THE ULTRASTRUCTURE OF THE EMBRYO SAC BEFORE FERTILIZATION IN *ARUNDO FORMOSANA* HACK.

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Abstract: The mature embryo sac of *Arundo formosana* Hack. contains an egg apparatus composed of an egg cell and two synergid cells at the micropylar end, a central cell with two large polar nuclei in the middle, and a mass of 8 to 18 antipodal cells at the chalazal end. The egg apparatus shares a cell wall with the central cell at the micropylar end and there is only a plasma membrane surrounding at the chalazal end. The cytoplasm of the egg is rich in mitochondria, starch-containing plastids and oil drops. Two synergid cells are very similar and strongly polarized; mitochondria are distributed at the micropylar end and surrounding the filiform apparatus; plastids are only distributed at the chalazal end; and dictyosomes and dilated ER vesicles are numerous. The central cell has a complex organized cytoplasm that is rich in organelles; the two polar nuclei are partially fused; and many ingrowth walls occur adjacent to the nucellus. The antipodal cells contain a large amount of ER and ribosomes. Plasmodesmata are present in the cell wall between the embryo sac cells, but not adjacent to the nucellus. After pollination, the egg shows a considerable increase in polarity. The persistent synergid cell retains its original constitution and the degenerated synergid cell is filled with the electron dense materials. The number of dictyosomes and the quantities of oil drops and starch increase in the central cell. In the antipodal cells, most of rough ER becomes parallel with the cell walls; some dense-staining particles may be present between the plasma membranes and the cell walls; and the ingrowth walls occur adjacent to the nucellus.

INTRODUCTION

The embryo sac development in most grasses is *Polygonium* type. The mature embryo contains an egg, two synergid cells, a central cell and a various number of antipodal cells (Aulbach-Smith and Herr, 1984; Cass and Jensen, 1970; Chao, 1971; Diboll, 1968; Diboll and Larson, 1966; Jones and Rost, 1989; Mahalingappa, 1977; Maze *et al.*, 1970; Maze and Bohm, 1973, 1974, 1977; Maze and Larson, 1975; Muniyamma, 1976; You and Jensen, 1985). Most of these studies are derived from light microscopy, and only few reports make use of EM.

Previous works on the ultrastructure of the mature embryo sac in grasses (Diboll, 1968; Diboll and Larson, 1966; Maze and Larson, 1975; You and Jensen, 1985) have shown that the egg and the central cell are similar in structures among these species, but the synergid cells and the antipodal cells show some variations. The differences in the synergid cells are the polarity and the degenerative time, and that in the antipodal cells are the polarity and the cell wall. However, except

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for the synergid cells, the changes of the mature embryo sac cells after pollination are not clear.

Arundo formosana Hack. is an endemic grass in Taiwan. It is bamboo-like and grows in groups on cliffs. It distributes from the coastal region to the high elevation as 1800 m. The purpose of this paper is to study the ultrastructure of the mature embryo sac before and after pollination, including the structures and the changes of the egg aparatus, the central cell and the antipodal cells.

MATERIALS AND METHODS

The mature pistils of *Arundo formosana* Hack. were collected from field grown plants. According to whether the pollen grains being at the stigmas or not, sample were distingushed post- from pre-pollination. Samples were fixed in 2.5% glutaraldehyde in 0.1 M phosphate buffer at 4°C overnight. After three 20 min rinses in the buffer, materials were postfixed in 0.1% OsO_4 in the same buffer for 4 h at room temperature, and then risned three times in the buffer, 20 min each. Dehydration was completed by an acetone series and Spurr's plastic was used for embedding (Spurr, 1969). Sectioning was done with Ultracut E ultramicrotome. Thick sections were stained with 0.5% toluidine blue and thin sections were stained with 6% uranyl acetate and lead citrate (Reynolds, 1963). A Hitachi-600 TEM or JEM 1200 EX II was used for viewing.

RESULTS

The structure of mature embryo sac

The embryo sac development of *Arundo formosana* Hack. is *Polygonum* type and the antipodal cells undergo considerable proliferation. The mature embryo sac contains an egg apparatus composed of an egg and two synergid cells at the micropylar end, a large central cell with two polor nuclei in the middle, and a mass of 8 to 18 antipodal cells at the chalazal end (Fig. 1).

The mature embryo sac before pollination

The egg

The egg in longitudinal section appears pear shape (Fig. 2). The egg is approximately 60 μm long. The width at the chalazal end is broader than that at the micropylar end. The widest portion in the middle is approximately 25 μm. The oval-shaped nucleus with a single nucleolus is centrally located and surrounded by the majority of the cytoplasm.

A large number of mitochondria, which have a simple interior organization and few cristae, are distributed in perinuclear region (Figs. 2, 3). Starch-containing plastids and oil drops are scattered in the cytoplasm and their density is higher than other embryo sac cells (Fig. 2). Plastids are less abundant than mitochondria, but they appear denser than mitochondria (Fig. 3). ER is scarce and uniformly distributed. Most of dictyosomes are found at the periphery of the cell, and they produce some dictyosome vesicles (Fig. 4), but their number is low. Ribosomes, which are either attached to ER or free in the cytoplasm, are numerous. Some rough ER arranges in parallel with the plasma membrane (Fig. 4).

The egg shares a cell wall with two synergid cells and the central cell at the micropylar end, while at the chalazal end no wall is present and two plasma membranes are in contact (Figs. 4, 5). The cell wall is the thickest at the micropylar end, and becomes thinner and thinner gradually toward the chalazal end. Plasmodesmata can be found in the cell wall of the micropylar end (Fig. 5). Sometimes, there are some wider regions between two plasma membranes and the electron dense materials are present in these regions (Fig. 4).

The synergid cells

The two synergid cells appear elongate oval-shaped and are about the same length as the egg (Fig. 6). The synergid cell walls are only present at the microplyar end of the cells (Fig. 7). The other parts are only surrounded by a plasma membrane. There are a large number of finger-like wall projections, that form the filiform apparatus, at the micropylar end (Figs. 6, 7). The filiform apparatus shows periodic acid Schiff's reaction-postive (not show).

Two synergid cells are similar in structures except that the cytoplasm of one cell is denser than that of the other (Fig. 6). The lighter one is the persistent synergid cell and the denser one will degenerate. At this stage, many organelles are present, especially mitochondria, dictyosomes and ER. Small vacuoles are scattered in the cytoplasm.

The synergid cells are strongly polarized. The nucleus occupies a middle-lateral position (Fig. 6). Most of mitochondria are distributed at the micropylar end and surround the filiform apparatus, and their number is very high (Fig. 7). Mitochondria contain some cristae and a slight dense matrix (Fig. 9). The plastids with some thylakoids are only present at the chalazal end (Figs. 6, 8). No starch is present. Dictyosomes are active in vesicle production and distributed from the micropylar end to the chalazal end of the cells, but a greater number near the filiform apparatus (Figs. 7, 9). Many small oil drops are proximal to the filiform apparatus.

Most of ER is present as dilated vesicles and scattered in the cytoplasm (Fig. 7). Some ribosomes are attached to the dilated vesicles (Fig. 10). Ribosomes are less abundant than in the egg. Plasmodesmata can be seen in the boundary walls of two synergid cells, synergid-egg and synergid-central cells.

The central cell

The central cell is the largest cell in the embryo sac. It contains some large and some small vacuoles (Fig. 1) and is surrounded by a cell wall except for the boundary with the chalazal end of the egg apparatus where it is only bordered by the plasma membrane (Fig. 2). A region of the central cell around the micropylar end of the egg apparatus is called the "apical pocket" (Diboll and Larson, 1966). The cytoplasm is restricted to the periphery of the cell, the apical pocket and the perinuclear region.

The two polar nuclei, which are very close to the egg apparatus, are large and approximately the same size (Fig. 11). Each of them has a conspicuous nucleolus and a smooth nuclear membrane. They are partially fused and the fusion bridges contain some mitochondria and ER (Fig. 12).

There are abundant organelles in the cytoplasm (Fig. 13). Mitochondria are large with few cristae and a clear matrix. Plastids, either with or without starch

Key to Labelling

AN:	Antipodal cell	ER:	Endoplasmic reticulum	Pl:	Plasmodesma
AP:	Apical pocket	FA:	Filiform apparatus	PM:	Plasma membrane
CC:	Central cell	IW:	Ingrowth wall	PN:	Polar nucleus
CW:	Cell wall	M:	Mitochondrion	R:	Ribosome
D:	Dictyosome	N:	Nucleus	RER:	Rough endoplasmic reticulum
DN:	Degenerated nucleus	NC:	Nucellus	ST:	Starch grain
DSy:	Degenerated synergid	Nu:	Nucleolus	Sy:	Synergid cell
DV:	Dictyosome vesicle	OD:	Oil drop	Th:	Thyalkoid
E:	Egg	P:	Plastid	V:	Vacuole

Figs. 1-16. The mature embryo sac before pollination.

Fig. 1. The light microscopic photograph of the longitudinal section of the ovule, showing the main structures of the embryo sac. (bar=15 μm)

Fig. 2. The longitudinal section of the embryo sac. Note the shape of the nucleus and the distribution of organelles in the egg. From the position of the arrowhead (▶), the egg with a common cell wall at the micropylar end, but surrounded by plasma membrane at the chalazal end. Most of the cytoplasm of the central cell distributed in the perinuclear region and the apical pocket. (bar=7 μm)

Fig. 3. Portion of the nucleus and the perinuclear cytoplasm in the egg, showing mitochondria, starch-containing plastids, ER, oil drops and vacuoles. (bar 1 μm)

Fig. 4. Portion of the cytoplasm between the egg and the central cell, showing two plasma membranes in contact and the electron dense materials in a wider region (▶). Note rough ER parallel with the plasma membrane in the egg. (bar=200 nm)

Fig. 5. Enlargement of Fig. 2. Showing from a common cell wall to only two plasma membranes in contact between the egg and the central cell. Note plasmodesmata in the cell wall. (bar=500 nm)

Fig. 6. The longitudinal section of two synergid cells. Note the density of the cytoplasm, the nucleus position, the distribution of plastids and the filiform apparatus. (bar=5 μm)

Fig. 7. Portion of a synergid cell and the central cell, showing the mitochondrial distribution of synergid cell at the micropylar end. Note the distribution of dilated ER vesicles (▶). (bar=1 μm)

Figs. 8-10. Enlargement of Fig. 6.

Fig. 8. Showing plastids and dilated ER vesicles (▶). (bar=500 nm)

Fig. 9. Showing mitochondria, dictyosomes and dictyosome vesicles. (bar=500 nm)

Fig. 10. Showing dilated ER vesicles (▶). Note some ribosomes attached to dilated ER vesicles. (bar=200 nm)

Fig. 11. Portion of the central cell and the egg, showing two polar nuclei very close to the egg apparatus. Note the shapes and the part fusion (▶) of two polar nuclei. (bar=2 μm)

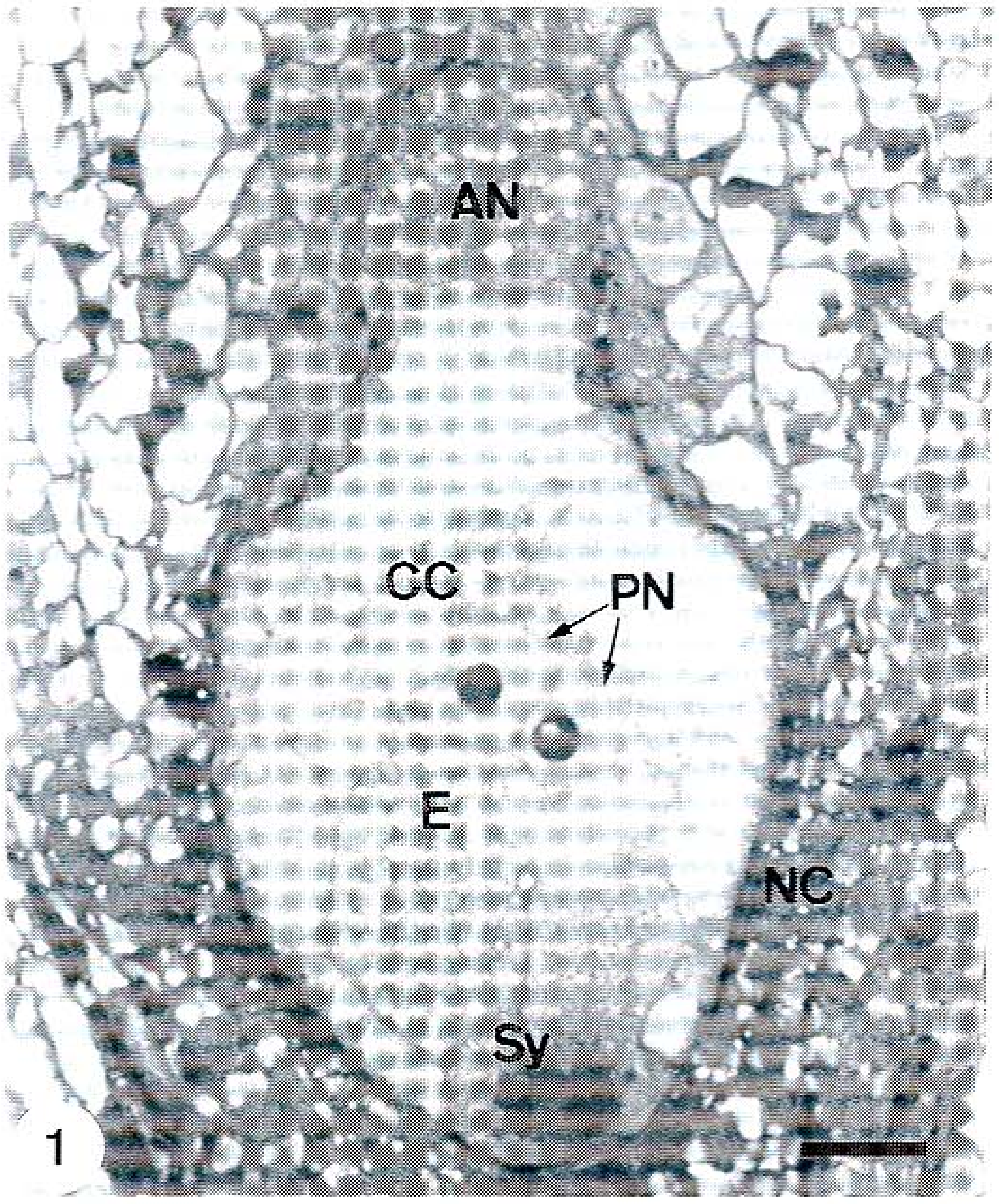
Fig. 12. Enlargement of Fig. 11. Showing the part fusion of two polar nuclei. Note some ER in the fusion bridge. (bar=500 nm)

Fig. 13. Portion of the central cell, showing mitochondria, plastids, ER, dictyosomes, dictyosome vesicles and vacuoles (bar=1 μm)

Fig. 14. Portion of the central cell, showing the ingrowth wall and its peripheral cytoplasm. (bar=200 nm)

Fig. 15. The longitudinal section of the antipodal cells. (bar=2 μm)

