MORPHOLOGICAL AND QUANTITATIVE CHANGES IN THE POPULATION OF CELL ORGANELLES DURING MICROSPOROGENESIS OF PINUS SYLVESTRIS L. II. MORPHOLOGICAL CHANGES FROM PROMETAPHASE I UNTIL THE TETRAD STAGE

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SUMMARY

A morphological study was made with respect to the changes during microsporogenesis of *Pinus sylvestris* L. from prometaphase I until the tetrad stage. Described and discussed are the breakdown and rebuilding of the nuclear membrane, the mixing of karyoplasm and cytoplasm with the transfer of ribosomal material, the nuclear invaginations, the kinetochore and microtubuli.

A decrease of starch in the plastids starts in interphase II. The mitochondria do not change.

The "lipid-complex" appears in telophase II. Many vesicles are present in the cytoplasm during the cell divisions. Ribosomes are observed in all stages, polysomes become visible during interphase II and telophase II. Rough endoplasmic reticulum is absent. The Golgi body produces small and large vesicles and long flat cisternae, similar to smooth endoplasmic reticulum. These Golgi vesicles fuse and form the primary cell wall. The presence of the plasma membrane is postulated as necessary for the synthesis of callose. No difference has been found between the morphological events during callose wall formation and cellulose wall formation. A relation may exist between the callose wall formation and the polysomes and lipid granules and "lipid complex", but a relation with smooth endoplasmic reticulum is not clear. During diplotene and early tetrad stage the formation of the callose wall proceeds in the same way.

1. INTRODUCTION

During meiotic cell division in *Pinus sylvestris* many events occur which are similar to those during the mitotic divisions in other organisms.

No consensus of opinion exists concerning the breakdown and the rebuilding of the nuclear membrane (ESAU & GILL 1969). The centriole in the plant cell shows the same variability. A polar centre may sometimes be absent (TANAKA 1970) or it may appear as a polar body (ESAU & GILL 1969), or a "polar hollow" (BURGESS 1970), or a vesicle aggregate (ROBBINS & JENTZSCH 1969). The kinetochore during metaphase I in *Tradescantia* (WILSON 1968) and in *Lilium candidum* (DIETRICH 1968) has the same morphological structure as has been found in pine. Nuclear invaginations, as appear in pine during the early tetrad stage, have already been reported in *Pinus banksiana* by DICKINSON & BELL (1970) and for *Podocarpus macrophyllus* by ALDRICH & VASIL (1970). After the breakdown of the nuclear membrane a mixing of the karyoplasm and cytoplasm takes place.

In *Lilium* the ribosome population increases mainly during diakinesis and metaphase I (MACKENZIE, HESLOP-HARRISON & DICKINSON 1967; LINSKENS & SCHRAUWEN 1968 and DICKINSON & HESLOP-HARRISON 1970). Transfer of ribosomal material from the nucleus to the cytoplasm during mitosis in *Vicia faba* is supposed by LAFONTAINE & CHOUINARD (1963) and in *Pinus sylvestris* during meiosis by WILLEMSE & LINSKENS (1968). MARUYAMA (1965, 1968) found no change in plastids, mitochondria and Golgi bodies during the meiotic divisions of *Tradescantia paludosa*. No change in mitochondria and Golgi bodies occurs during mitosis (ROTH, WILSON & CHAKRABORTY 1966).

During the early tetrad stage callose wall formation takes place. MARTENS, WATERKEYN & HUYSKENS (1967) showed that a callose wall surrounds the whole microspore of *Pinus sylvestris* during the tetrad stage. Some studies are known about the callose wall formation between the generative and vegetative cell of the microspore. In *Helleborus foetidus* the earliest wall separating the microspore is formed by aggregation of Golgi vesicles, which contain callose (ECHLIN & GODWIN 1968). In *Dactylorchis fuchsii* and *D. purpurella* the vesicles forming the cell-plate contain callose or callose precursors (HESLOP-HARRISON 1968). During the formation of the generative cell wall in *Endymion non-scriptus*, vesicles, microtubules and tubular endoplasmic reticulum (ER) are present. It has been suggested by ANGOLD (1968), that the structure of the generative cell wall contains callose, because tubular ER is present. TSINGER & PETROVSKAYA-BARANOVA (1965) report that sphaerosomes are connected with the formation of callose plugs in pollen tubes of *Lathyrus odoratus*.

In cellulose walls the formation of the cell-plate starts in the phragmoplast which consists of microtubules oriented at right angles to the plane of the future cell wall, in which many Golgi vesicles fuse (FREY-WYSSLING *et al.* 1964; NORTHCOTE & PICKETT-HEAPS 1966; PICKETT-HEAPS 1967; HEPLER & JACKSON 1968 and HEPLER & NEWCOMB 1967). In general during the formation of the cellulose wall the Golgi vesicles contain and transport material for the primary cell wall (SIEVERS 1963; SASSEN 1964; JORDAN 1970). NORTHCOTE & PICKETT-HEAPS (1966) supposed that in a separate way cellulose should synthesize and they restrict the function of the Golgi body to the synthesis of pectic substances only. The multiple enzymatical function of the Golgi bodies has been supposed by PICKETT-HEAPS (1967) and demonstrated by WISE & FLICKINGER (1970). In the cisternae of the Golgi body many particulate enzymes have been found (WERZ & KELLNER 1970; STAEHELIN & KIERMAYER 1970).

Cellulose formation may take place on the plasma membrane and is not related to a distinct cell organelle. During cellulose formation, D-glucose is transferred to a glucolipid, which acts as a carrier and is translocated outside the cell, where the D-glucose is polymerized to cellulose (HASSID 1969). Chemical intact membrane fragments are necessary for cellulose synthetase activity (PINSKY & ORDIN 1969). Polysaccharide-synthesizing particles are present on the plasma membrane (RAY 1967; VILLEMEZ *et al.* 1968). However, BROWN (1969) suggests that a transport of cellulose by the Golgi vesicles takes place in *Pleurochrysis scherffelii*.

