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Aggregations of organelles in meiotic cells of higher plants

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Abstract

During early prophase I in microsporocytes and sporocytes of various plants all mitochondria and plastids aggregate in a group, where some plastids seem to undergo division. This group desintegrates by middle prophase I. Further aggregations of plastids and mitochondria occur in microsporogenesis and sporogenesis is of a simultaneous type. Organelles aggregate the second time at the end of prophase I and during or after telophase I they form a dense equatorial plate which lasts until telophase II. Since the phragmoplast is dismantled after telophase I and there is no cytokinesis, organelles aggregated in the plate apparently prevent merging of the nuclei and spindles of meiosis II, thus taking over a role of a phragmoplast and cell wall. In some plants after telophase II organelle aggregation changes shape and occupies the planes where cell walls will be built in simultaneous cytokinesis. Positioning of plastids and mitochondria along these planes may facilitate their equal apportionment among the postmeiotic cells.

Key words: organelles in meiocytes, mitochondria, plastids, microsporogenesis, sporogenesis

INTRODUCTION

Regular rearrangement of cytoplasmic organelles in the cells undergoing meiosis in sporogenesis and microsporogenesis and also during mitosis have been described since the turn of the century. It was assumed that moving organelles may follow some patterns of grouping and regrouping. Several patterns of this movement, called then chondriokinesis, were presented by Bąkowski (1938). Interest in the problem seems to have dimished in the thirties after extensive investigations made by Py (1932) under the auspices of the eminent French plant cytologist Guiliermond, who was interested in ontogenetic and developmental relationship between plastids and mitochondria rather than in their movements in the cell. In her work Py was unable to

find any regular organelle groupings, which implied baselessness of different descriptions of chondriokinesis.

Only since the sixties papers began to appear which were showing that during microsporogenesis cytoplasmic organelles, mainly plastids and mitochondria, form aggregations in certain periods of meiosis (ref. Rodkiewicz et al. 1985, Sheffield and Bell 1987). Therefore we may assume that at least in some higher plants there exist regular patterns of organelle behaviour. During sporogenesis and microsporogenesis of a simultaneous type we can distinguish two cycles of aggregation and disaggregation, one in early prophase I and the second in telophase I, or even late prophase I to telophase II. Presumably at least the second cycle of aggregation occurs in megasporogenesis of some ferns, characteristic by formation of tetrahedral megaspore tetrad (Bell 1981).

There is very little information how organelles change their place in microsporogenesis of successive type; it seems that mitochondria and plastids form only an early prophase I aggregation. This aggregation confers on the microsporocyte, in both types of sporogenesis, highly polarised appearance, which, however, disappears after organelles become scattered.

Similar aggregation was also described in orchid megasporogenesis where at early prophase I all plastids and mitochondria group in the micropylar part of meiocyte (Rodkiewicz and Stobiecka 1978, Bednara et al. 1981). The group disperses but the megasporocyte continues development as a polarized unit, since in megasporogenesis there are some more symptoms of polarization presented in reviews (Rodkiewicz 1978, Willemse and Bednara 1979, Willemse and De Boer-de Jeu 1981, Willemse 1982, Noher de Halac and Harte 1985, Fougère-Rifot 1987).

Quite different is megasporogenesis in *Onagraceae* where plastids form two constant aggregations at the apices of elongated prophase I megasporocyte, while mitochondria remain scattered. The aggregations last until the formation of linear tetrads, finally only two megaspores, micropylar and chalazal, contain plastids, which influences further development of megaspores (Jalouzot 1971, Rodkiewicz and Bednara 1974, Rodkiewicz et al. 1976, Śnieżko 1984, Śnieżko and Harte 1984a, b, 1986).

During prophase I in some gymnosperm megasporocytes organelles are moved into chalazal apex and are only, or mainly, transmitted to functional megaspores (Stewart and Gifford 1967, Fiordi and Mangini 1977).

PROPHASE I IN SPOROGENESIS AND MICROSPOROGENESIS

Plastids and mitochondria in microsporocytes and sporocytes of several species were described to form aggregations at certain points from early to middle prophase I. The aggregations occur in both simultaneous and succes-

sive types of spore and microspore development in plants belonging to *Pteridophyta*, gymnosperms and angiosperms.

First descriptions of regular organelle aggregations in prophase I meiocytes were made by the beginning of the century (Marquette 1907, 1908) and later by several other authors. The aggregated organelles were referred to as plastids and mitochondria, mitochondria or cytoplasmic granules. They were grouped at one side of meiocyte, which might have been slightly elongated, with the nucleus shifted towards the other side. The aggregation occured at some time during the leptotene-zygotene period; very often concurrently with a bouquet (or syniezis) stage of chromosomes lying together in one group.

Such or basically similar arrangements of organelles were seen by light microscopists in: sporocytes of several species of *Equisetum* (Marquette 1907, Lewitsky 1926, Jungers 1934), (though Lenoir (1934) could not confirm all their descriptions), in *Marsilia quadrifolia* (Marquette 1908), in microsporocytes of *Tetraclinis articulata* (Saxton 1913) and *Aucuba japonica* (Yu 1938 after Bąkowski 1938). Some authors drew the aggregation without, however, mentioning it in the text, like in a microsporocyte at the bouquet stage of *Gentiana lutea* (Wójcicki 1932).