Fig. 16. Portion of a antipodal cell adjacent to the central cell, showing mitochondria, plastids, ER and vacuoles. Note the parallel ER encircling vacuoles and plasmodesmata present in the cell wall. (bar=500 nm)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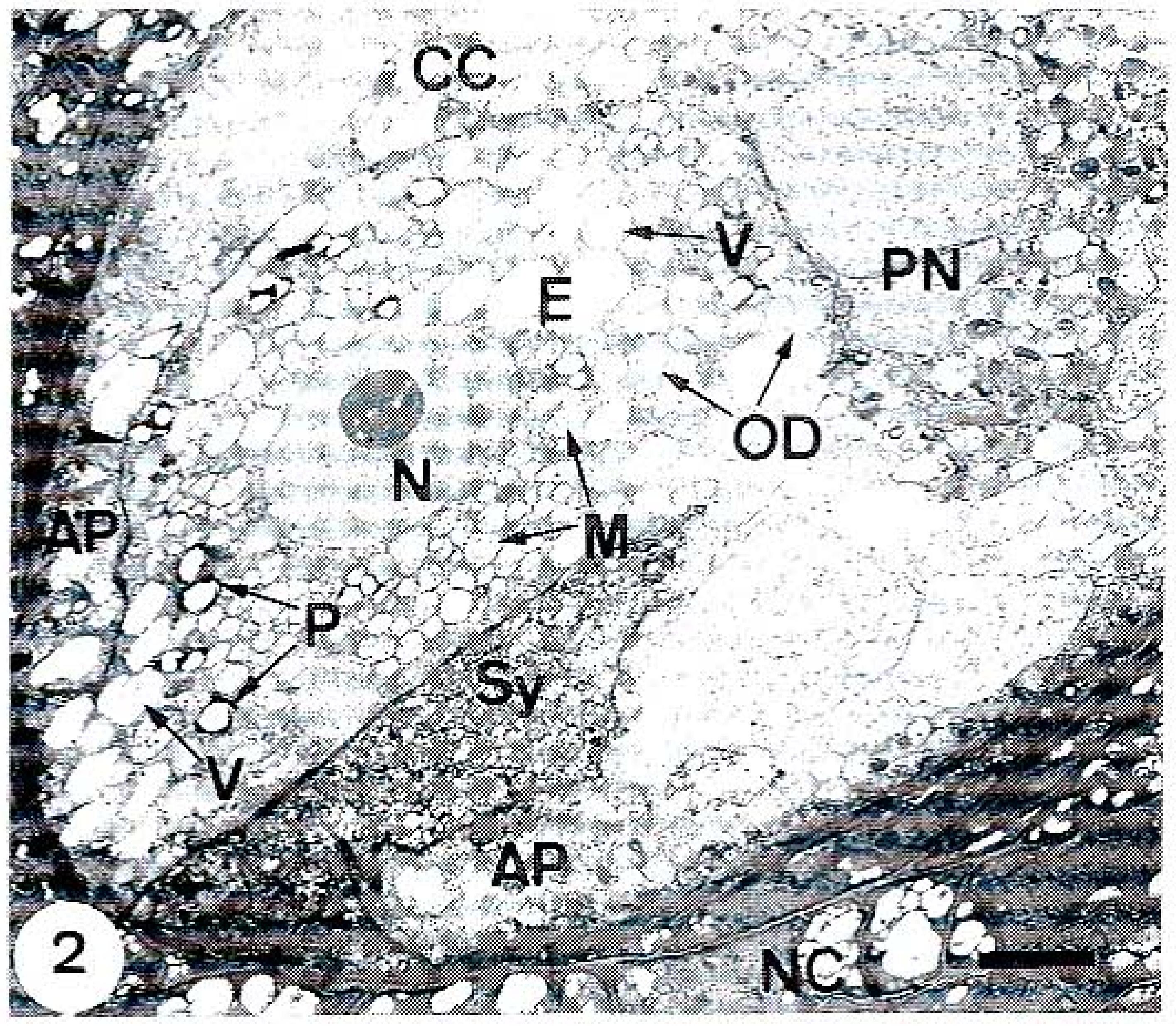
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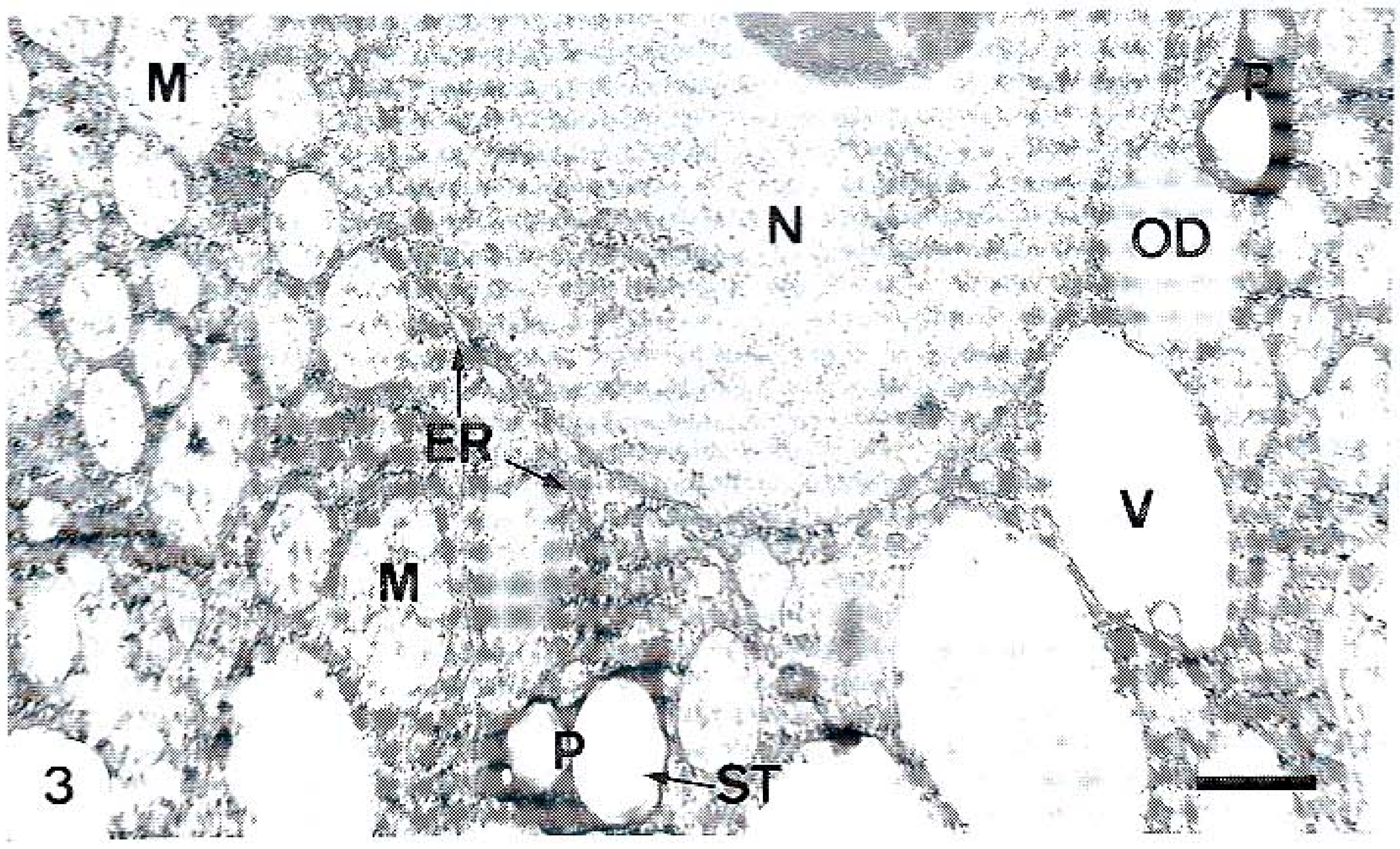
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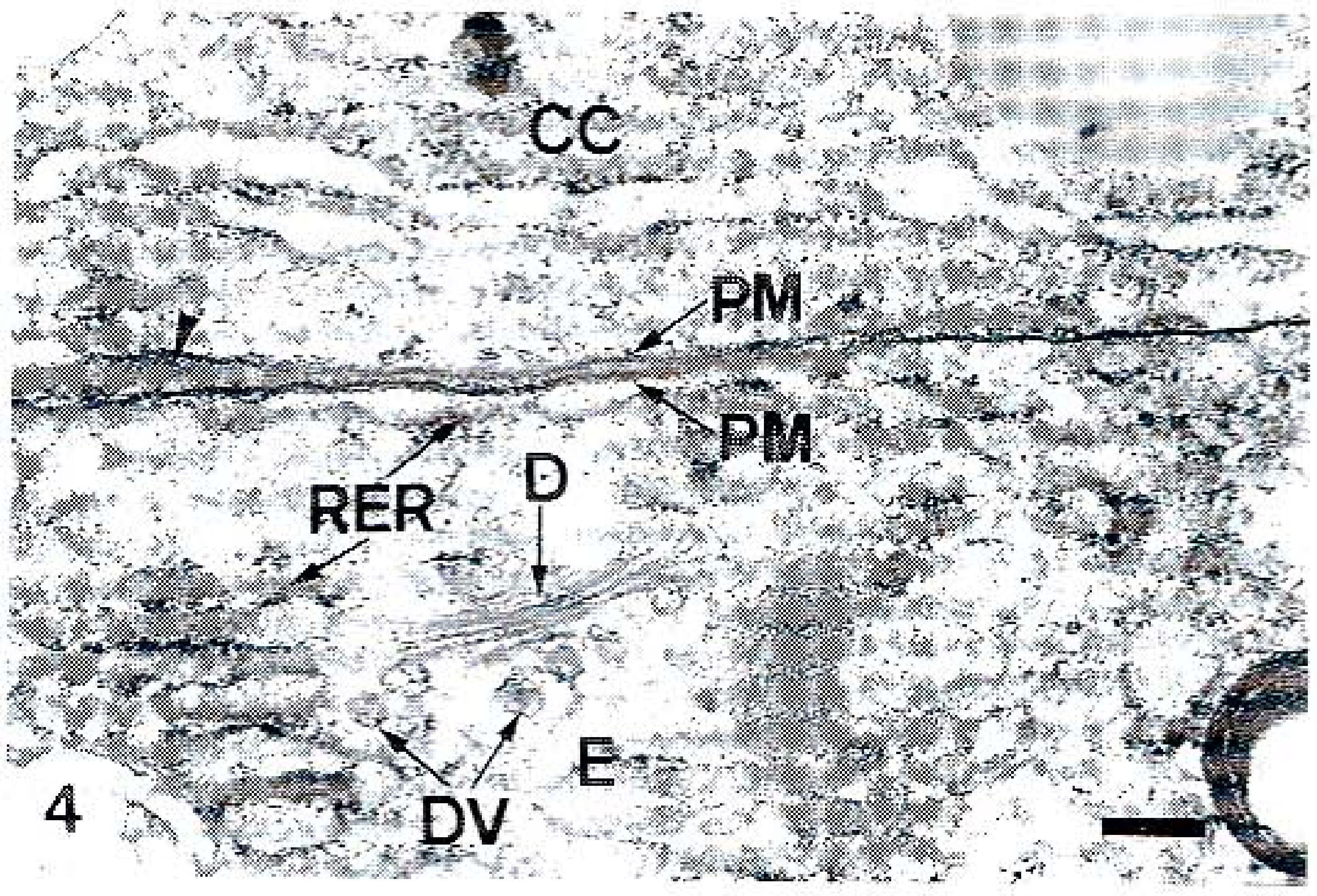
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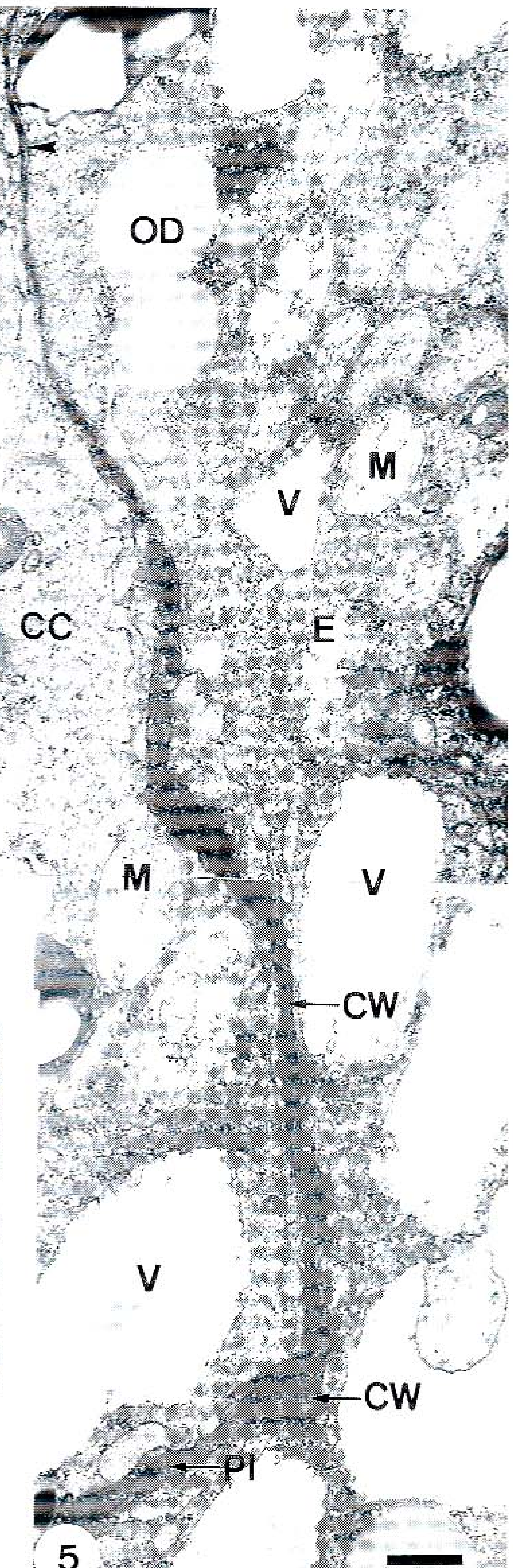