PICKETT-HEAPS (1967), HEPLER & NEWCOMB (1967) and HEPLER & JACKSON (1968) suppose, on the basis of the labeling pattern of applied ^{3}H-glucose and the presence of ER near the cell-plate, that the ER plays a role in cell wall synthesis. ER is present where callose is formed at the pore sites of the sieve plate in *Cucurbita* (ESAU *et al.* 1962).

In pine, primary cell wall materials are produced in the Golgi body and transported by Golgi vesicles. The callose is probably synthesized on the plasma membrane. The products necessary for the formation of the callose wall are probably stored in the lipid granules or "lipid complex" and in the plastids.

2. MATERIAL AND METHODS

The same material and methods were used as is described in the preceding part of this paper (WILLEMSE 1971).

3. RESULTS

3.1. Prometaphase I until telophase I

During these stages of cell division, the volume of the cell increases. The cell is surrounded by a thin cell wall and a callose wall (*fig. 1*).

Fragments of the nuclear membrane are visible on the border between karyoplasm and cytoplasm (*fig. 1, 2*). The karyoplasm contains granules with a diameter of approximately 30 nm and 15 nm (*fig. 3, 4*). The microtubuli are situated near the chromosomes. During prometaphase the kinetochore is visible as a globular less electron dense structure on the chromosome (*fig. 3*). During anaphase I microtubules are attached on the kinetochore, which is more granular (*fig. 4*). The microtubuli between the chromosomes extending from pole to pole are present in anaphase I. A centriole or a marked direction point in relation to the microtubules could not be observed. On the polar ends of the cell elements similar to smooth ER (SER) are lying together in several distinct groups (*fig. 5*).

Many plastids contain a large starch granule (*fig. 1*). The mitochondria have few cristae and an electron transparent content. The lipid granules contain an electron dense material. The Golgi bodies with few vesicles are situated mainly around the granular zone with the chromosomes (*fig. 2*). In the cytoplasm many vesicles of the same type as found during diakinesis are present. A small population of ribosomes is situated in the cytoplasm.

3.2. Telophase I

In the polar ends of the cell a close contact exists between the somewhat homogeneous mass of chromosomes and the new nuclear membrane (*fig. 6*). Remarkable is the presence of many Golgi bodies around the chromosome mass. They produce small vesicles which fuse and locally form a new nuclear membrane (*fig. 7*).

In the centre of the cell many granules are present, most of them are approxi-

mately 15 nm in diameter. In the equatorial plane the microtubuli end in an accumulation of small vesicles which seem to represent a club-shaped end of the microtubule (*fig. 8, 9*). The number of vesicles in the cytoplasm decreases. Mainly vesicles with a clear membrane remain visible.

3.3. Interphase II

The cell has a rather large volume and at each pole lies a nucleus. The callose wall shows thickening on the polar ends and has grown in comparison with prometaphase I (*fig. 10*).

The nucleus contains homogeneous nucleoli and sometimes inclusions. The karyoplasm has few granules of about 30 nm in diameter.

In the cytoplasm the starch granule in the plastids decreases in size (*fig. 10*). Golgi bodies, producing few small vesicles, are spread throughout the cytoplasm. In the centre of the cell many polysomes, ribosomes and some microtubuli are present (*fig. 11*).

3.4. Prometaphase II until the early tetrad stage

The breakdown of the nuclear envelope starts locally with the appearance of dilatations between the two membranes, followed by the fading of the two membranes (*fig. 12*). Here the breakdown initiates at the pole. The karyoplasm has many granules of approximately 15 nm in diameter (*fig. 13*). In metaphase II many microtubules show in cross section a crescent form (*fig. 14*). A centriole or a direction point has not been observed. Vesicles and elements of SER or similar to SER are found only in these regions (*fig. 13*).

The decrease of starch in the plastids continues. Some fragments of membranes become visible around the starch granule. Plastids without starch have sometimes a bowed appearance. The lipid granules contain an electron dense material. During telophase II lipid granules are connected with electron transparent vesicles and the whole group is surrounded by dark dots: the "lipid complex" appears (*fig. 15*). Golgi bodies, producing vesicles, are lying close to the region of the dividing nucleus (*fig. 12*). During cell division the cytoplasm contains many vesicles with a clear membrane and dilated cisternae of SER and Golgi vesicles similar to those found during diakinesis. Ribosomes including some polysomes are observed mainly around the plastids. The number of polysomes increases during telophase II; remarkable are the helical polysomes in this stage (*fig. 16*). During metaphase II and telophase II small concentric membranes are observed in the cytoplasm (*fig. 13, 15*).

3.5. The early tetrad stage

The four nuclei are arranged opposite to each other near the plasma membrane. The nuclei contain homogeneous nucleoli (*fig. 17*). Vesicles surrounded by two unit membranes, possibly an invagination of the nuclear membrane, occupy the periphery of the nucleus. These vesicles contain thin fibrillar material and are surrounded with karyoplasm or chromatin material (*fig. 18*).

In the cytoplasm the decrease of starch in the plastids continues. The lipid

granules have a different electron density, the "lipid complex" is also present. The Golgi bodies are dispersed in the cytoplasm (*fig. 17*). Many polysomes and ribosomes are present. Some electron transparent zones in the cytoplasm contain fibrillar material, resembling thin threads of chromatin, which converts into more electron dense threads (*fig. 19, 34*).

3.6. The callose wall formation

The callose wall between the four cells grows in centripetal direction (*fig. 33*). First the fusing vesicles of the cell-plate are visible everywhere at the same time (*fig. 17*).