Later, groups of aggregated organelles were also seen by means of electron microscopy in microsporocytes of *Ribes rubrum* (Genevès 1967, 1971). The group consisting almost exclusively of proplastids was positioned at one side of the nucleus, on its opposite side there was a group of mitochondria. In *Ceratozamia mexicana* microsporocyte proplastids were grouped at one side of the nucleus whereas mitochondria were scattered on the other side (Audran 1979). Slightly different disposition of plastids and mitochondria was noticed in microsporocytes of *Stangeria eriopus* (Rodkiewicz et al. 1988a, b, c) and *Nymphaea alba* (Rodkiewicz et al. 1988a, b). There all plastids and mitochondria were grouped at one side of the nucleus while the remaining mitochondria were scattered around the nucleus.

Separate groups of plastids and mitochondria were seen in sporocytes of *Equisetum hiemale* v. *japonicum* at a bouquet stage (Hiraoka 1986). Plastids together with mitochondria were grouped in the middle prophase I sporocytes of *Pteridium aquilinum* (Sheffield 1978) and somewhat earlier in sporocytes of *Polystichum lonhitis* (Bednara and Rodkiewicz 1988), in early prophase I microsporocytes of *Pinus silvestris* (Walles and Rowley 1982), *Stangeria eriopus* (Rodkiewicz et al. 1988a, b), *Larix europea* (Bednara and Rodkiewicz 1988). These somewhat differing descriptions, as we assume, present various stages of plastids and mitochondria aggregating and disaggregating during the time from early to middle prophase I (Fig. 1 a-e).

It was easy to follow in the light microscope positions of plastids containing starch grains during entire meiosis or a part of it. Such plastids, after staining of starch, were visible in simple squash preparations of *Equisetum* sporangia (Bednara et al. 1986), microsporangia or anthers of

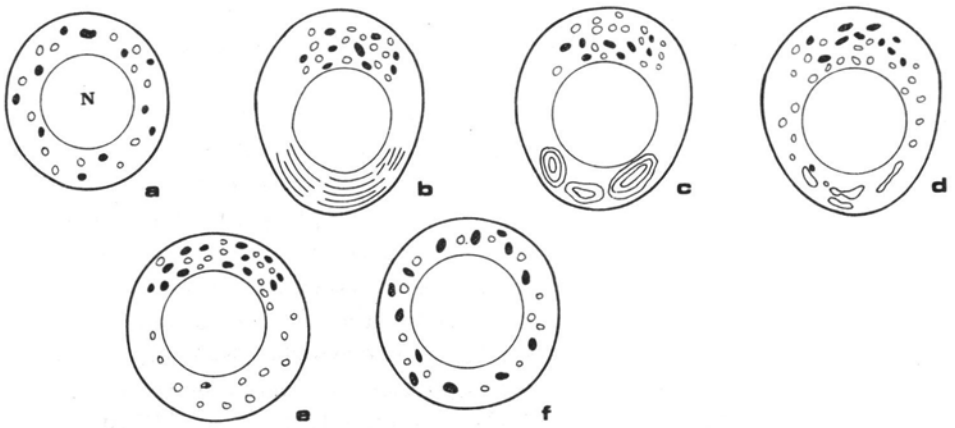

Fig. 1. Plastids (black) and mitochondria in a microsporocyte or sporocyte during early to middle prophase I. The assumed sequence was envisaged by piecing together data on stages which were observed in different species: a – Plastids and mitochondria around the nucleus entering prophase I. b – Group of both kinds of organelles and stacks of ER cisternae (seen in *Stangeria* and *Larix*). c – ER cisternae in circular arrangements. d – Group of plastids and mitochondria, some mitochondria outside the group. Systems of ER greatly reduced (in *Stangeria* and *Polystichum*). e – Group of plastids and mitochondria, some mitochondria around the nucleus, mostly on the opposite side: ER systems disappeared. f – Organelles around the nucleus

Stangeria (Rodkiewicz et al. 1986), *Tradescantia* and *Impatiens* (Rodkiewicz et al. 1985, 1986), *Larix* (Bednara and Rodkiewicz 1988) and *Nymphaea* (Rodkiewicz et al. 1988d). By comparing positions of plastids in light microscope preparations with electron microscope preparations we may conclude that in some stages both kinds of organelles are gathered together (Fig. 1b, c) and in some stages their positions do not coincide (Fig. 1e).

From the data on microsporogenesis and sporogenesis we may assume that during late leptotene or zygotene the organelles aggregate at one side of the nucleus which usually is slightly shifted from the centre of the cell. In *Larix, Polystichum* and *Stangeria* the group consists of all or almost all plastids and mitochondria, sometimes it also contains small ER (endoplasmic reticulum) elements, vesicles and in *Nymphaea* there are some osmiophilic bodies. These additional components seem to be accidental since they are present in greater number outside the organelle group, but not always in the group itself. At this stage ER cisternae form a parallel array on the opposite side of the nucleus in microsporocytes of *Stangeria* (Fig. 6) and *Larix* (Bednara and Rodkiewicz 1988). In *Stangeria* microsporocytes the parallel arrangements of cisternae gradually change into concentric (Rodkiewicz et al. 1988d).