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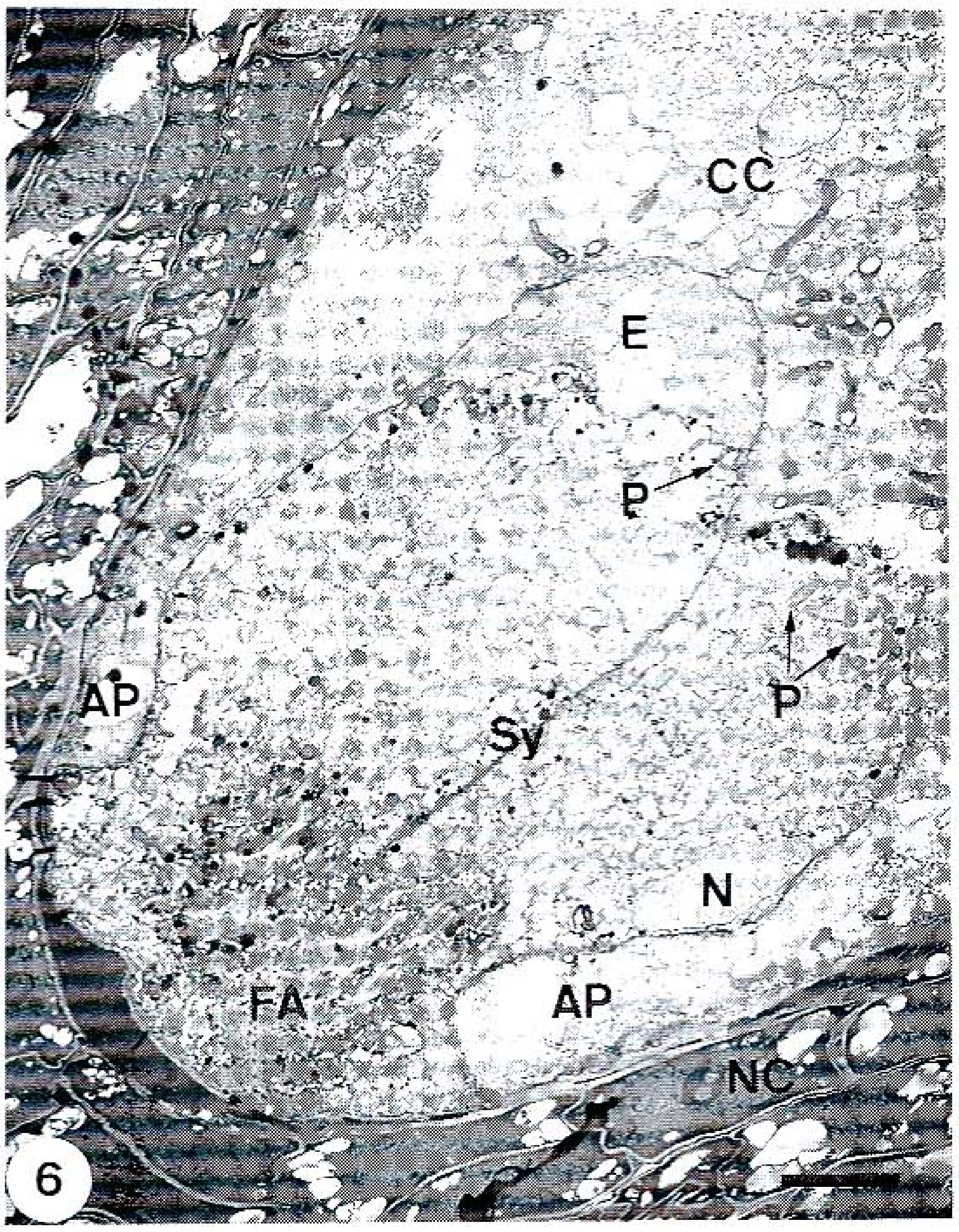
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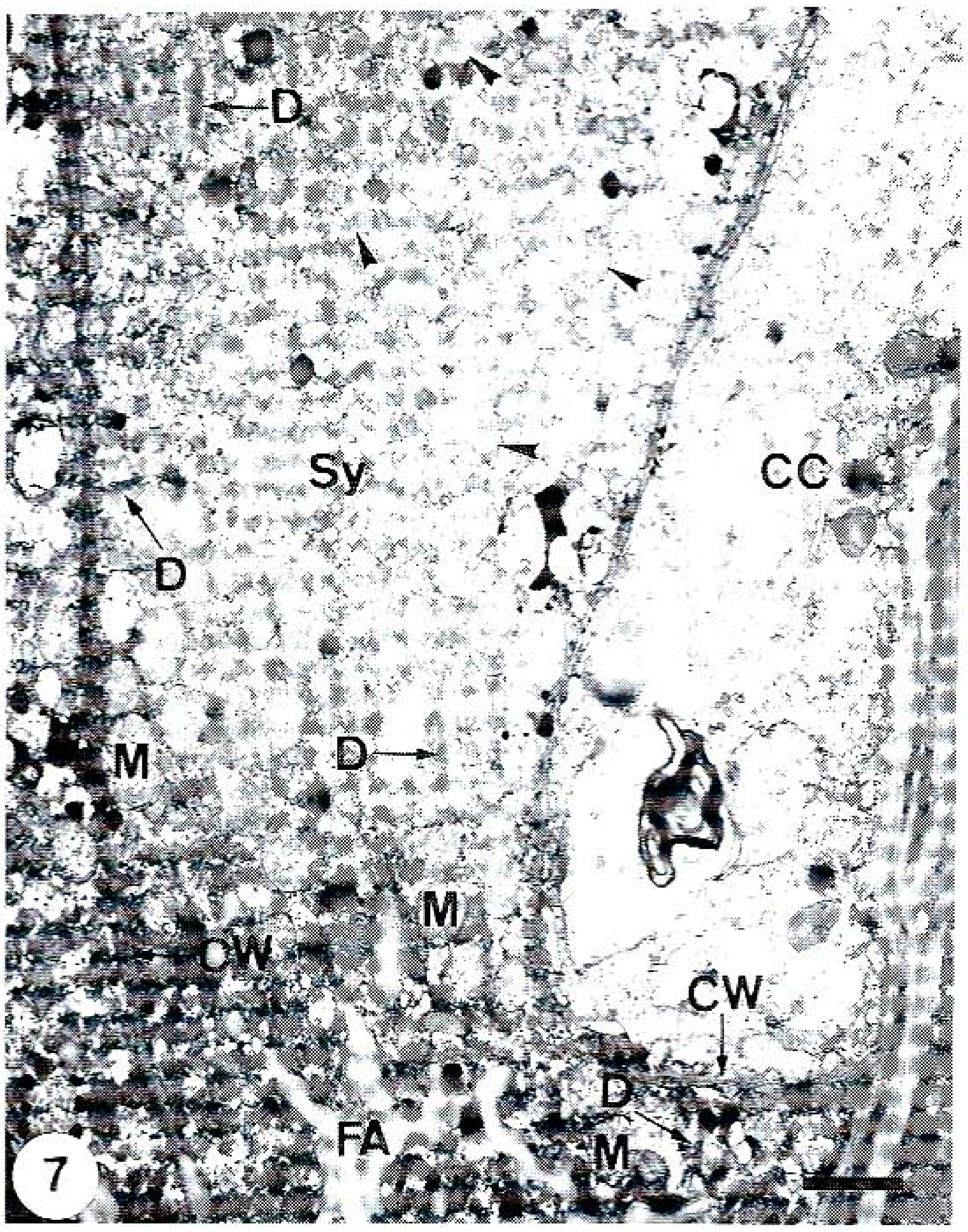
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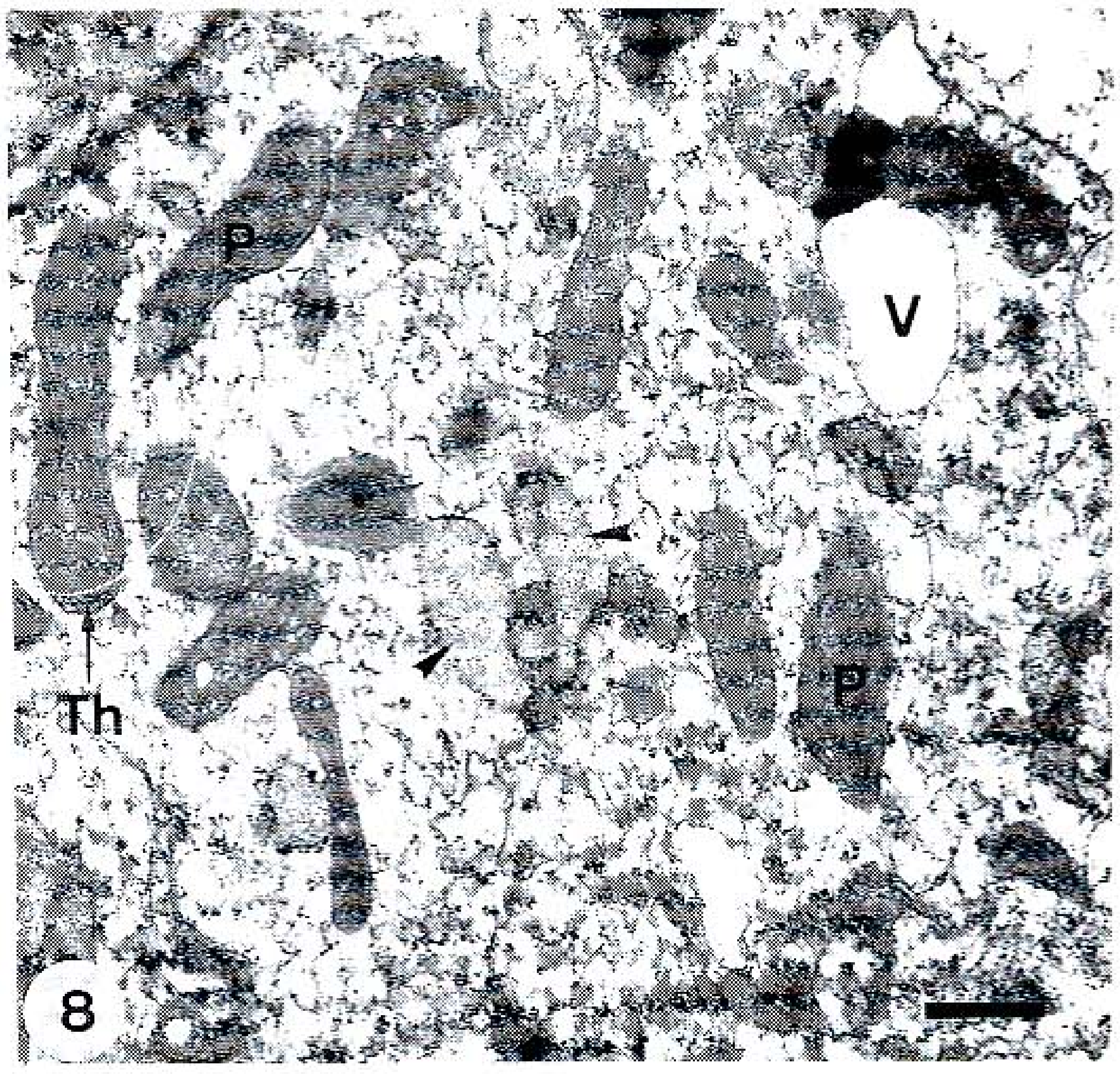
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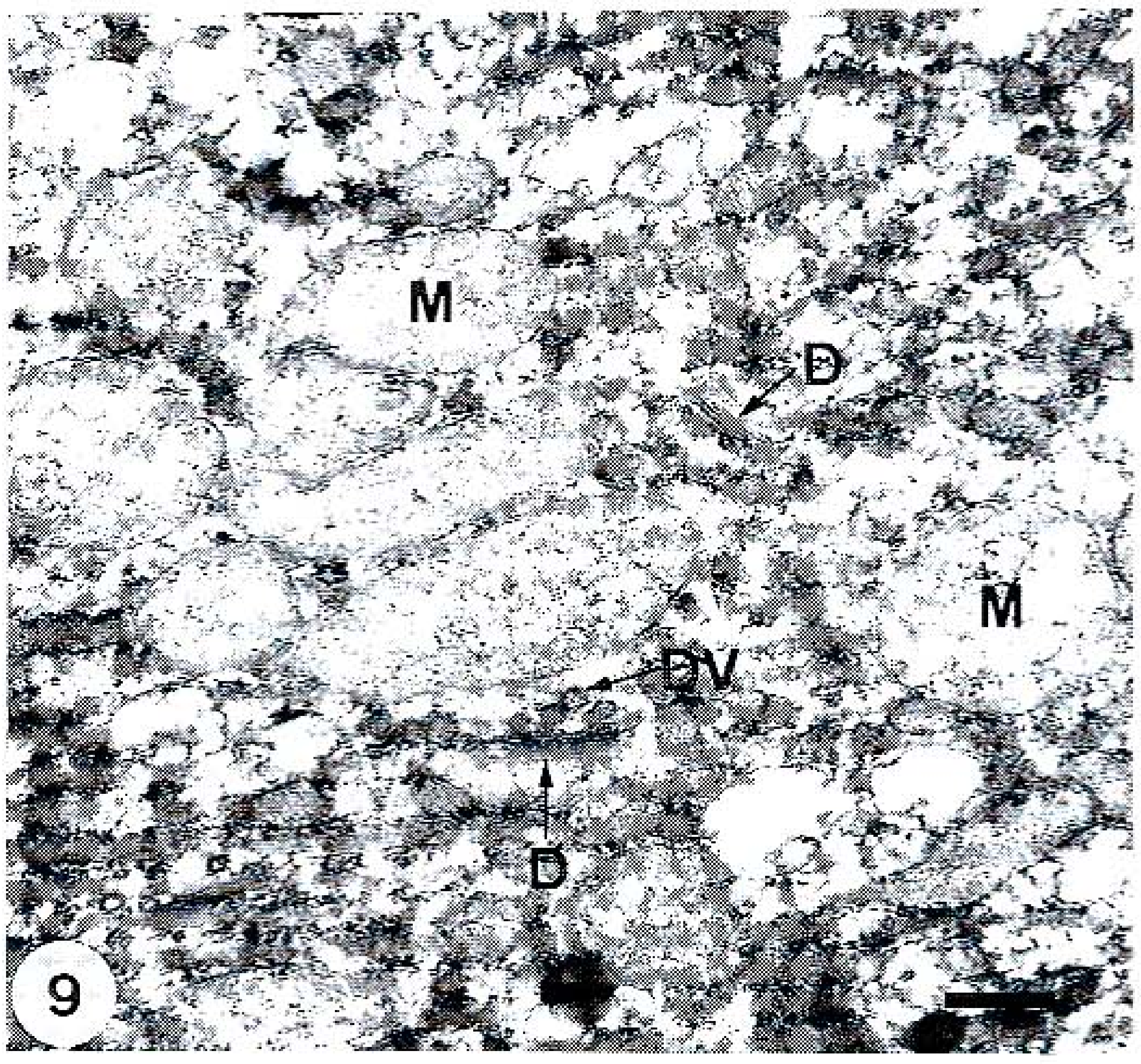
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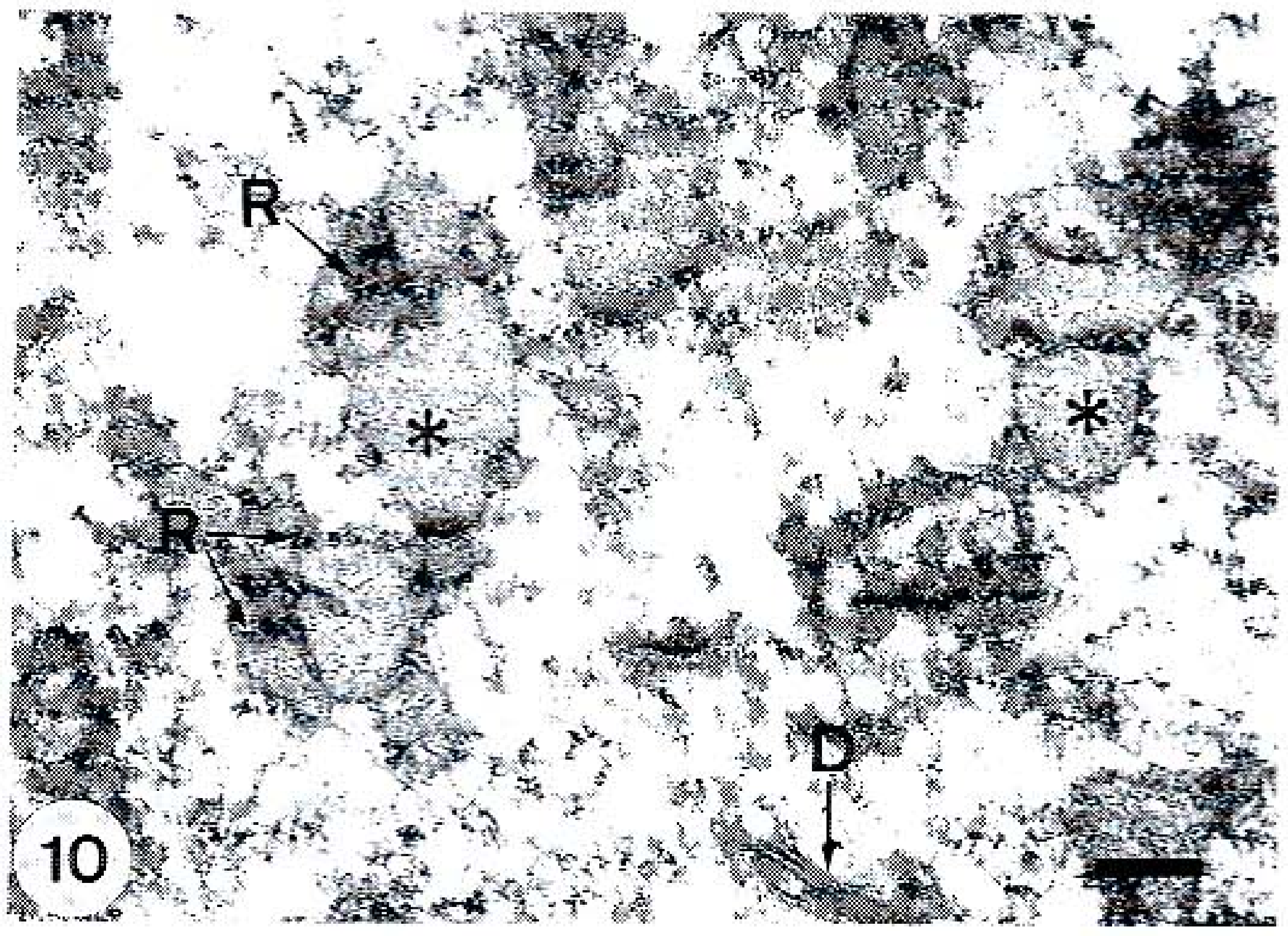
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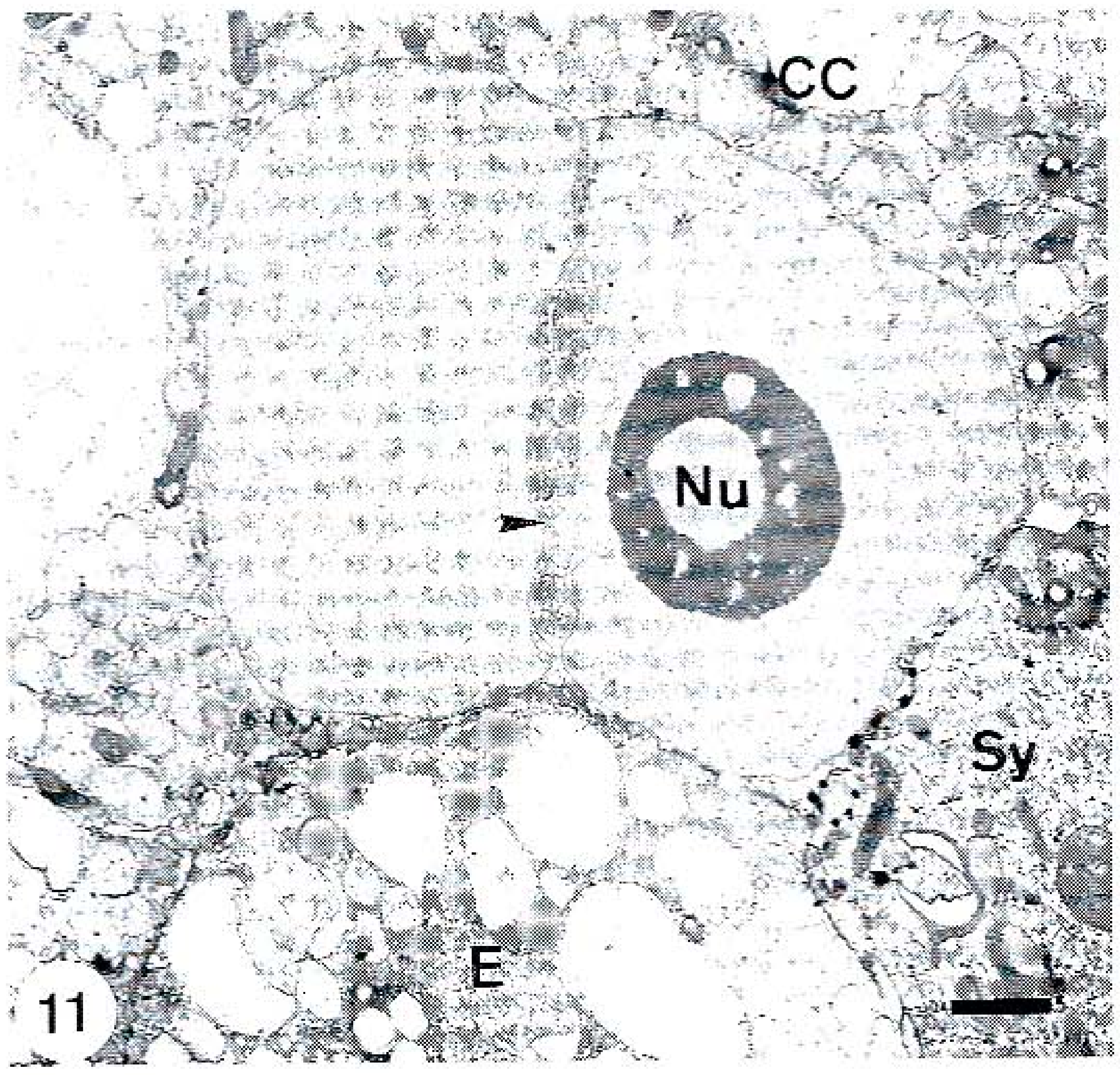
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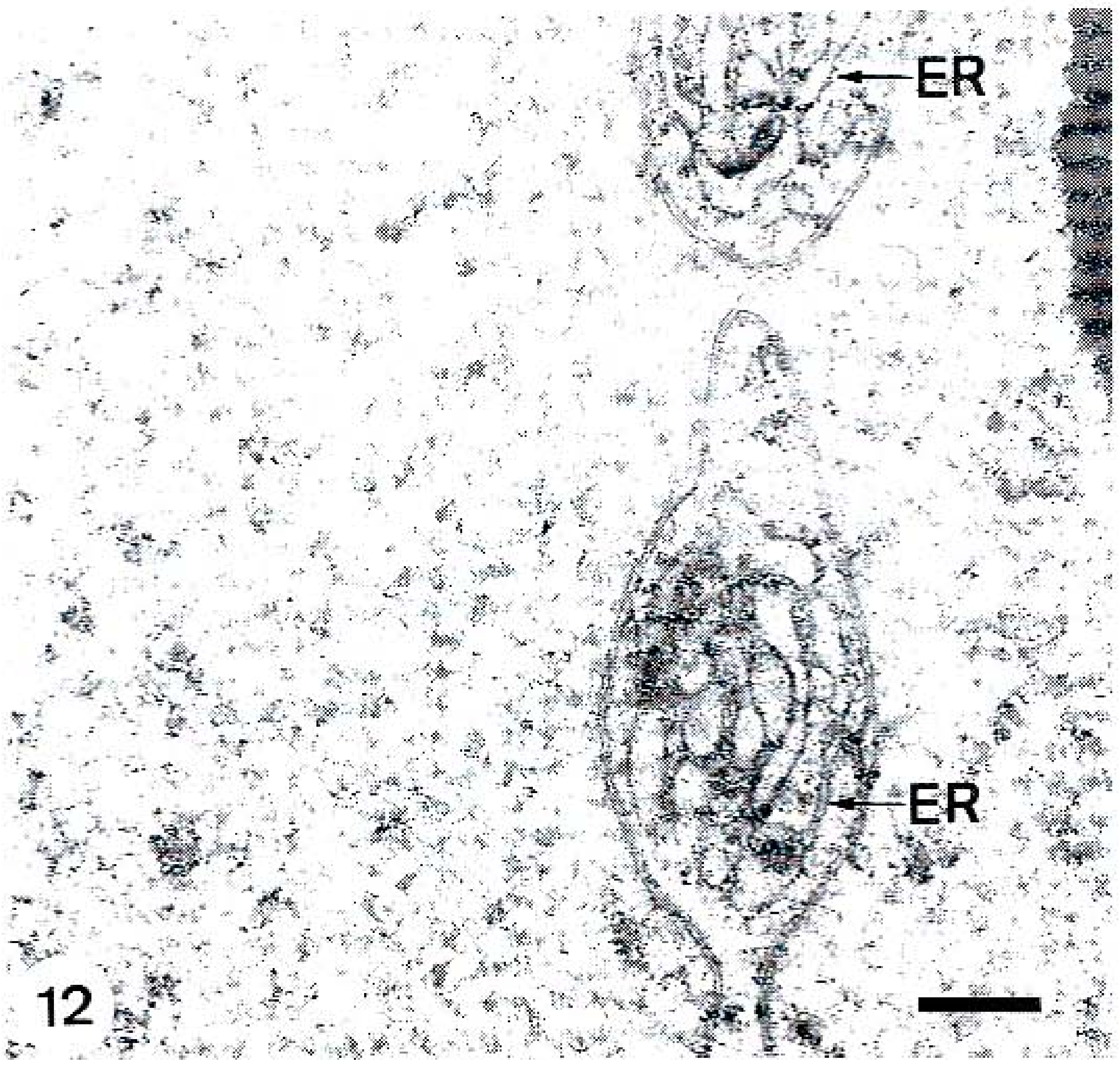