During anaphase II and telophase II many irregular shaped vesicles are present near the chromosomes. In the early tetrad stage vesicles connected with ribosomes have been observed near the nucleus (*fig. 20*). The ribosomes on the vesicles disappear and the result is a very dilated vesicle or cisterna, similar to SER. Except the large vesicles, many small irregular shaped vesicles, small round vesicles and long flat cisternae are present in the early tetrad stage (*fig. 21*). The long flat cisternae look like SER. However, the Golgi bodies produce small round vesicles, large vesicles as well as long flat cisternae (*fig. 22, 23*). The long flat cisternae in the cytoplasm and in the vicinity of the future cell-plate, looking like SER, originate from Golgi bodies. Many Golgi vesicles and long flat Golgi cisternae are situated in the region of the future cell-plate (*fig. 24*). These Golgi cisternae and vesicles fuse by making contact with their membranes. The two layers of the unit membrane become now clearly distinguishable (*fig. 25, 26, 27*). In the places where the membranes touch each other, sometimes some remnants of these membranes remain visible in the vesicles (*fig. 30*).

The fused vesicles are the first elements for the cell-plate (*fig.* 26). A very thin line in the direction of the cell-plate becomes now visible in the somewhat electron transparent centre of the vesicles (*fig, 25, 27*). The content becomes then more electron transparent, the volume increases and in the centre of the vesicle fine fibrillar material appears in the plane of the future cell-plate (*fig. 28*). The fine fibrillar material disappears in the electron transparent content of the large vesicle (*fig. 29, 30*). Thereafter the callose becomes visible as a very electron transparent line (*fig. 31, 32*). Remarkable is the persistence of lead-containing particles mainly near the membrane of the callose containing vesicles and near the callose wall, which surrounds the whole cell (*fig. 21, 30*).

During the cell-plate formation microtubules are found perpendicularly to the fusing vesicles (*fig. 34*).

4. DISCUSSION AND CONCLUSION

4.1. The nucleus

A local breakdown, possibly enzymatical, of the nuclear membrane in diakinese and prometaphase II starts at the pole, which has also been reported for *Haemanthus* (BAJER & MOLÈ-BAJER 1969). Remnants of the nuclear membrane remain visible in the cytoplasm. After diplotene no rough ER (RER), but only short

cisternae of SER are present, therefore the membrane bundles, which are visible during the division stages, have to be considered as remnants of the nuclear membrane. In pine the new nuclear envelope may be formed from the remnants of the nuclear membranes and of Golgi vesicles, which fuse to rebuild partly the lacking nuclear membrane parts. Many Golgi bodies surround the telophase nucleus, while also fusing vesicles, forming a new nuclear membrane, are present. In HeLa cells ROBBINS & JENTSCH (1969) supposed the re-formation of the nuclear membrane from spheroids derived from polar vesicular aggregates. Fusion of vesicles and cisternae of the ER have also been described as to reform the nuclear membrane (ESAU & GILL 1969). The capacity of the Golgi vesicles to rebuild the plasma membrane is shown by the formation of the cell-plate in *Phaseolus* roots (HELPER & NEWCOMB 1967) or in pine, as is described here, and in the cell coat of several types of rat cells (RAMBOURG *et al.* 1969). In pine the nuclear membrane originates also partly from fusing Golgi vesicles.

During prometaphase I the kinetochore in pine is visible as a less electron dense structure on the chromosomes as has been observed in *Tradescantia* (WILSON 1968) and *Lilium* (DIETRICH 1968). In metaphase I the microtubuli become visible on the kinetochore. An organized structure resembling a centriole or polar body (ESAU & GILL 1969; BURGESS 1970) has not been observed in pine as in the fungus *Basidiobolus ranarum* (TANAKA 1970). As WILSON (1971) postulates, ER may function as a polar centre. In pine SER is found in the polar ends, but a relation with microtubules is not present.

In interphase II inclusions have been observed in the nucleus. In the early tetrad stage invaginations of the nuclear membrane become visible, similar to those described during the tetrad stage for *Podocarpus* by VASIL & ALDRICH (1970) and for *Pinus* by DICKINSON & BELL (1970). In *Podocarpus* the invaginations may function as channels for the transport of some exine precursors which are synthetized within the nucleus. In *Pinus* the invaginations contain and transport probably nucleic acids to the cytoplasm. In *Pinus sylvestris* the vesicles are probably also invaginations. If there is a transport of material out of the nucleus the thin fibrillar material present in electron transparent zones in the cytoplasm of *Pinus sylvestris* may possibly be delivered from the nucleus by means of the invaginations. This material possibly plays a role in the pollen wall formation which starts after the early tetrad stage. However, a direct relation has not been demonstrated clearly.

After breakdown of the nuclear envelope, the granules in the karyoplasm are mixed in the cytoplasm and not included again in the new nuclei. During diplotene granules of approximately 30 nm, probably ribonucleoproteins, and 15 nm originate from nucleoli. The 15 nm granules strongly resemble ribosomes. Many polysomes become visible during interphase II and telophase II after mixture with the cytoplasm in the cell centre. LAFONTAINE & CHOUINARD (1963) described in mitotic cells of *Vicia faba* a nucleolar production of granules and a mixture of these karyoplasmic granules with the cytoplasm, which have a strong resemblance with ribosomes. ESAU & GILL (1969) show the presence of ribosomes in the spindle of dividing mesophyll cells of *Nicotiana* and suggest an

entry of ribosomes in the nuclear region. In pine the karyoplasmic granules are precursors of ribosomes. They become clearly visible in the diplotene nucleus and are not included in the telophase I nucleus. A rise in the number of ribosomes during metaphase I in *Lilium* meiocytes has been reported by DICKINSON & HESLOP-HARRISON (1970) and LINSKENS & SCHRAUWEN (1968), and in *Lilium* and *Trillium* by MACKENZIE *et al.* (1967). This outburst of ribosomes derived from the nucleus during the meiotic cell divisions is a way to provide the cytoplasm with new nuclear information (WILLEMSE & LINSKENS 1968). This phenomenon may not be restricted to the meiotic division only.

During prometaphase I and II some microtubuli have mainly a crescent form. These structures are the C-filaments like those found in the ciliate *Nassula* (TUCKER 1967). These C-filaments are either artefacts or a development stage in the microtubule formation. In pine the C-filaments are observed during prometaphase and they are situated mainly in the region of the nucleus. They can be interpreted as a stage of microtubule development. No links or cross bridges between microtubuli have been observed as reported by WILSON (1969), HEPLER & JACKSON (1968) and KRISHAN & BUCK (1964).