Concentrically arranged ER cisternae were also described in microsporocytes of *Ceratozamia* (Audran 1979), *Lilium henryi* (Dickinson and Heslop-Harrison 1977, Dickinson 1981), *Pinus silvestris* (Rowley and

Walles 1985a, b). They were related to hydrolysis of portions of cytoplasm which might have brought about a loss of optical density characteristic for early meiosis. The authors, however, give no evidence on position of these ER bound areas.

Cisternae in concentric arrays extend and are transformed into vacuoles or vesicles, the arrays then disappear completely; we may assume that this stage of development is represented by a sporocyte of *Polystichum* (Bednara and Rodkiewicz 1988) in which areas of aggregated organelles and vesicular or vacuolated cytoplasm are situated at the opposite sides of the nucleus. The organelle aggregation begins to disperse concurrently with ER vesiculation. In microsporocytes of *Stangeria* and *Nymphaea* some mitochondria begin to leave the aggregation and become scattered around the nucleus (Fig. 1e). We may assume that mitochondria are first to be removed from the organelle aggregation and separate groups of both kinds of organelles are present as described in *Equisetum* (Hiraoka 1986) or in *Ribes* (Genevès 1967). Finally all organelles are scattered more or less evenly throughout cytoplasm (Fig. 1a-f).

There is no explanation of plastids and mitochondria gathering in one group which confers to the relatively early prophase I meiocyte a polarized appearance (Figs. 6 and 7), It is only suggested that the organelle aggregation is related with plastid divisions (Rodkiewicz et al. 1988b). Such divisions may take place since constricted plastids, commonly believed as being in the course of division, are often present in organelle aggregations (Fig. 8). Some other facts support this assumption. There is no doubt that during prophase I a single plastid in moss sporocytes undergoes division two times (Brown and Lemmon 1982a, b, further references in Birky 1983). Each of four resulting plastids is inherited by one of four spores in a tetrad. In certain tissues or unicellular plants mitotic prophase is also a time of plastid divisions. In prophase I microsporocyte of *Lilium henryi* cytoplasmic DNA of plastids and mitochondria incorporates a large amount of labeled (^{3}H)thymidine. It is suggested that this synthesis of DNA may precede divisions of organelles (Smyth and Shaw 1979). Dickinson and Heslop-Harrison (1970) describe plastids grouped during the tetrad stage in *Lilium longiflorum* microsporogenesis and suggest that some division of plastids appears to take place there.

LATE PROPHASE I ORGANELLE GROUPING

In some plants scattered mitochondria and plastids are gathering again by the end of prophase I. The regular groupings of organelles were described in sporocytes and microsporocytes which by the end of meiosis undergo synchronous cytokinesis. In such meiotic cells of *Equisetum* (Bednara and

Rodkiewicz 1985), *Onoclea sensibilis* (Marengo 1977), *Stangeria* (Rodkiewicz et al. 1988b) and *Impatiens balsamina* (Rodkiewicz et al. 1986) plastids and mitochondria are grouped at the opposite sides of the nucleus presumably by the enucleation sites. This supposition may be arrived at studying the position of organelle groups in early metaphase I; in *Stangeria* and particularly in *Equisetum* meiocytes distinct groups of organelles, corresponding to those in late prophase I, lie very close to the meiotic spindle apices (Fig. 2a-b).

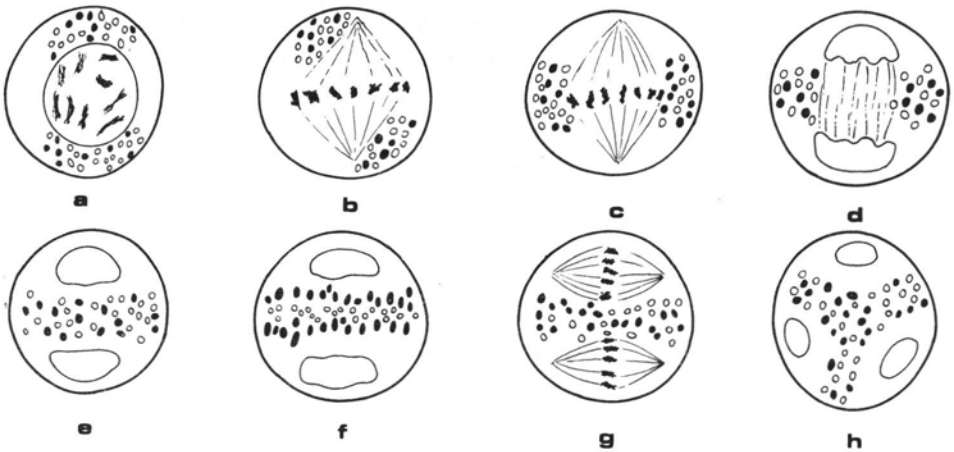

Fig. 2. Plastids and mitochondria, late prophase I to post-telophase II, in microsporogenesis or sporogenesis concluding by simultaneous cytokinesis. a — Late prophase I, groups of organelles at the opposite sides of the nucleus (seen in *Equisetum, Onoclea, Stangeria, Impatiens*). b — Metaphase I, organelles grouped at the apices of the spindle (in *Equisetum*). c — Metaphase I, organelles grouped at the level of chromosomes (in *Equisetum, Impatiens*, compare Fig. 9. of *Nymphaea* microsporocyte). d — Telophase I or post-telophase I, organelles invade the equatorial space. e — Late telophase I or post-telophase I, organelles aggregated in a form of a plate or a disk. Its thickness may differ in various species. f — Organelles segregated into three layers: plastids — mitochondria — plastids, for a short time during post-telophase period; before and after organelles are intermingled (in *Equisetum* and *Nymphaea*). g — Metaphase II, organelles separate the spindles. h — Post-telophase II, layers of organelles take place between four nuclei in tetrahedral arrangement (in *Equisetum, Impatiens, Nymphaea*)

