozwiniętym systemem membran wewnętrznych, zdolne są jedynie do gromadzenia dużej liczby ziaren skrobi. Trzeci typ chloroplastów znajduje się w komórkach miękiszowych części naczyniowej wiązek waskularnych. Chloroplasty te znacznie mniejsze od opisanych powyżej, mają zredukowany system membran wewnętrznych i nie są zdolne do gromadzenia skrobi, ani kropli lipidowych; w stromie znajdują się tylko plastoglobule. Prekursorami tych różnorodnych typów chloroplastów są prawdopodobnie jednakowe morfologicznie proplastydy, których sekwencja rozwojowa zdeterminowana jest stopniem zróżnicowania komórki, rodzajem komórki, a także pełnioną przez nią funkcją.