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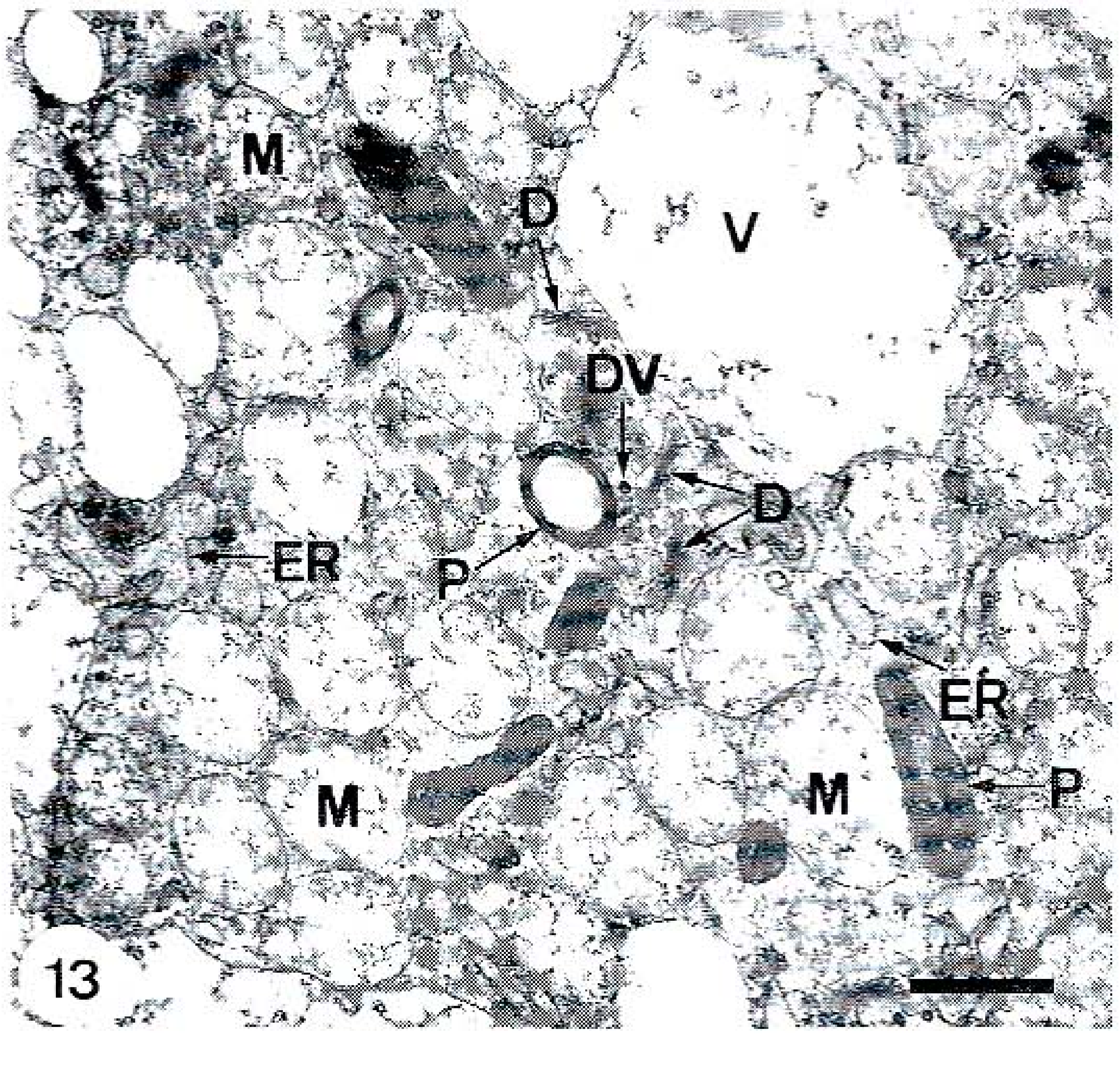
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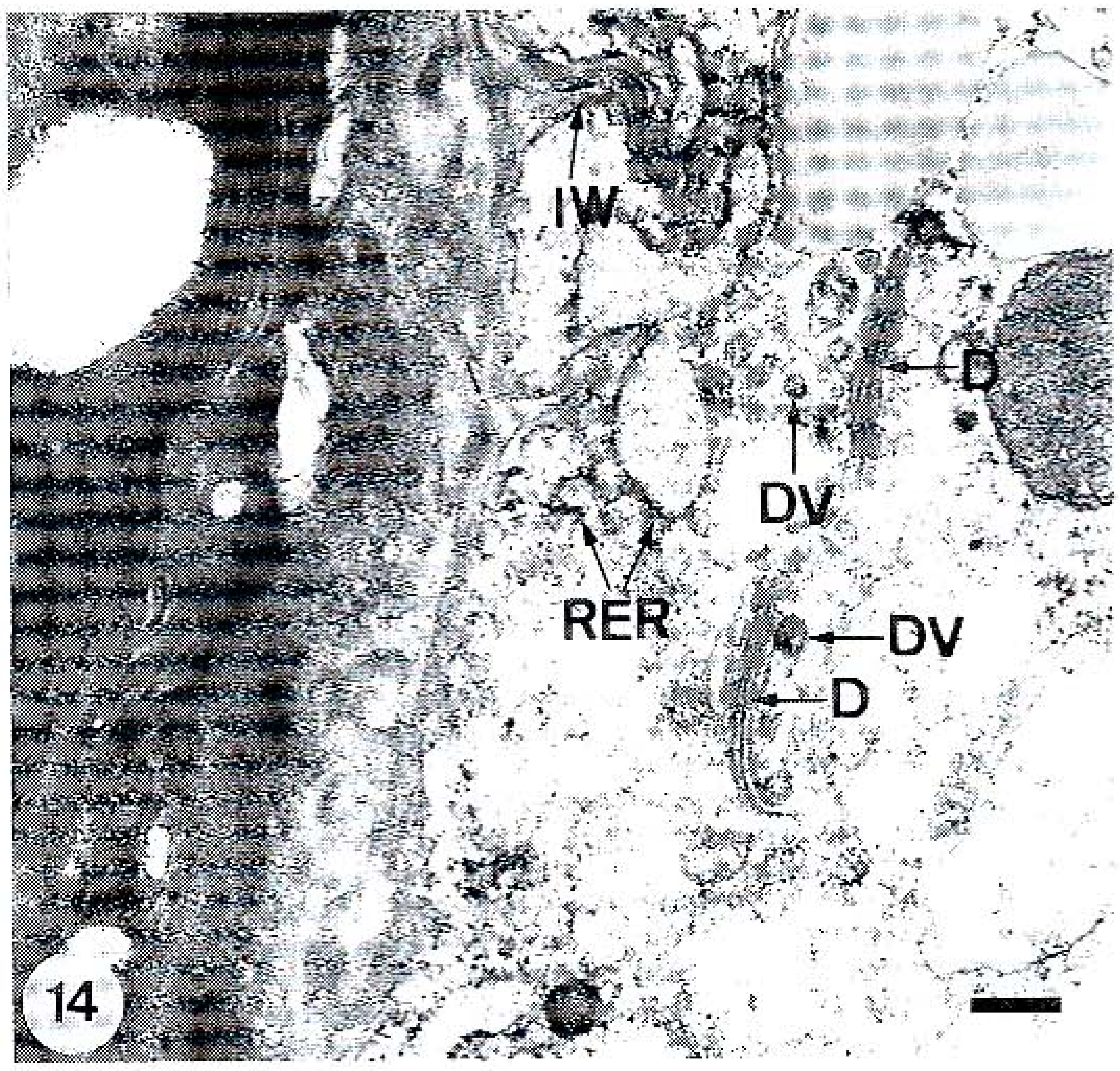
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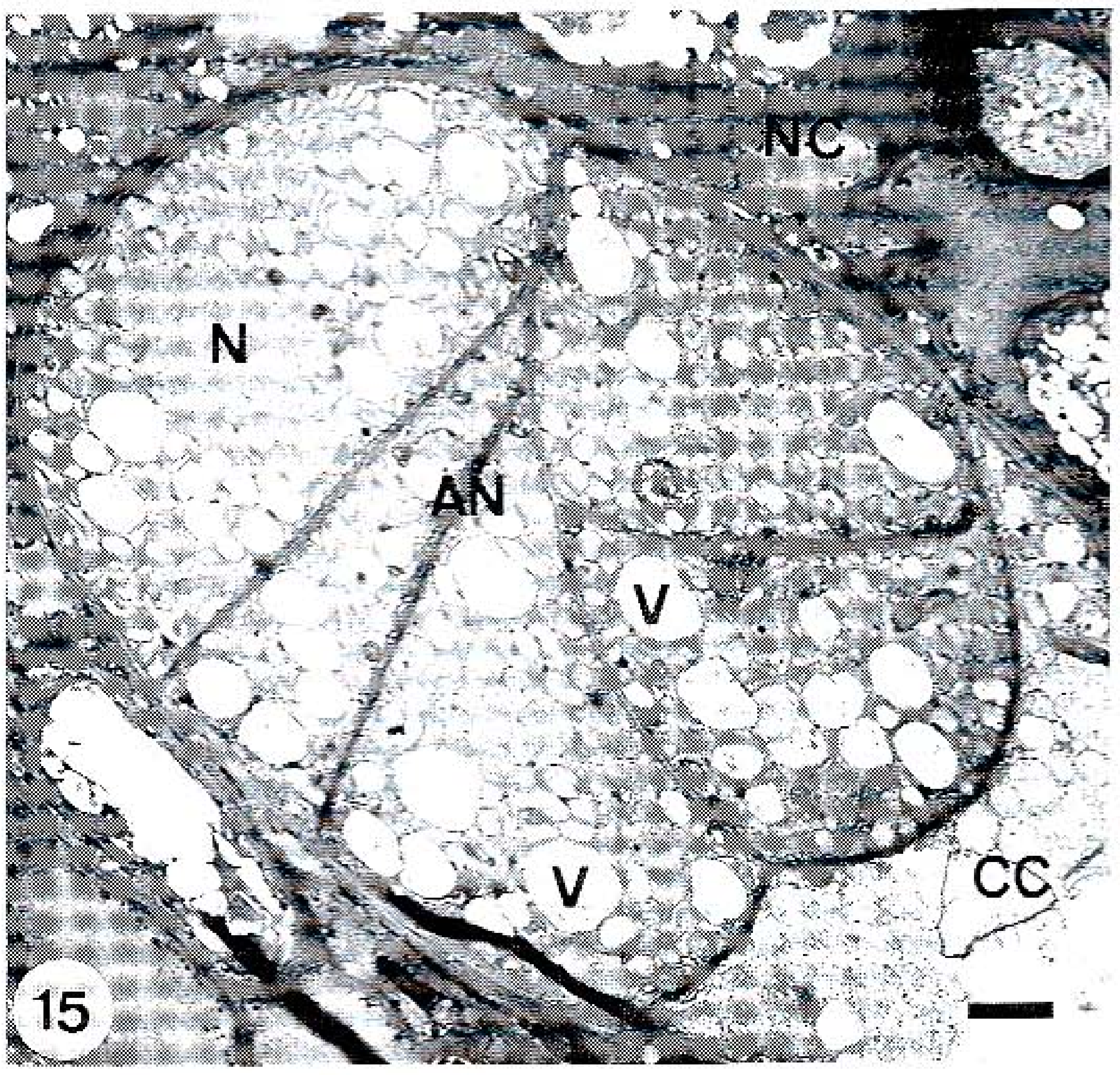
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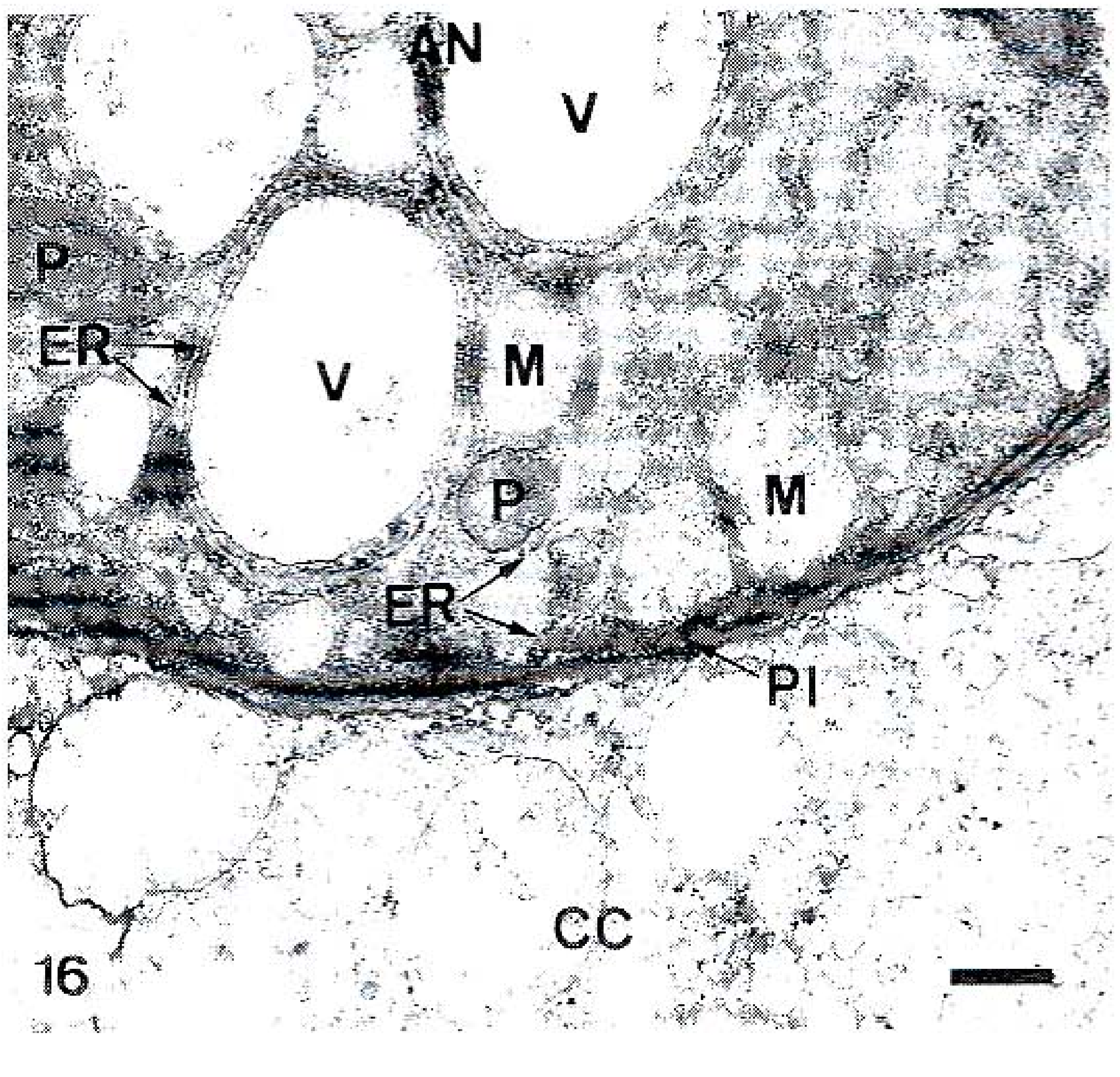
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grains, are rod or oval shape. Dictyosomes are uniformly distributed in the cytoplasm and produce many vesciles. Oil drops, ER and ribosomes are scattered in the cytoplam. Ribosomes and ER are numerous.