Another kind of organelle disposition occurs in late prophase I microsporocytes of *Nymphaea*, where Guignard, already in 1898, noticed the formation of a large group of starch grains. In fact all plastids together with all mitochondria are just in one large aggregation which lies side by side with the nucleus (Fig. 4a). One group of apparently similar organelles is formed in sporocytes of *Marsilia quadrifolia* (Marquette 1908) and somewhat different grouping is present in microsporocytes of *Petunia violaceae* (Matsuda 1928).

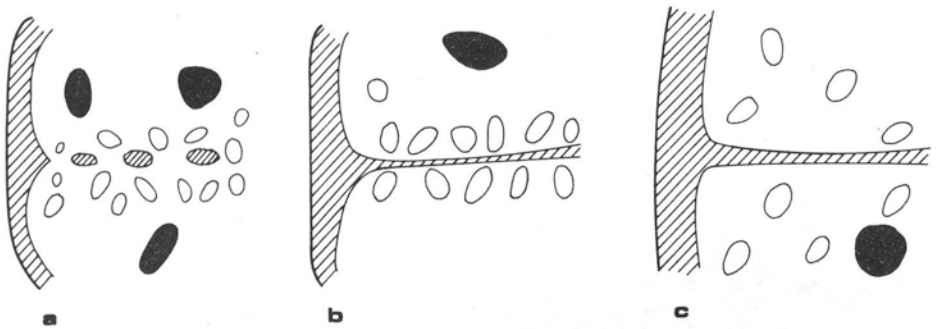

Fig. 3. *Equisetum hyemale*, formation of a cell plate between the spores of a tetrad. a — Rows of mitochondria with incipient cell plate vesicles. b — Continuous cell plate bordered by mitochondria, plastids shown black. c — Mitochondria moved from a peripherial position

The third quite different kind of grouping is formed by organelles in late prophase I microsporocytes of *Malva silvestris* (Rodkiewicz et al. 1988d) and *Lavatera trimestris*. The organelles gather in a dense layer around the nucleus (Fig. 5a). This coating of the nucleus was described by several authors, though some considered it a fixation artefact (ref. Bąkowski 1938).

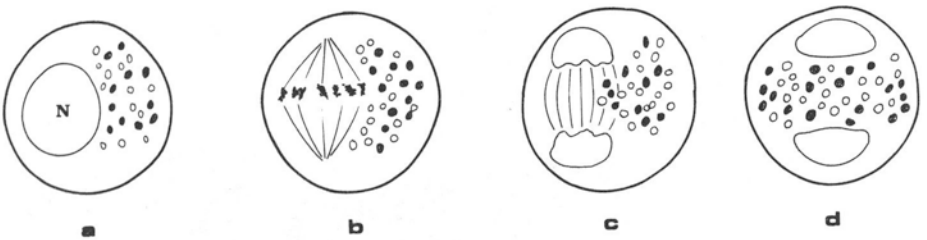

Fig. 4. Microsporogenesis in *Nymphaea alba*. a — Late prophase I, aggregated mitochondria and plastids (black) adjacent to the nucleus. b — Metaphase I, one group of organelles along the spindle (also in Fig. 9). c — Telophase I, organelles moving into the equatorial space. d — Post-telophase I, equatorial arrangement of organelles (also in Fig. 10)

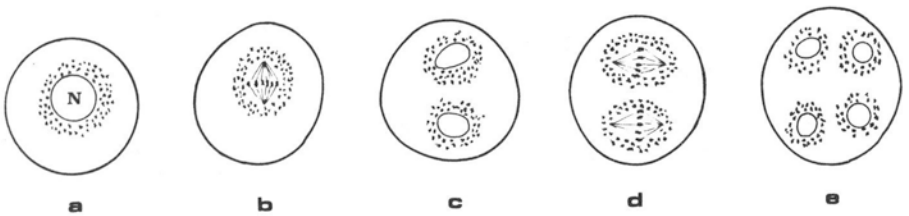

Fig. 5. Microsporogenesis in *Malva silvestris*. a — Late prophase I, dense layer of organelles around the nucleus. b — Metaphase I inside the area coated by a dense layer. c — Post-telophase I. d — Metaphase II. e — A tetrad of nuclei before simultaneous cytokinesis