4.2. The cytoplasm

The decrease of the starch content of the plastids starting in interphase II, is in contrast with the unchanging starch content in the plastids of *Tradescantia*. The rod-like mitochondria disappear in *Tradescantia*, but in pine both spherical and rod-like mitochondria persist (MARUYAMA 1968). During microsporogenesis in pine the mitochondria have an electron transparent content and few cristae. ROTH *et al.* (1966) supposed that no changes in the number of mitochondria and Golgi bodies during the mitotic division take place. It is possible that during microsporogenesis in pine no changes in the mitochondria occur, but the Golgi body changes in production of vesicles and changes in position in the cell. The small concentric membranes found during metaphase II and telophase II may be compared with the multilayered rings in *Tradescantia* microspores, interpreted by MARUYAMA (1966, 1968) as an early Golgi body stage. In all stages lipid granules are present .An aggregation of lipid granula during absence of the nuclear membrane as in *Lilium* has not been observed (HESLOP-HARRISON & DICKINSON 1967). As in zygotene and pachytene, the "lipid complex" appears again in prometaphase II. Many vesicles with an electron transparent content and a clear membrane have been observed in all stages of development. Mainly during the division stages many vesicles, mainly Golgi vesicles and cisternae of SER, surround the dividing nuclei. A local accumulation of SER as has been found in dividing rat hepatic cells (DOUGHERTY & LEE 1967) could not be observed. The RER is absent. After the nuclear divisions polysomes are found in the cytoplasm. Ribosomes are always present. The presence of helical polysomes has also been reported in pollen mother cells of *Ipomoea* (ECHLIN 1965).

4.3. Callose wall formation

Callose wall formation takes place during diplotene and the early tetrad stage.

During telophase I and II microtubuli were observed, standing perpendicularly to the plane of the future cell-plate. In telophase I no cell wall is formed and vesicles are absent. The microtubuli, the phragmoplast fibres (BAJER & JENSEN 1969) lie in clusters in amorphous material and end knobs are found like those reported by HEPLER & JACKSON (1968) for *Haemanthus*. In the early tetrad stage of pine, some microtubuli are standing perpendicularly to the callose wall which surrounds the cell. In diplotene no relation between microtubuli and the callose wall formation has been found.

During the formation of the cell-plate many vesicles and SER-like elements appear. These vesicles and the long flat cisternae similar to the SER are produced by the Golgi bodies. The production of small and large Golgi vesicles on one Golgi body has been reported by PICKETT-HEAPS (1967), as well as the transport of the whole cisternae (BROWN 1969). In pine the production of long flat cisternae similar to SER has to be adjointed to the features of the Golgi body. A fuzzy coated membrane of the Golgi vesicles as reported for *Phaseolus* by HEPLER & NEWCOMB (1967) was not observed.

In the plane of the cell-plate the small or large vesicles and long flat cisternae of the Golgi body fuse. The surrounding unit membrane of these Golgi products becomes more accentuated during the fusion. This membrane is the future plasma membrane (HEPLER & NEWCOMB 1967). In pine these accentuations of the unit membrane of the vesicles in the plane of the cell-plate, but not in the cytoplasm or near a Golgi body, give rise to the supposition that this phenomenon is not the result of normal sectioning as HEPLER & NEWCOMB (1967) suggested. The change in the unit membrane of the vesicles may be a sign of the presence of particulate enzymes on these membranes with relation to the synthesis of callose (VILLEMEZ *et al.* 1968; HASSID 1969; RAY 1967). This may be also the reason for the always dark stained membranes of the Golgi body on which particulate enzymes are present (STAEHELIN & KIERMAYER 1970; WERZ & KELLNER 1970). Probably the enzymes are located between the two layers of the unit membrane (WEHRLI *et al.* 1969). In the Golgi vesicles particulate enzymes could be present derived from the Golgi cisternae. If enzymes are present for the synthesis of callose (or cellulose in another case), they have to function on the membranes of fused vesicles or on the plasma membrane, since the appearance of callose starts within fused vesicles and not during the transport. The necessity of the presence of the plasma membrane appears from the further growth of the cell wall after the disappearance of the Golgi vesicles (HEPLER & NEWCOMB 1967) and the contact of the plasma membrane with the callose wall during the formation of the protrusions in the tetrad stage, when the pollen wall formation starts (WILLEMSE 1971a) as will be described in the next part.

In the fused vesicles fine fibrillar material appears in line with the plane of the future cell-plate; thereafter the callose becomes visible first as an electron transparent central region, which subsequently changes into an electron transparent line in the plane of the cell-plate. During diplotene the same phenomena are observed: small and large Golgi vesicles, SER, possibly also the long flat cisternae derived from the Golgi body, then outside the plasma membrane first

the fine fibrillar material and finally the electron transparent line of the callose wall. Callose wall formation depends on the Golgi vesicles containing materials for the primary cell wall and the presence of the plasma membrane. Callose wall formation does not differ from the cellulose wall formation in its morphological description.

In pine the role of the SER is not clear. A transition of RER to SER before diplotene has been described. The vesicles coated with ribosomes in the early tetrad stage, as reported also by ROBBINS & JENTZ (1967) in dividing HeLa cells, may be analogous to the transition from RER to SER, because of the disappearing ribosomes. ER is related to the formation of plasmodesmata (HEPLER & NEWCOMB 1967), to the pore sites of sieve plates (ESAU *et al.* 1962) and SER to the formation of the callose wall of generative cells (ANGOLD 1968) and of the callose wall around the microspore (ANGOLD 1967; HESLOP-HARRISON 1966). In pine the difficulty is to distinguish the SER from the long flat cisternae of the Golgi bodies. Therefore, their relation to the formation of the callose wall remains hypothetical. Remarkable is the presence of polysomes during callose wall formation. Besides the plastids, the "lipid complex" and the lipid granules may be a storage for polysaccharides as TSINGER & PETROVSKAYA (1965) suggested.