There are many ingrowth walls in the cell wall adjacent to the nucellus. Near ingrowth walls there are many rough ER, dictyosomes with dictyosome vesicles and oil drops (Fig. 14). Sometimes, the coated vesicles can be seen to fuse with the plasma membrane which surrounds the ingrowth walls.

The antipodal cells

The antipodal cells appear lighter than the other cell types in the embryo sac. Each antipodal cell contains large and small vacuoles (Fig. 15). A large irregularly shaped nucleus with a conspicuous nucleolus is located near the center of the cell. The organelles are uniformly distributed in the cytoplasm.

The most conspicuous characteristic of the antipodal cells is that they contain a large amount of ER and ribosomes. ER is present in parallel stacked cisternae and many regions show cisternal dilations (Fig. 16). The parallel ER sometimes encircles vacuoles. Mitochondria have a simple internal structure and few cristae. Plastids with some thylakoids are without starch.

Plasmodesmata can be found between the antipodal cells or between any antipodal cell and the central cell (Fig. 16), but are not present between any antipodal cell and the nucellus. Oil drops are seldom found.

The mature embryo sac in the interval between pollination and fertilization

The egg

Some changes occur in the egg after pollination. The majority of the cytoplasm is restricted to the micropylar half of the egg. The shape of the nucleus becomes irregular and the nuclear membrane forms some lobed edges (Fig. 17). Most of ER is parallel with the plasma membrane (Fig. 22). The quantities of oil drops and starch increase. Most of the plastids are distributed at the micropylar end. The vacuolation of the chalazal half increases.

The synergid cells

The persistent synergid cell and the degenerated one appear similar in structure before pollination and gradually become different after pollination. The persistent synergid cell retains its original constitution, but the degenerated one changes drastically.

Figs. 17-29. The mature embryo sac in the interval between pollination and fertilization.

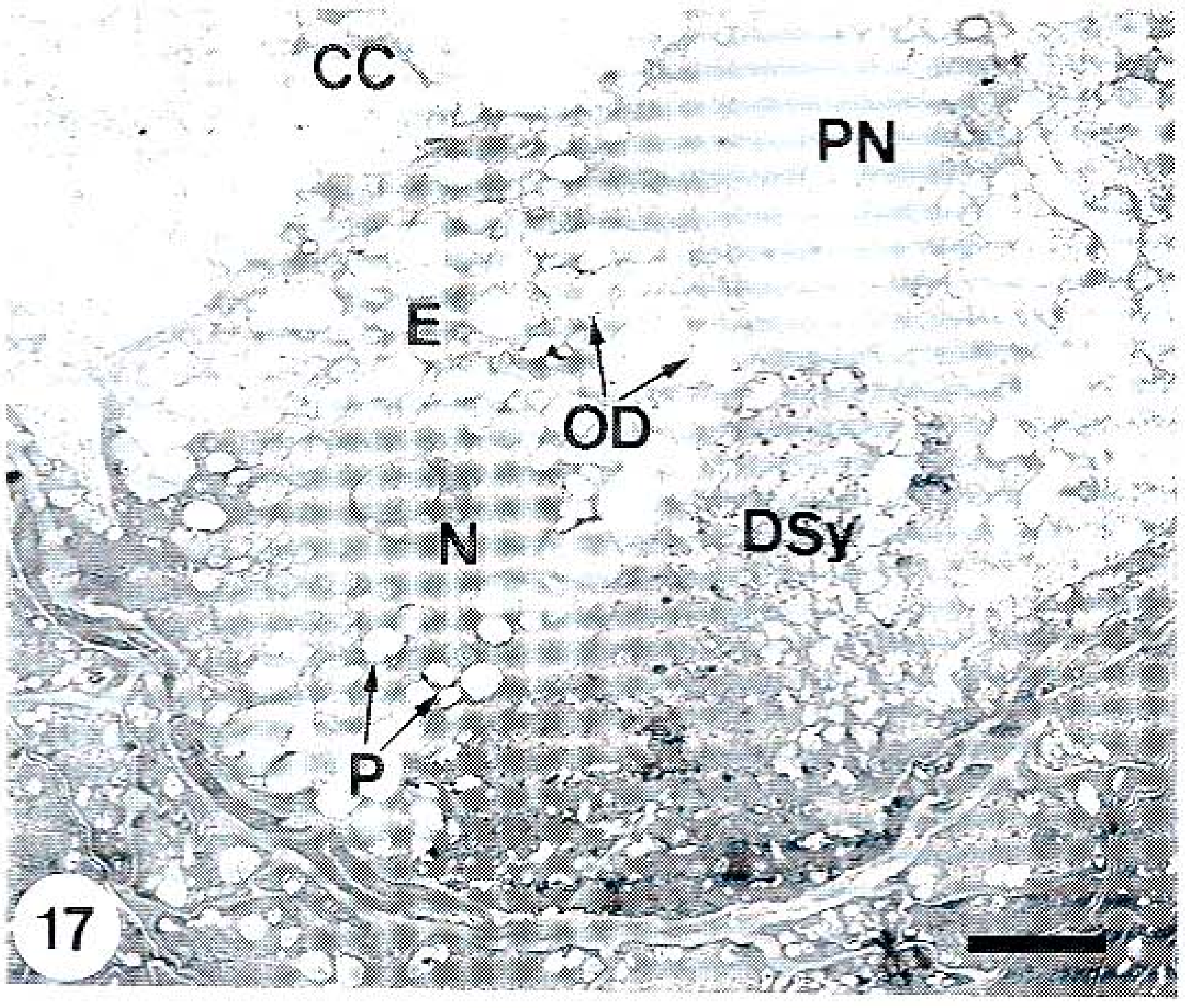
Fig. 17. The longitudinal section of the embryo sac, showing the egg, the degenerated synergid cell and portion of the central cell. Note the nucleus shape and the distribution of the cytoplasm in the egg. (bar=5 μm)