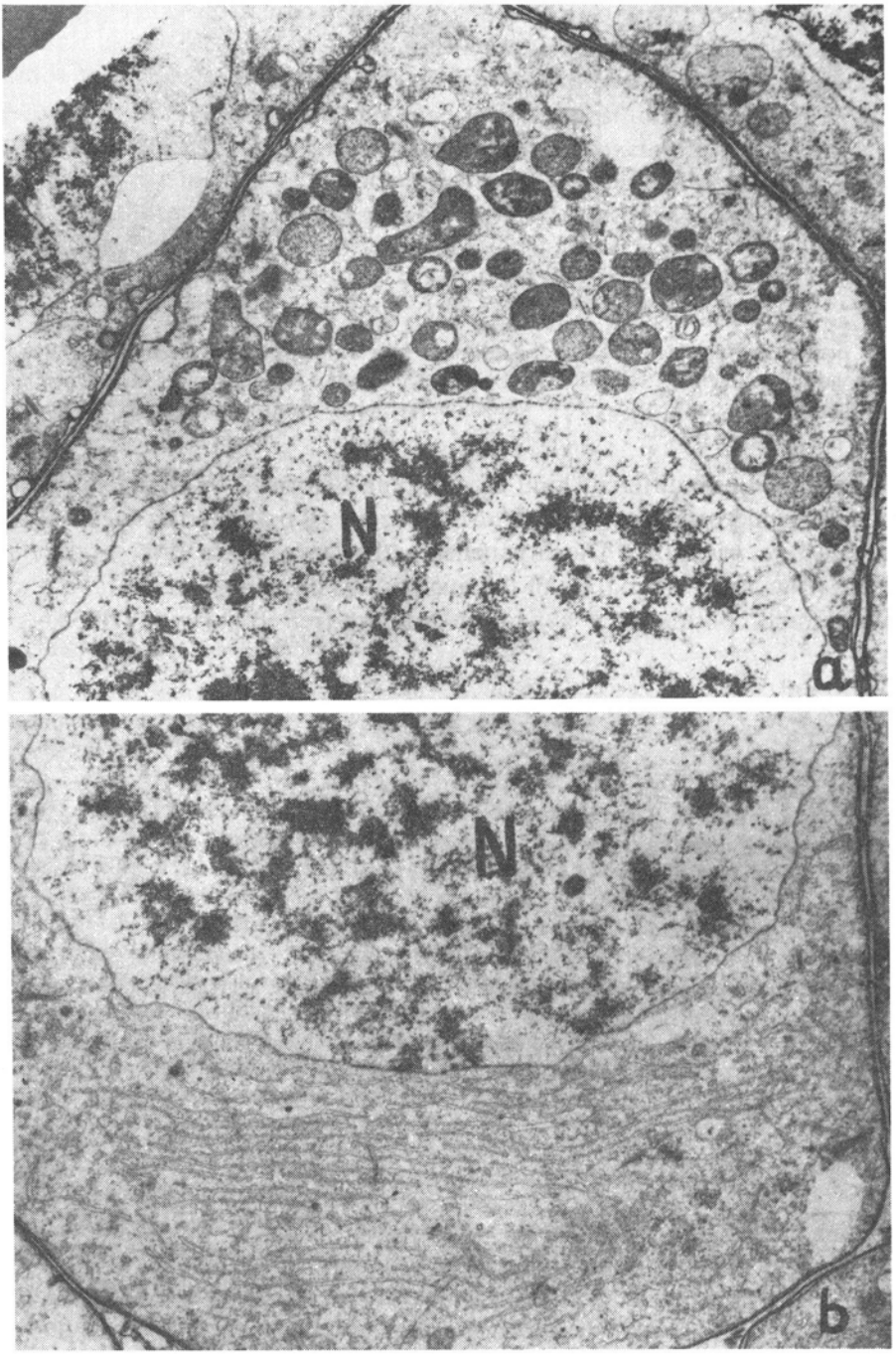

Fig. 6. Early prophase I microsporocyte of *Stangeria eriopus*, × 4000. a — Part of nucleus and aggregation of plastids and mitochondria. b — Part of nucleus and ER cisternae. See Fig. 7