The centripetal ingrowth and the polar thickenings of the callose wall may be connected with the high number of Golgi vesicles at the onset, because the volume of cytoplasm is great on the polar ends of the cell and at the border of the cell centre after the divisions. The orientation of the Golgi vesicles may depend on the presence of microtubuli (HEPLER & NEWCOMB 1967). The orientation of the fine fibrillar material around the cell during diplotene and in the Golgi vesicles during the cell-plate formation may depend on the position of the plasma membrane. The pattern of growth of the cell-plate may be regulated by the adjacent cytoplasm as HEPLER & NEWCOMB (1967) suggested.

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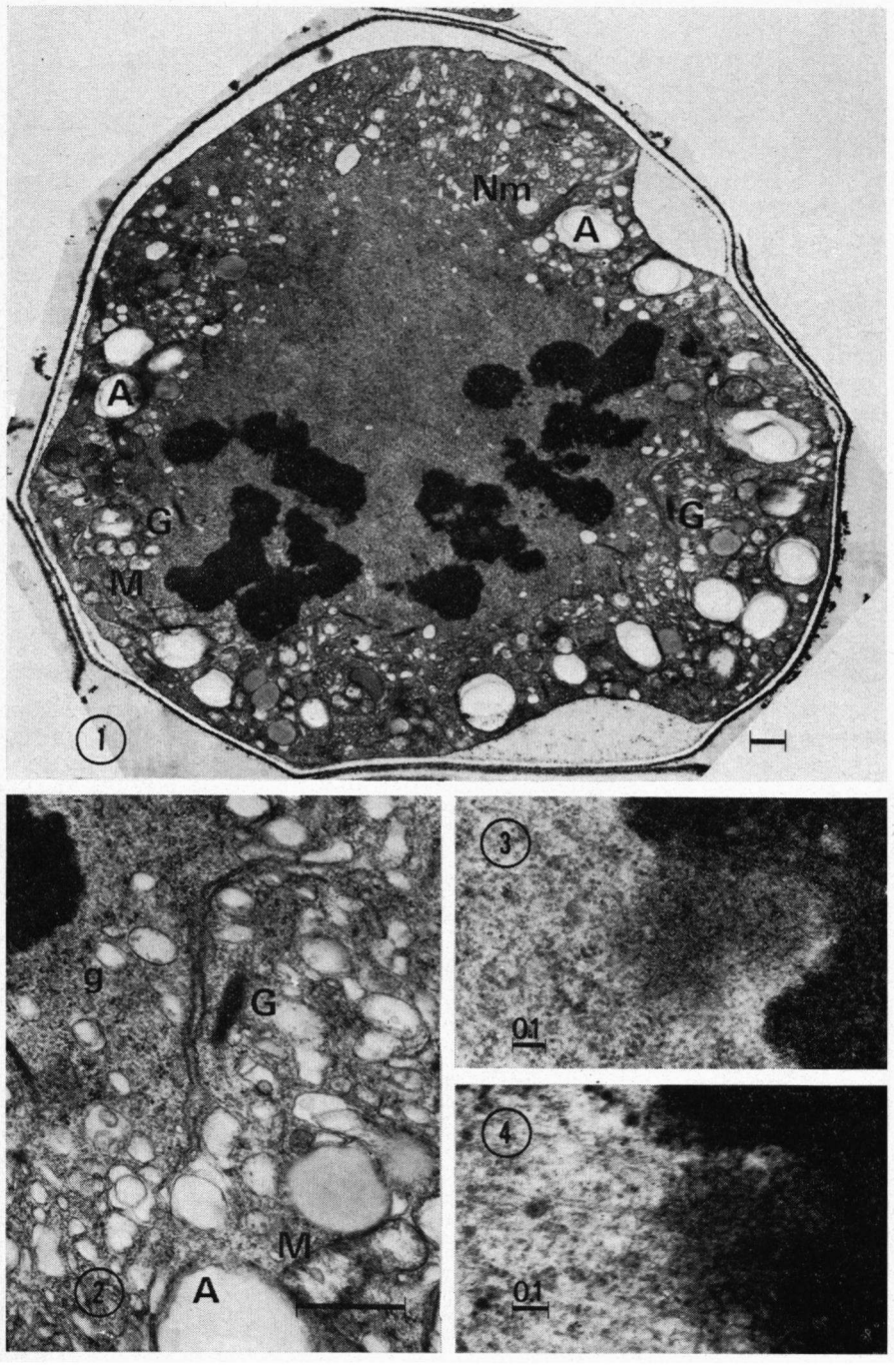
Fig. 1. Prometaphase I. Note the Golgi bodies (G) and remnants of the nuclear membrane (Nm), × 4,770.
Fig. 2. Detail cytoplasm. Golgi bodies (G) round the karyoplasm with many granules (g). Plastids with starch (A) and mitochondria (M), × 15,000.
Fig. 3. Kinetochore during prometaphase I. Granular karyoplasm, × 41,000