Fig. 18. Portion of the degenerated synergid cell, showing the cell lumen filled with the electron dense materials. (bar=2 μm)

Fig. 19. Portion of the degenerated synergid cell, showing the electron dense materials proximal to the filiform apparatus and the degenerated nucleus. (bar=1 μm)

Figs. 20-21. Portion of the degenerated synergid cell, showing degenerated organelles. (bar=500 nm)

Fig. 22. A contact portion of the degenerated synergid cell, the egg and the central cell. Note many small vesicles (▶) formation between two plasma membranes and the long ER parallel to the plasma membrane in the egg. (bar=500 nm)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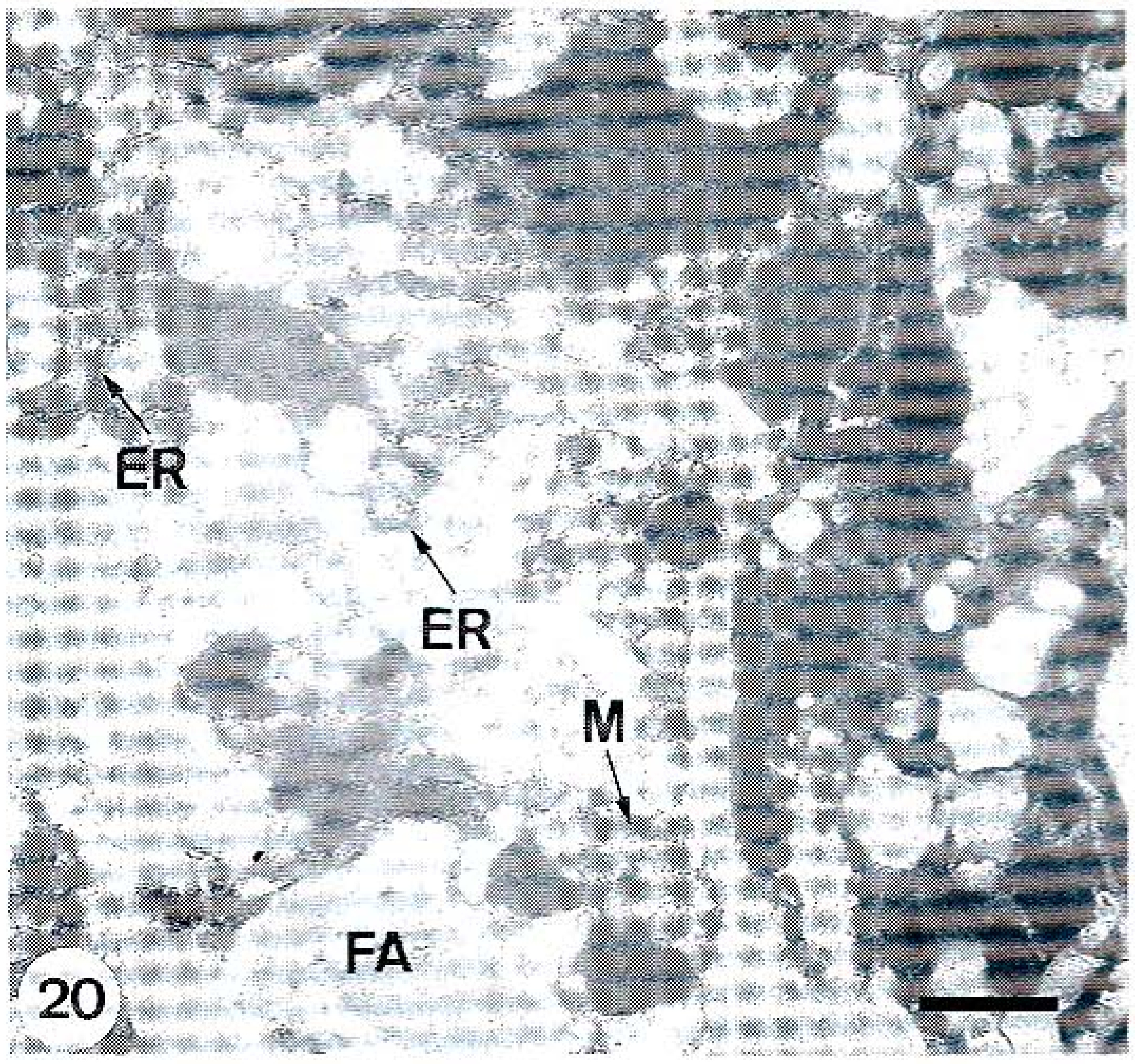
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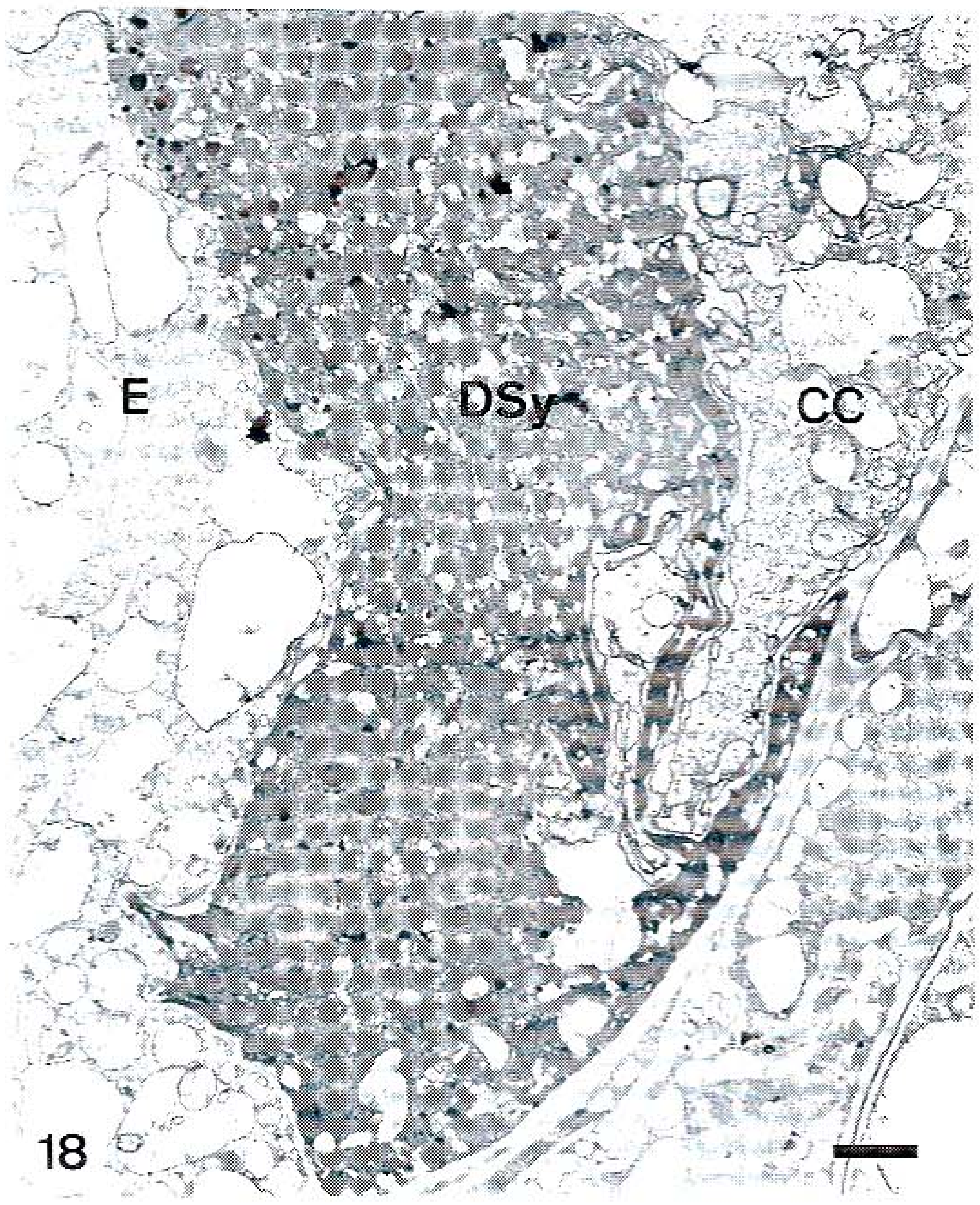
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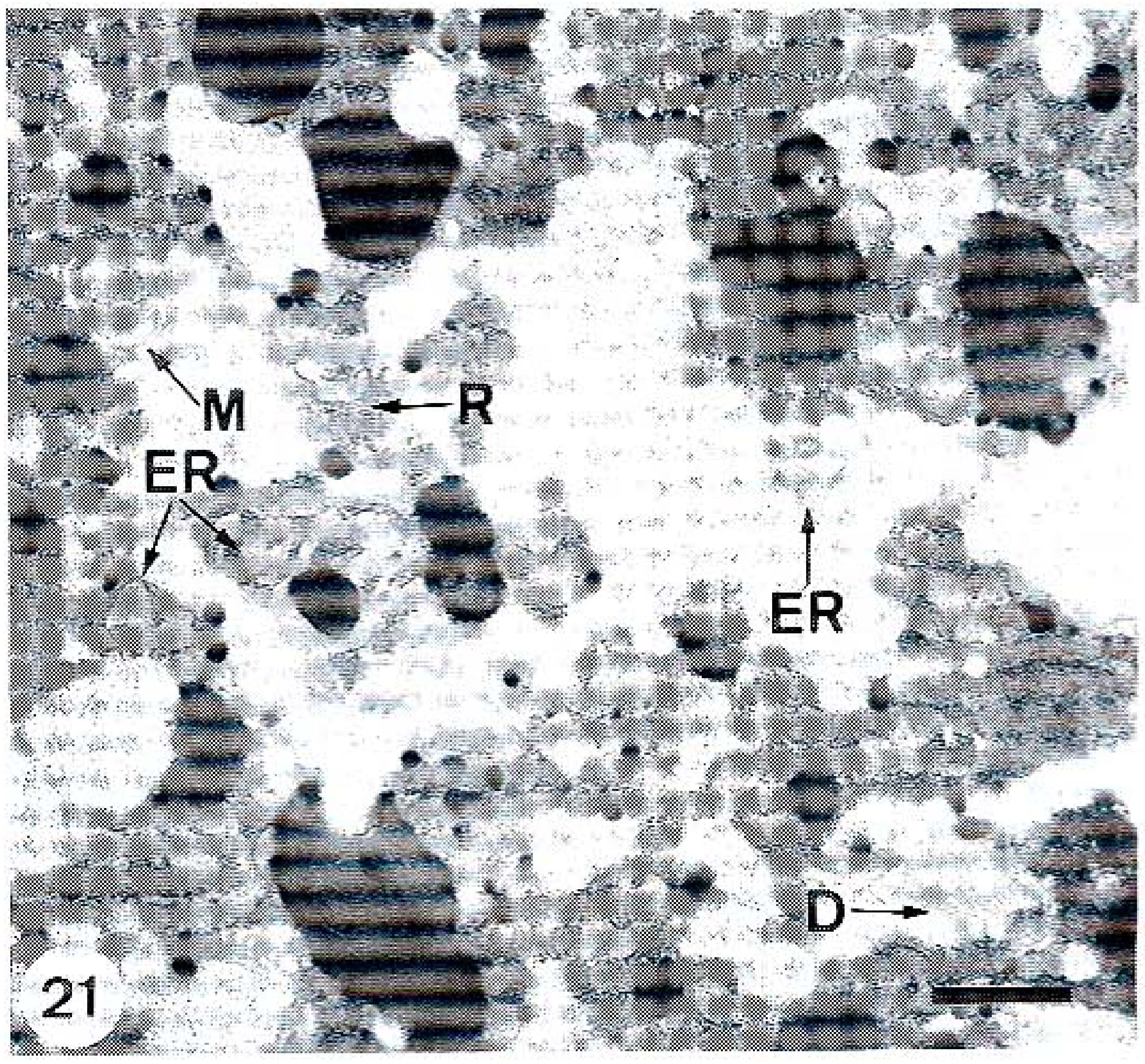
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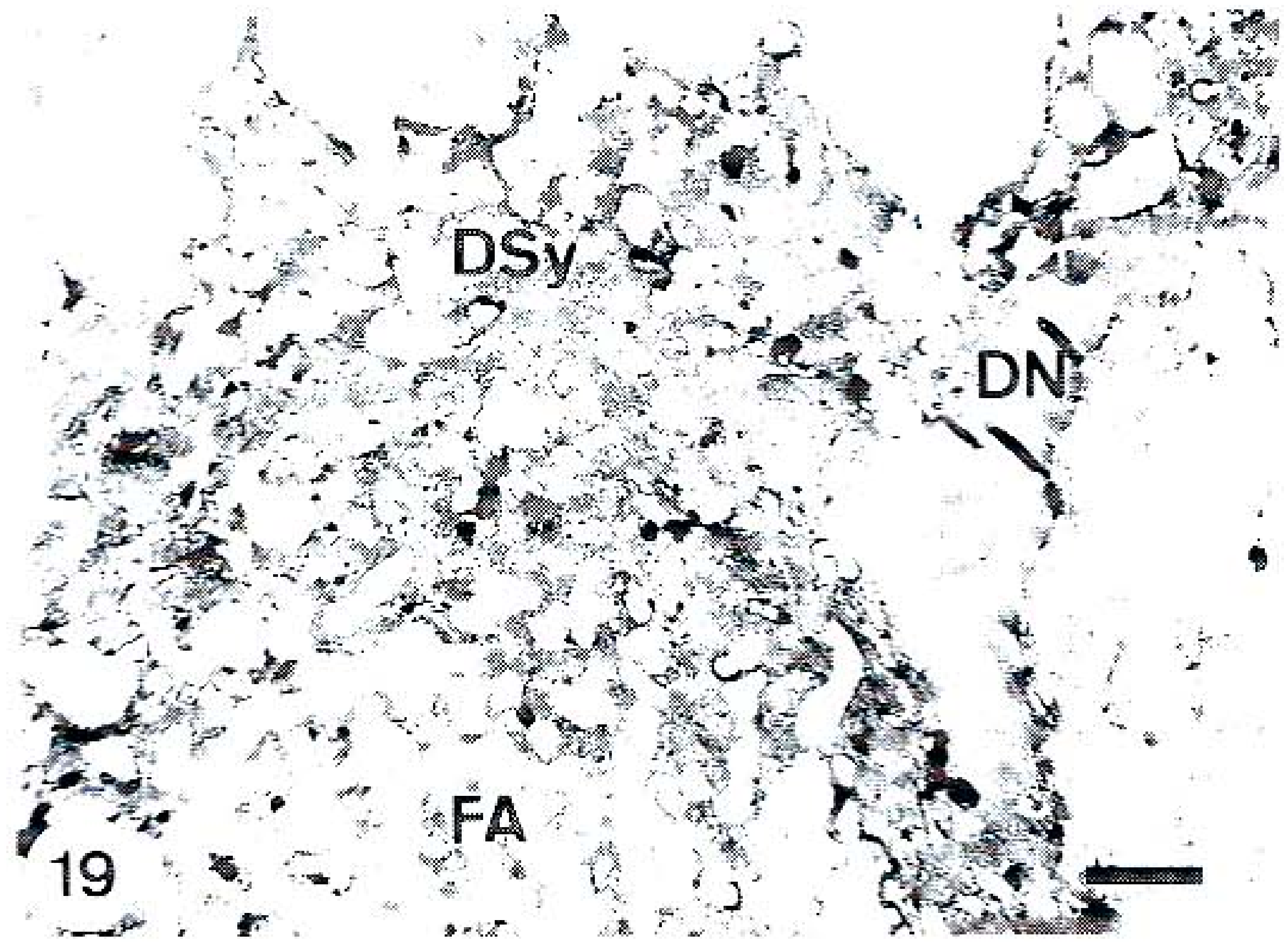
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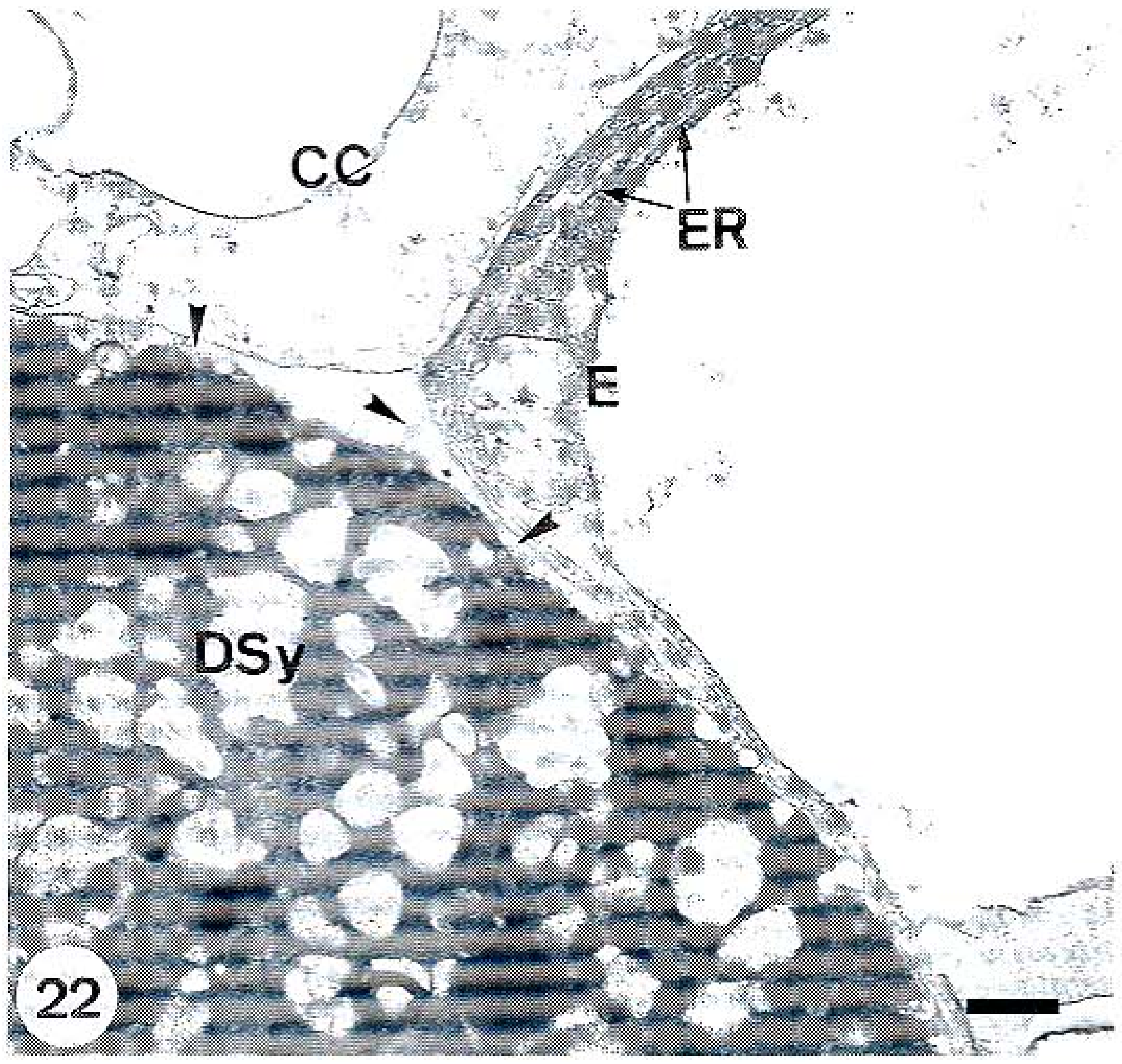
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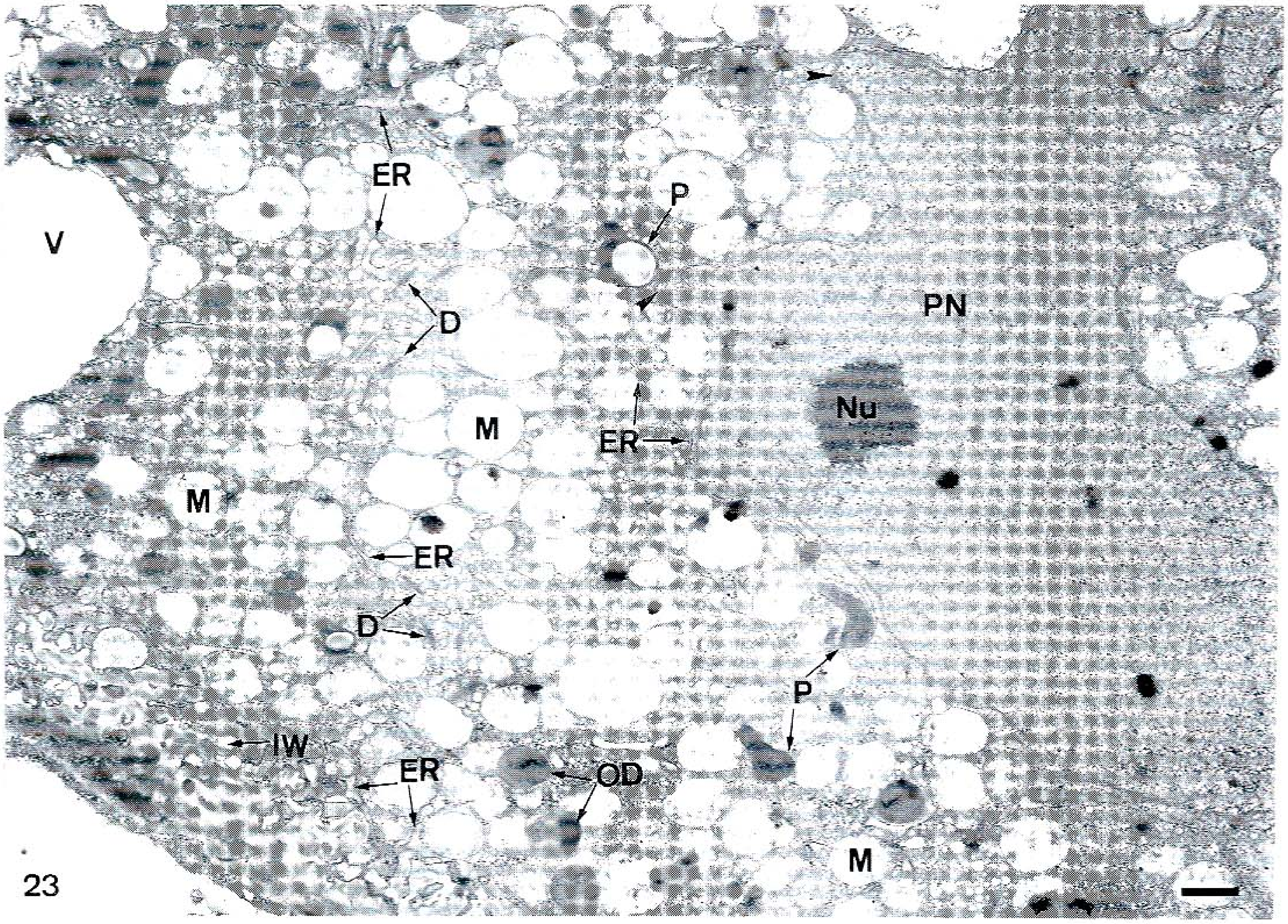