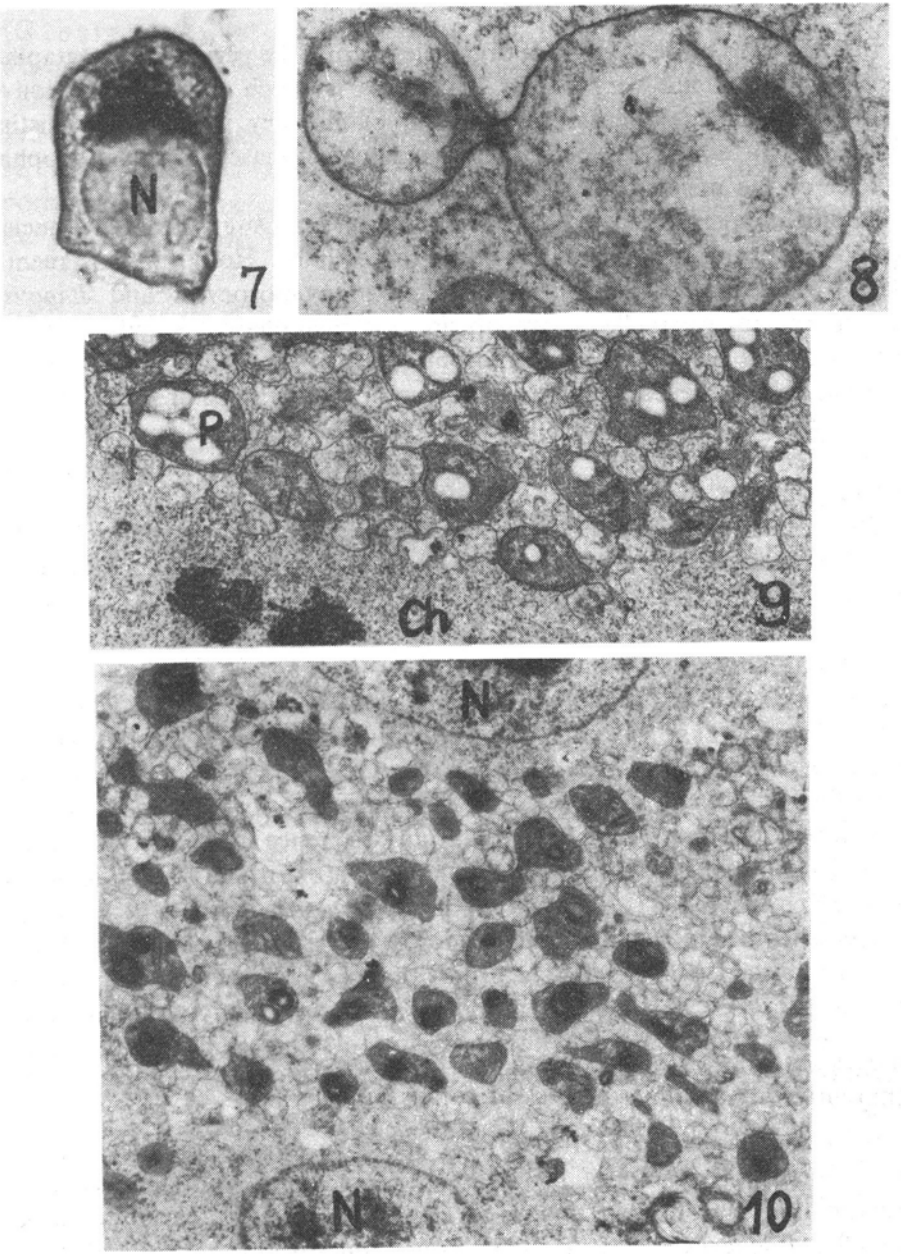

Fig. 7. Early prophase I *Stangeria eriopus* meiocyte. Group of plastids after staining of starch (PAS). Fig. 8. Constricted plastid in microsporocyte of *Stangeria,* × 20000.
Fig. 9. Metaphase I in *Nymphaea alba* microsporocyte, Ch — chromosomes, P — plastids and mitochondria, × 5000. Fig. 10. Microsporocyte of *Nymphaea alba* after telophase 1, equatorial aggregation of plastids (dark) and mitochondria (light), N — nucleus, × 4000

FORMATION OF AN EQUATORIAL ORGANELLE PLATE

Informations on behaviour of organelles during the period from metaphase I to telophase I are very scarce, but there is much more description of organelles in late telophase I. In several plants they form a very distinct aggregation in equatorial plane between late telophase I or post-telophase I nuclei of the meiocyte (Figs. 2e and 10).

Organelles aggregated by late prophase I on opposite sides of the nucleus are moved during metaphase I towards the equator. How this movement is carried out remains unresolved. In *Equisetum* sporocytes and *Impatiens* microsporocytes organelles move outside the metaphase I spindle and take position at the level of the chromosome plate (Figs. 2c, d). It is not clear wheather the organelles constitute there two or more groups or form a ring. By the end of telophase I organelles begin to move into the equatorial space, where after conclusion of telophase I they form a thick plate-like layer stretching across the cell (Figs. 2e, 10).

These equatorial plates are fairly easy to notice in the light microscope and were described in: sporocytes of *Equisetum palustre* (Lewitsky 1926) and *E. limosum* (Jungers 1934), *Nephridium molle* (Senjaninova 1927), *Adiantum hispidum* (Marengo 1962), in microsporocytes of *Stangeria paradoxa* (Audran 1964), *Ginkgo biloba* (Mann 1924), *Helleborus foetidus* (Nicolosi-Roncati 1910), *Tropaeolum perignum* (Sugiura 1928), *Chamaedorea Karvinskiana* (Suessenguth 1921). *Petunia violacea* (Matsuda 1928), *Lysimachia thyrsiflora* and *Clarkia elegans* (Rodkiewicz et al. 1986). In some papers the layer of organelles is shown in pictures as a strip of dense cytoplasm between post-telophase I nuclei, without any reference in the text which deals with microsporogenesis in *Elatina hydropiper* (Friesendahl 1927), *Empetrum nigrum* (Frejberg 1983), *Laurelia novae-zelandiae* (Sampson 1969). A similar layer is formed in *Nymphaea* microsporocytes by one organelle group set up at late prophase I (Fig. 4a-d). The group changes its shape gradually entering between telophase I nuclei. Such type of layer formation occurs also in sporocytes of *Marsilia quadrifolia* (Marquette 1908). Depicting the layer in microsporocytes of *Nymphaea alba* Guignard (1898) refers only to the starch grains.