Fig. 4. Kinetochore during anaphase I with microtubuli. Granular karyoplasm, × 51,800.
Fig. 5. Detail cytoplasm anaphase I near the pole of the cell, SER and microtubuli (m), × 21,900.
Fig. 6. Telophase I; rebuilding of the nuclear membrane, many Golgi bodies (G) surround the new nucleus, × 17,400.
Fig. 7. Detail of nuclear membrane (Nm) with Golgi body producing vesicles (v) which fuse (arrow), × 28,800.
Fig. 8. Telophase I; ending microtubuli in the cell centre (arrow), × 21,600.
Fig. 9. Detail microtubule with club-shaped end (arrow), × 108,000.
Fig. 10. Interphase II. Cell with callose wall (C) and decreasing starch (A) in the plastids, × 3,060.
Fig. 11. Interphase II. In the cell centre microtubules (m) and polysomes (p), × 21,900.
Fig. 12. Prometaphase II. Breakdown of the nuclear membrane (Nm). Karyoplasm with granules (g) and Golgi bodies (G), × 24,800.
Fig. 13. Anaphase II. Many vesicles (v) around the granular zone. No distinct polar centre. Concentric membranes are present (c), × 5,400.
Fig. 14. Microtubules near the chromosomes. Some have a crescent form (arrow), × 32.200.
Fig. 15. Telophase II. "Lipid complex" in the cytoplasm (Lc). Concentric membranes (c) and decreasing starch (A) in the plastids, × 31,500.