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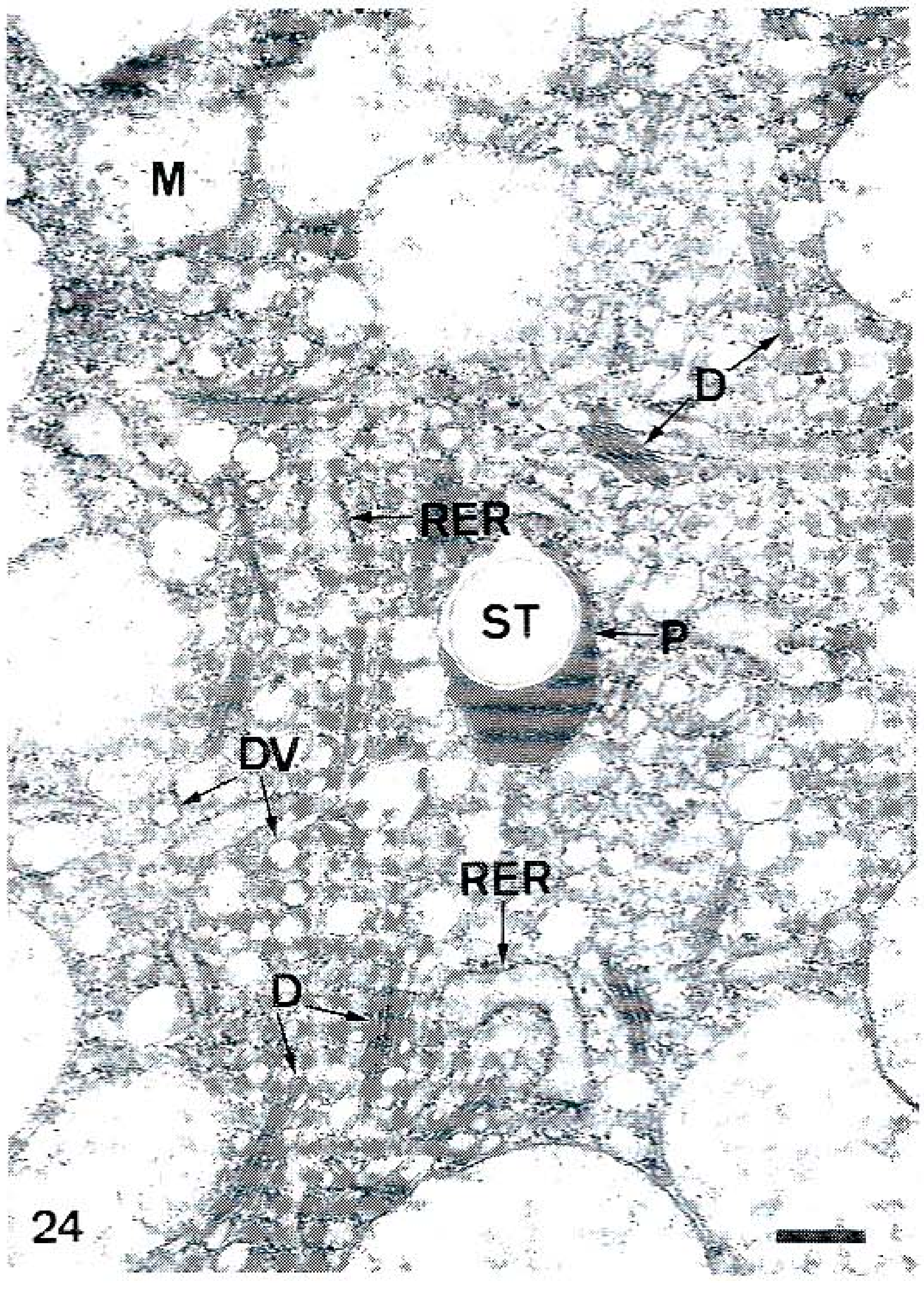

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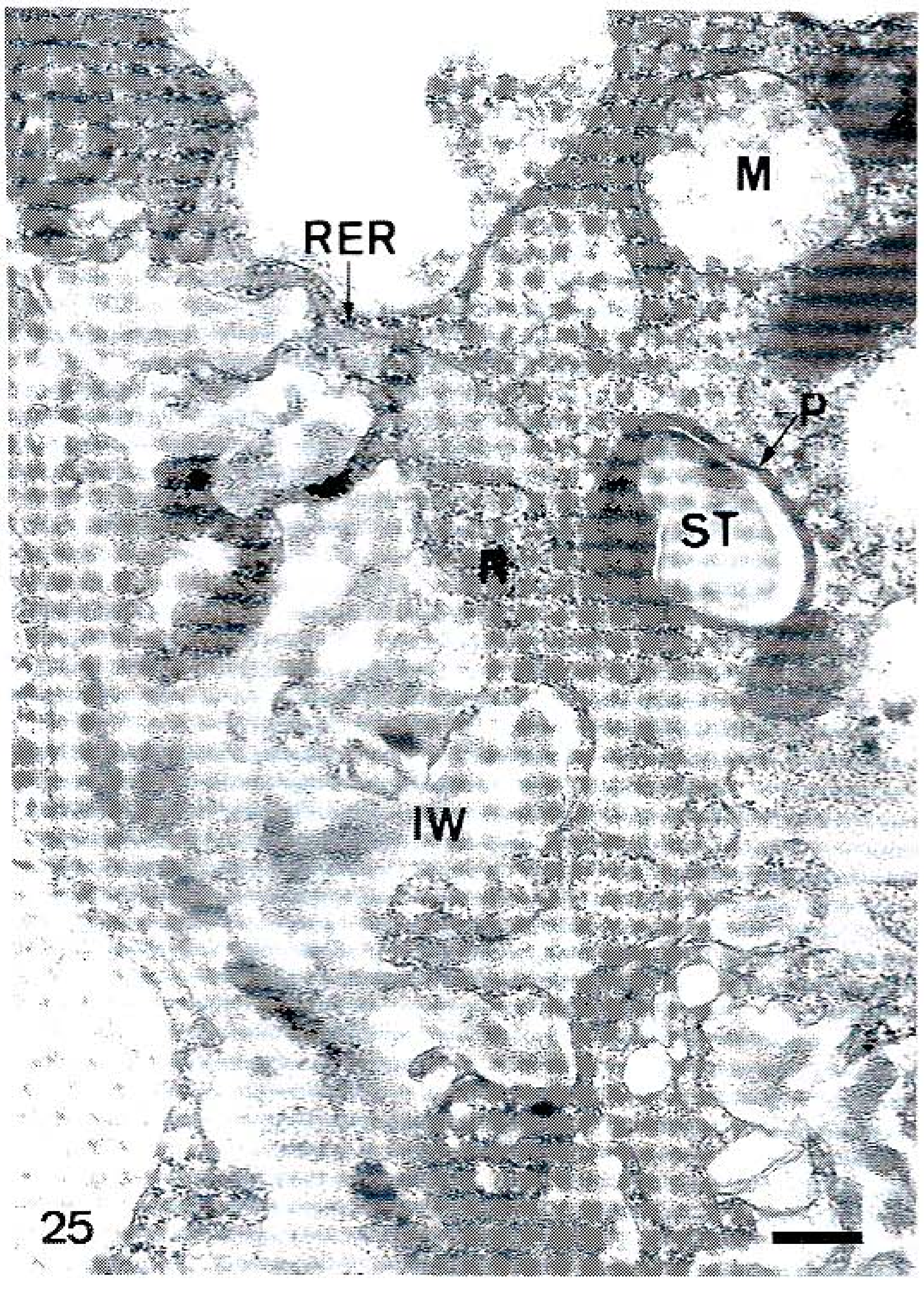

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Before the pollen tube reaches to the embryo sac, organelles of the degenerated synergid cell degenerate almost completely. A large amount of the electron dense materials almost fill the cell lumen (Fig. 18), but some areas appear electron transparency. Some degenerated organelles, which include nucleus (Fig. 19), mitochondria, dictyosomes and ER (Figs. 20, 21), can be found, especially near the filiform apparatus. At the micropylar end, some small vesicles are present between two plasma membranes (Fig. 22). The plasma membrane of the degenerated synergid cell is almost not discernible.