By means of electron microscopy the organelle equatorial plates were seen first in microsporogenesis of *Ribes rubrum* (Genevès 1967). They consist of mitochondria, plastids and undefined elements called by the author special organelles (Genevès 1971). In telophase I microsporocytes of *Helleborus foetidus*, according to Echlin and Godwin (1968), mitochondria and plastids tend to be arranged parallel to the plance where cell division would be expected. Aggregated organelles were later seen in various plants. Mainly plastids and mitochondria form equatorial plates in: four species of *Equisetum* (Bednara and Rodkiewicz 1985, Bednara et al. 1986), *Onoclea sensibilis* (Marengo 1977), *Pteridium aquilinum* (Sheffield and Bell 1979), *Dryopteris*

borrei (Sheffield et al. 1983), *Psiliotum* (Lee 1982), *Psiliotum nudum* (Gabarayeva 1985), *Ginkgo biloba* (Wolniak 1976, Wang et al. 1988), *Paeonia tenuifolia* and *Campanula rapanculoides* (Dietrich 1973), *Impatiens balsamina* (Dupuis 1978), *Lycopersicon peruvianum* (Pacini and Juniper 1984), *Datura inoxia, Nicotiana tabacum* and *Antirrhinum majus* (Dupuis et al. 1988), *Solanum nigrum* (Bhandari and Sharma 1988). In microsporocytes of *Podocarpus macrophylla* a layer of spherosomes was diescribed in the equatorial plane (Vasil and Aldrich 1970).

The mitochondrial plate was described in meiocytes of *Polypodium aureum* (Marengo and Marengo 1972). Organelle equatorial plates in moss sporocytes are formed mainly by mitochondria together with some osmiophilic bodies, short ER cisternae and vesicles. Plastids do not participate in their formation being, already in prophase I, positioned at four poles of sporocyte (Brown and Lemmon 1982a, b, 1987a, b).

The post-telophase I plate of plastids and mitochondria is also formed in megasporocytes of ferns belonging to a small group of *Hydropterideae* (Bell 1981). Their megasporogensis is quite unusual because the megasporocyte after synchronous cytokinesis divides into four equal megaspores in tetrahedral arrangement. Such set up of postmeiotic cells is very common in microsporogenesis, but exceptional in megasporogenesis; megaspores are most often in linear or T-shaped tetrads.

Microsporogenesis, sporogenesis and in one example megasporogenesis of all these described plants is concluded by synchronous cytokinesis and tetrahedral tetrads. The equatorial plates were not reported in plants with sporogenesis or microsporogenesis of successive type, though in the space between telophase nuclei there is accumulation of mitochondria and plastids as in microsporocytes of *Tradescantia reflexa* (Sakai and Shigenaga 1964), *Tradescantia virginiana* (Rodkiewicz et al. 1985) and *Larix* (Trenin 1986, Bednara and Rodkiewicz 1988).

All or almost all mitochondria and plastids together with some other cytoplasmic elements of the cell are included into the equatorial plate (except in moss sporocytes). The organelles remain aggregated during interkinesis and the second meiotic division apparently withstanding the pressure of streaming cytoplasm and moving chromosomes, which may only slightly affect the shape of the organelle plate, like in a *Polystichum* sporocyte (Bednara and Rodkiewicz 1988). It is not known how in these circumstances the organelle plate keeps its integrity.

REARRANGEMENTS OF ORGANELLE PLATE

Plastids intermingled with mitochondria invade the equatorial space of telophase I meiocyte. In *Equisetum* after formation of a dense aggregation in a shape of a plate, organelles segregate into three distinct layers (Fig. 2f). The middle layer of mitochondria is coverd on both sides by layers of plastids

(Bednara and Rodkiewicz 1985). Similar though not so distinctly segregated organelle aggregation is present in microsporocytes of *Nymphaea* (Rodkiewicz et al. 1988c). At this stage in *Equisetum* elongated plastids and mitochondria of the aggregation are oriented along the microtubules of the phragmoplast stretching between the nuclei. The phragmoplast is not clearly visible since it may undergo decomposition. Later this orderly arrangement of organelles disappears and during at least of the most of the second meiotic division mitochondria are intermingled with plastids (Fig. 2g).

The organelle aggregation lasts to the conclusion of telophase II, as it was noted by many authors, and is dispersed during cytokinesis. In *Pyrola japonica* organelles occupy the center of four-nucleate microsporocyte (Takahashi and Sohuma 1980). In *Impatiens* (Rodkiewicz et al. 1986), *Equisetum* (Bednara et al. 1986) and *Nymphaea* (Rodkiewicz et al. 1988c). organelle aggregation changes its shape and partitions a cell into four mononucleate regions (Fig. 2h). The aggregated organelles seem to delineate the planes of future cell walls which will be set up in simultaneous cytokinesis.

The process was followed with some detail in *Equisetum hyemale* sporocytes. There originally intermingled mitochondria and plastids segregate, in a similar manner like after telophase I, into three layers, but plastids almost at once are moving off the layers into cytoplasm closer to the nuclei, while mitochondria remain in tight aggregation forming boundaries between differentiating spores. Apparently such layers of mitochondria were also described in *Equisetum fluviatilis* (Lehmann et al. 1984).

Along the middle of mitochondrial aggregation occurs a row of small vesicles (Fig. 3a). From the confluence of these vesicles a continuous cell plate arises. Each surface of the new cell plate is studed with numerous mitochondria, which a little later are shifted deeper into cytoplasm (Fig. 3b, c). A row of mitochondria along both sides of a cell plate (or a cell wall) between young megaspores in tetrahedral tetrad in *Marsilia vestita* were clearly shown by Bell (1981).