Fig. 16. Helical polysomes in the telophase II cell, × 47,300.
Fig. 17. Early tetrad stage. Cell-plate becomes visible between the cells. In the cell light zones with fibrillar material (arrow). Note the "lipid complex" (Lc), × 8,640.
Fig. 18. Nuclear invaginations, × 44,400.
Fig. 19. Electron transparent zone with fine fibrillar material, × 43,750.
Fig. 20. Vesicles with ribosomes near the nucleus. Polysomes are visible (p), × 29,400.
Fig. 21. Golgi bodies (G) in the cytoplasm with many vesicles (v) and long flat cisternae (arrow), × 21,900.
Fig. 22. Golgi body with small and large vesicle, × 35,000.
Fig. 23. Golgi bodies producing long flat cisternae, × 50,600.
Fig. 24. Cell-plate formation. Many Golgi vesicles and cisternae in the cell centre, × 44,400.
Fig. 25. Fusing Golgi vesicles and cisternae, the membrane becomes clearer. Within the vesicles a thin line becomes visible (arrow), × 39,900.
Fig. 26. Fused vesicles with a clear membrane, × 39,900.
Fig. 27. The thin line is visible in the vesicles, × 48,900.
Fig. 28. Detail of fused vesicle with more electron transparent content and fine fibrils in plane of the future cell-plate, × 36,800.
Fig. 29. The content of the vesicles becomes more electron transparent. Note the black, lead containing particles, × 21,900.
Fig. 30. Detail of the vesicles, in the vesicles remnants of membranes are visible, × 46,000.
Fig. 31. In the vesicles the callose becomes visible (arrow), × 18,900.
Fig. 32. Detail of the callose containing vesicle, × 47,500.
Fig. 33. Centripetal ingrowth of the callose wall. Note the Golgi bodies (G), × 14,700.
Fig. 34. Microtubules perpendicular to the coming cell-plate (m). Note the electron dense threads (arrow), × 22,000.
Unless mentioned otherwise, the line in the figures represents a length of 1 μm.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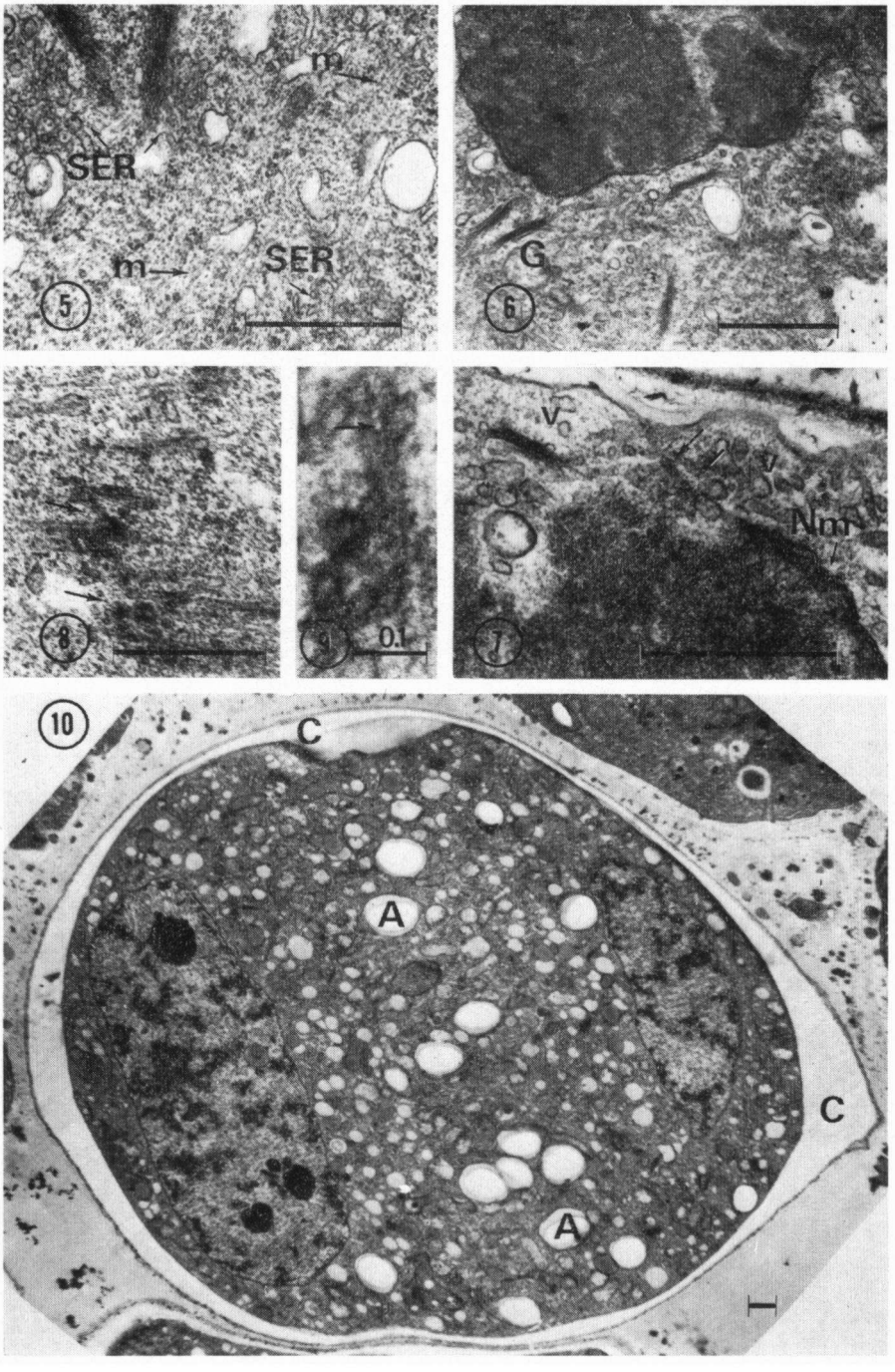
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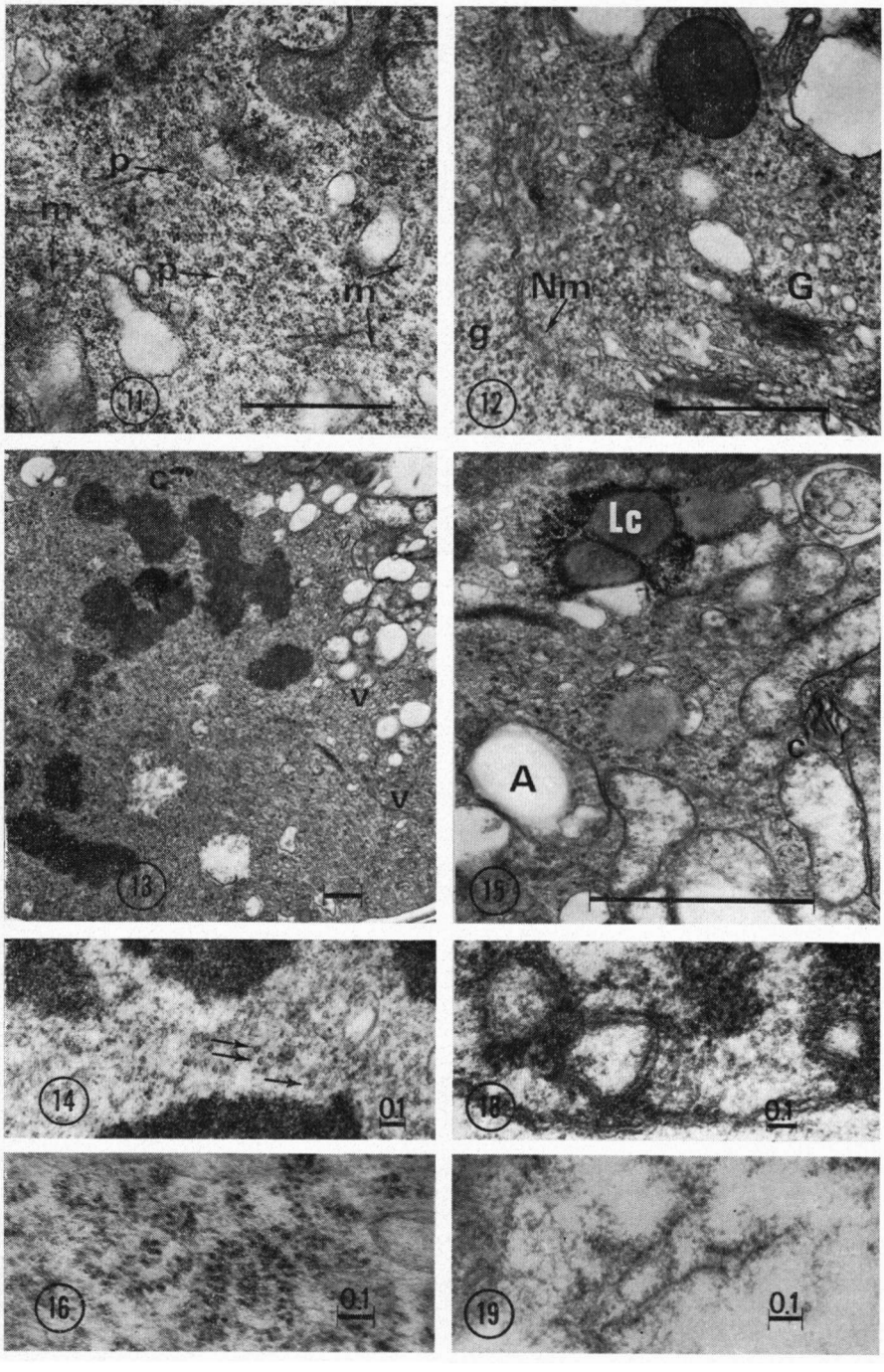
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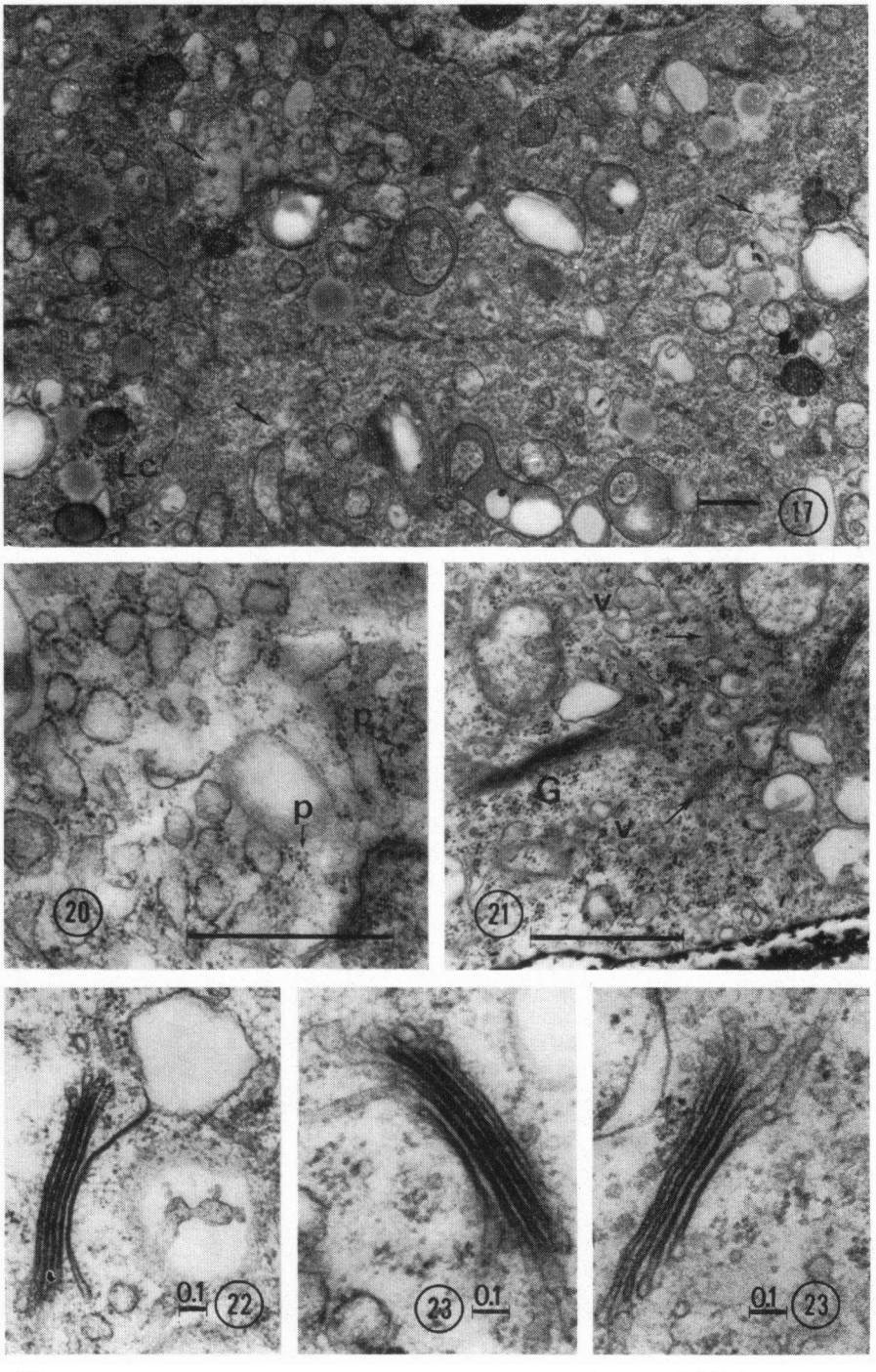
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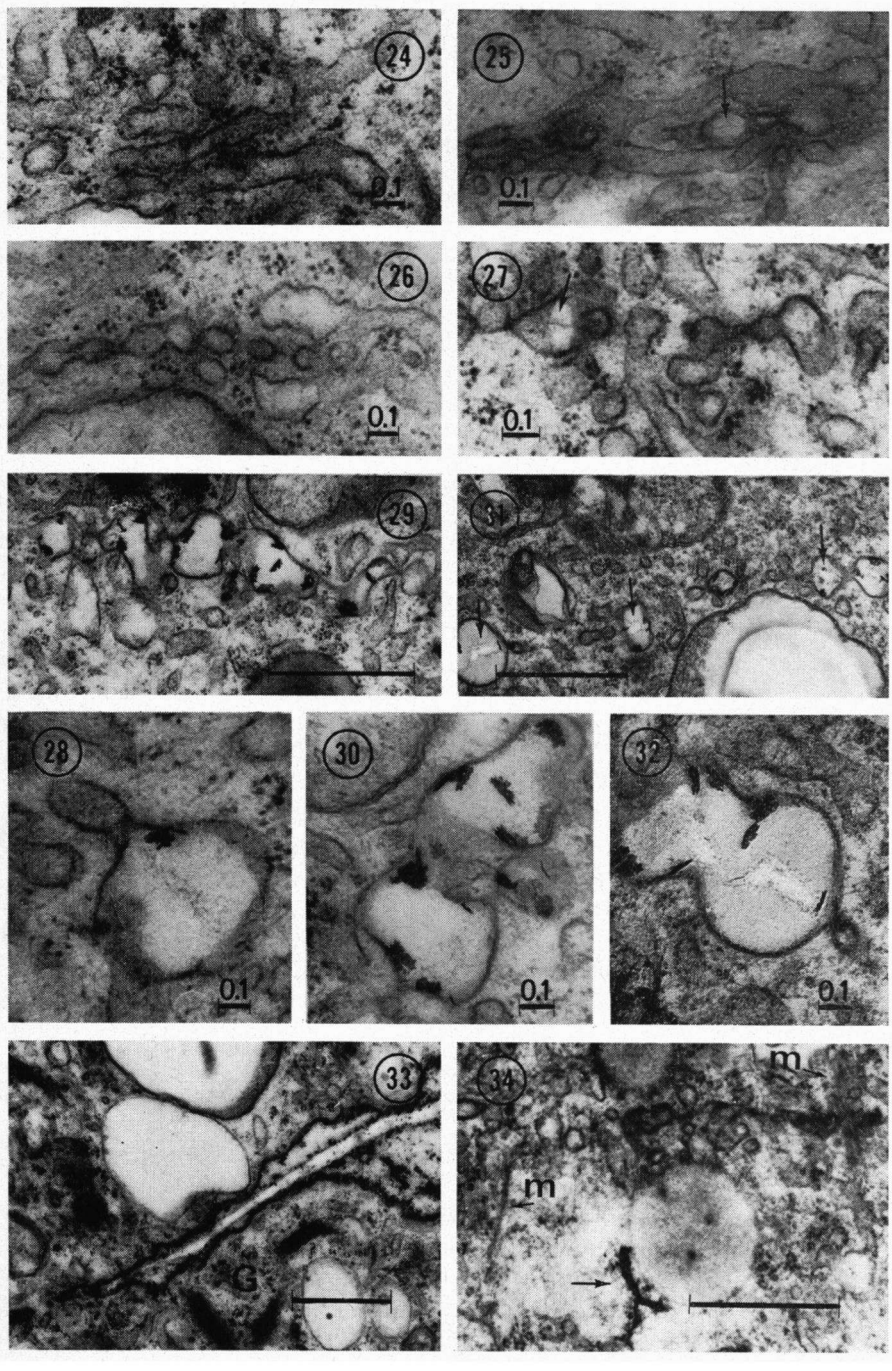
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