The equatorial organelle aggregation in *Gingko* microsporocytes does not change its shape after telophase II and undergoes about equal partitioning by simultaneous cytokinesis among four microspores (Wolniak 1976). Mitochondrial band (or equatorial aggregation) in moss sporocytes also remain in its original position after telophase II. The band is involved in formation of certain cell walls between the spores in a tetrad. These walls originate inside the mitochondrial band, other walls are built in the equatorial planes of phragmoplasts of the second meiotic division (Brown and Lemmon 1987b).

ORGANELLE COATS IN *MALVA* MICROSPOROCYTES

Organelles in microsporocytes of *Malva* and *Lavatera* (*Malvaceae*) behave quite differently than those in other described plants (Rodkiewicz et al. 1988d). The dense cytoplasmic coating of late prophase nucleus remains during

the next stages of meiosis I as a kind of envelope enclosing the area in which meiotic spindle is acting. After the first meiotic division, there is no cytokinesis, but each of resulting nuclei is again coated by a similar dense layer. Again inside the areas encircled by these layers both nuclear divisions are proceeding and finally each of four nuclei is coated by a similar layer (Fig. 5a-e). There is no information how the coating layers of mitochondria and plastids are divided and closed after nuclear divisions.

PHRAGMOPLAST, ORGANELLE AGGREGATION AND APPORTIONMENT

During telophase I an extensive microtubular phragmoplast is set up between the sister nuclei. It was particularly clearly shown by immunofluorescence technique in microsporocytes of angiosperms with synchronous cytokinesis (Van Lammeren 1985, Van Lammeren et al. 1985, Hogan 1987) and in sporocytes of mosses (Brown and Lemmon 1987a, b). Microtubules of phragmoplast may prevent the nuclei to become reunited and form a restitution nucleus, thus reversing the result of meiosis.

After telophase I there are two principal courses of further development: one characterized by successive cytokinesis, the other by simultaneous cytokinesis. In the first type of development phragmoplast disappears after telophase I, but meanwhile a callose cell plate is set up by cytokinetic mechanism. There is no cytokinesis after telophase I in the second type of development. The phragmoplast likewise disappears and its components apparently take part in formation of two spindles at the nuclei lying in common cytoplasm, but neither the nuclei nor spindles do not merge since they are separated by a massive plate of aggregated organelles (Rodkiewicz et al. 1985, Bednara et al. 1986).

The distribution of plastids and mitochondria at cell divisions appears to be on the whole approximately equal (Birky 1983, Hennis and Birky 1984). It may be assumed that nonrandom disposition of organelles after the second telophase facilitates their more or less equal apportionement among four cells. This was also supposed by the authors who observed telophase I – telophase II aggregation (Senjaninova 1927, Genevès 1967, 1971, Dietrich 1973, Wolniak 1976, Dupuis 1978). Genevès even wrote that organelles were as precisely distributed as chromosomes.

The fairly elaborate process of organelle rearrangements after telophase I in *Equisetum, Impatiens* and *Nymphaea* serves, assumingly, to equalize the number of plastids and mitochondria in spores or microspores and pollen grains. The pollen grain of angiosperms however, transmits, via a male gamete, to a zygote a very small portion of its mitochondria and usually no plastids. We may ascribe to this equalization process a role in a competition of pollen tubes which takes place in the style.

Selection of competing male gametophytes may bring about changes in

genetical structure of sporophyte populations (Mulcahy 1971, 1979, Mulcahy et al. 1975, Ottaviano et al. 1982), since a large part (about 60%) of structural genes expressed in germinating pollen and growing pollen tubes are also expressed in the sporophyte (Tanksley et al. 1981, Mascarenhas et al. 1985). By equalizing the number of mitochondria and plastids a similar cytoplasmic background is provided for all genomes and expressing of genetical differences is not influenced by variable numbers of organelles.

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Grupowanie się organelli w komórkach mejotycznych roślin wyższych

Streszczenie

Podczas wczesnej I profazy wszystkie mitochondria i plastydy mikrosporocytu lub sporocytu skupiają się w jedną grupę. Niektóre plastydy tej grupy dzielą się. W połowie I profazy grupa organelli jest już rozproszona. W mikrosporogenezie i sporogenezie typu równoczesnego organelle skupiają się znowu pod koniec I profazy. W niektórych gatunkach agregaty te pod koniec I telofazy tworzą równikowe płytki z gęsto ułożonych organelli. Taka płytka prawdopodobnie zapobiega łączeniu się jąder komórkowych i wrzecion II podziału mejotycznego, w roślinach tych bowiem po zniknięciu fragmoplastu nie ma utworzonej przegrody pierwotnej. Po II telofazie płytka organelli mejocytów niektórych roślin zmienia kształt i zajmuje płaszczyzny, w których mają powstać ściany komórkowe rozdzielające komórki tetrady, powstającej po równoczesnej cytokinezie. Tak ułożone organelle (plastydy i mitochondria) mogą być łatwiej rozdzielone równomiernie między komórki (zarodniki) niż gdyby były rozmieszczone przypadkowo.