The central cell

Most of the cytoplasm is restricted to the perinuclear region. Compared with pre-pollination, the numbers of the dictyosomes and dictyosome vesicles increase evidently (Figs. 23, 24). The quantities of oil drops and starch also slightly increase. The nuclei become irregular in shape and have some lobed edges (Fig. 23). The polar nuclei retain partially fused. There are many ingrowth walls in the cell wall adjacent to the nucellus. The degree of the wall ingrowth is generally homogenenous, although some sections show that they decrease slightly from the chalazal end to the micropylar end. Many rough ER, ribosomes, mitochondria and oil drops are still near the ingrowth walls (Fig. 25).

The antipodal cells

The vacuolation of the antipodal cells increases slightly. Most of the parallel stacked rough ER becomes to be parallel to the cell walls and some regions show cisternal dilations (Figs. 26-29).

The relative numbers of mitochondria, rough ER, ribosomes and dictyosomes increase in the antipodal cells. Sometimes, the dense-staining particles can be found between the plasma membranes and the cell walls (Fig. 28). The ingrowth walls are present in the antipodal cells adjacent to the nucellus, but their degree is much less than that in the central cell (Fig. 29). The quantity of oil drops increases slightly and plastids are still without starch.

DISCUSSION

The mature embryo sac

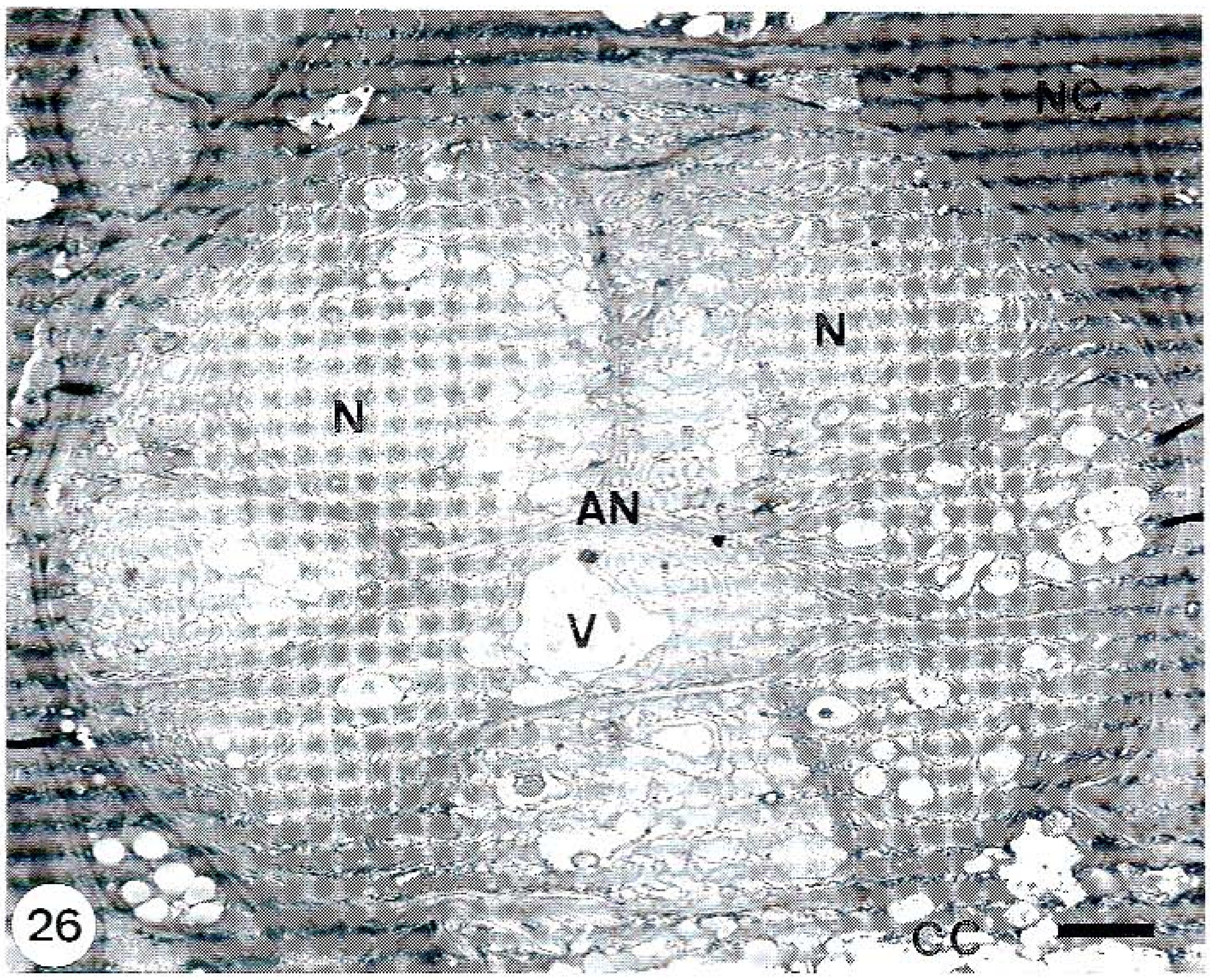
The mature embryo sac of *Arundo formosana* Hack. consists of an egg, two synergid cells, a diploid central cell and a various number of antipodal cells. This is typical of the Poaceae, including *Eustachys* (Aulbach-Smith and Herr, 1984), *Paspalum* (Chao, 1971), *Zea* (Diboll and Larson, 1966), most of *Eleusine* (Mahalingappa, 1977), *Oryza* (Jones and Rost, 1989), *Agrostis interrupta* (Maze and Bohm, 1974), *Stipa* (Maze and Bohm, 1973; Maze and Lin, 1975) and *Triticum* (You and Jensen, 1985).

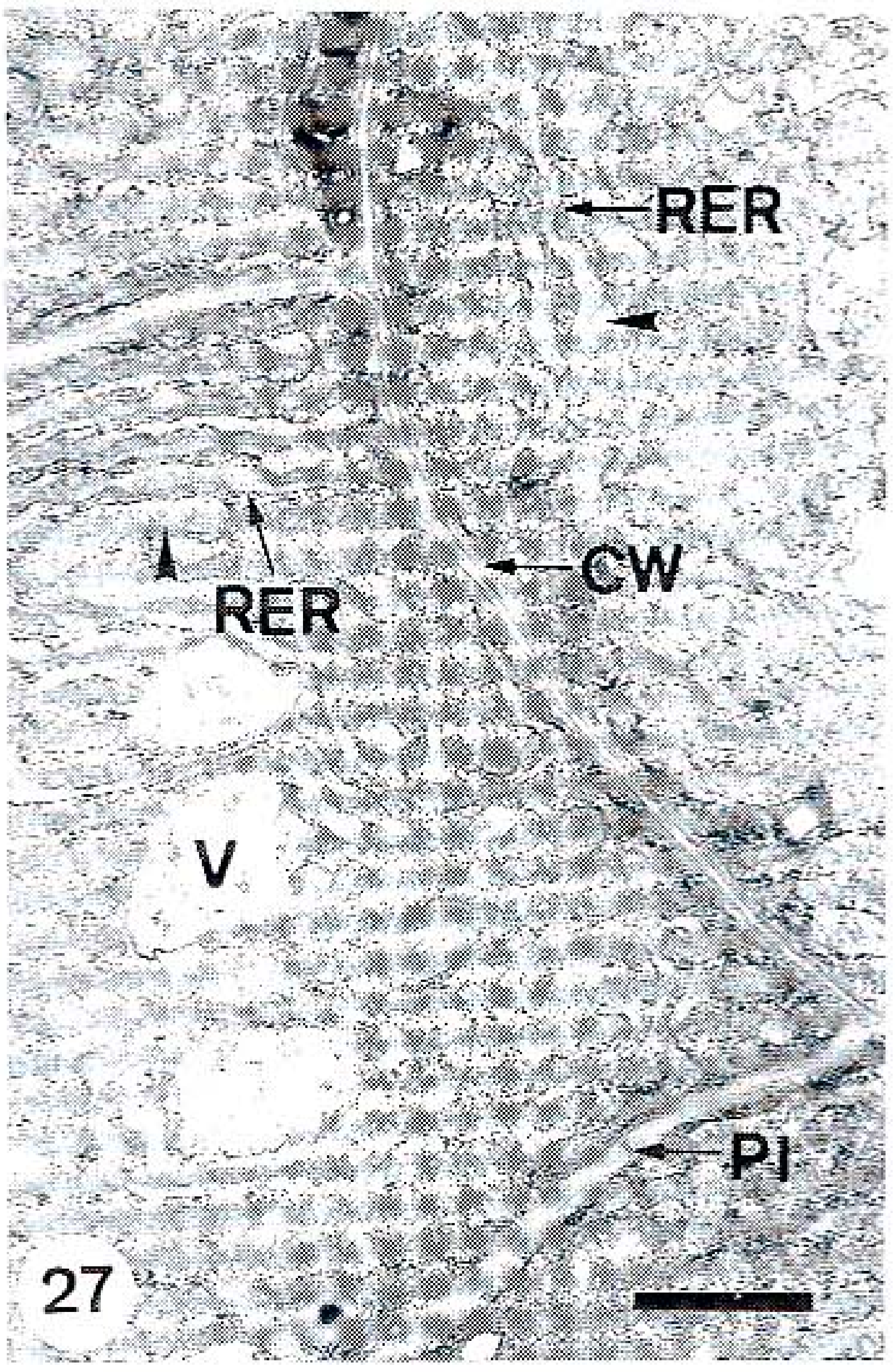
Figs. 23-25. Portion of the central cell.

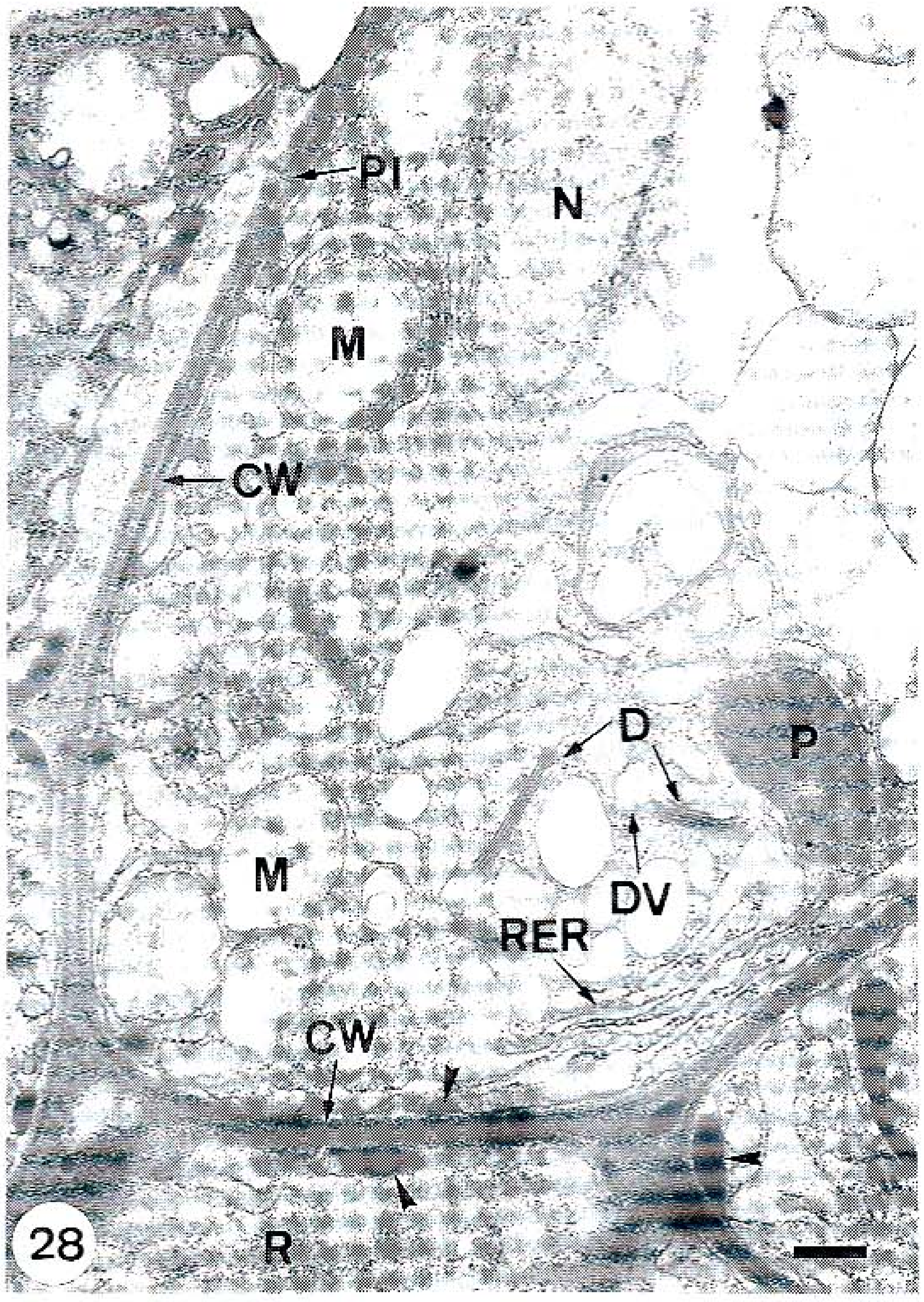
Fig. 23. Showing the polar nuclei, the perinuclear cytoplasm and the ingrowth wall. Note the polar nuclear membranes to form some lobed edges (▶). (bar=1 μm)

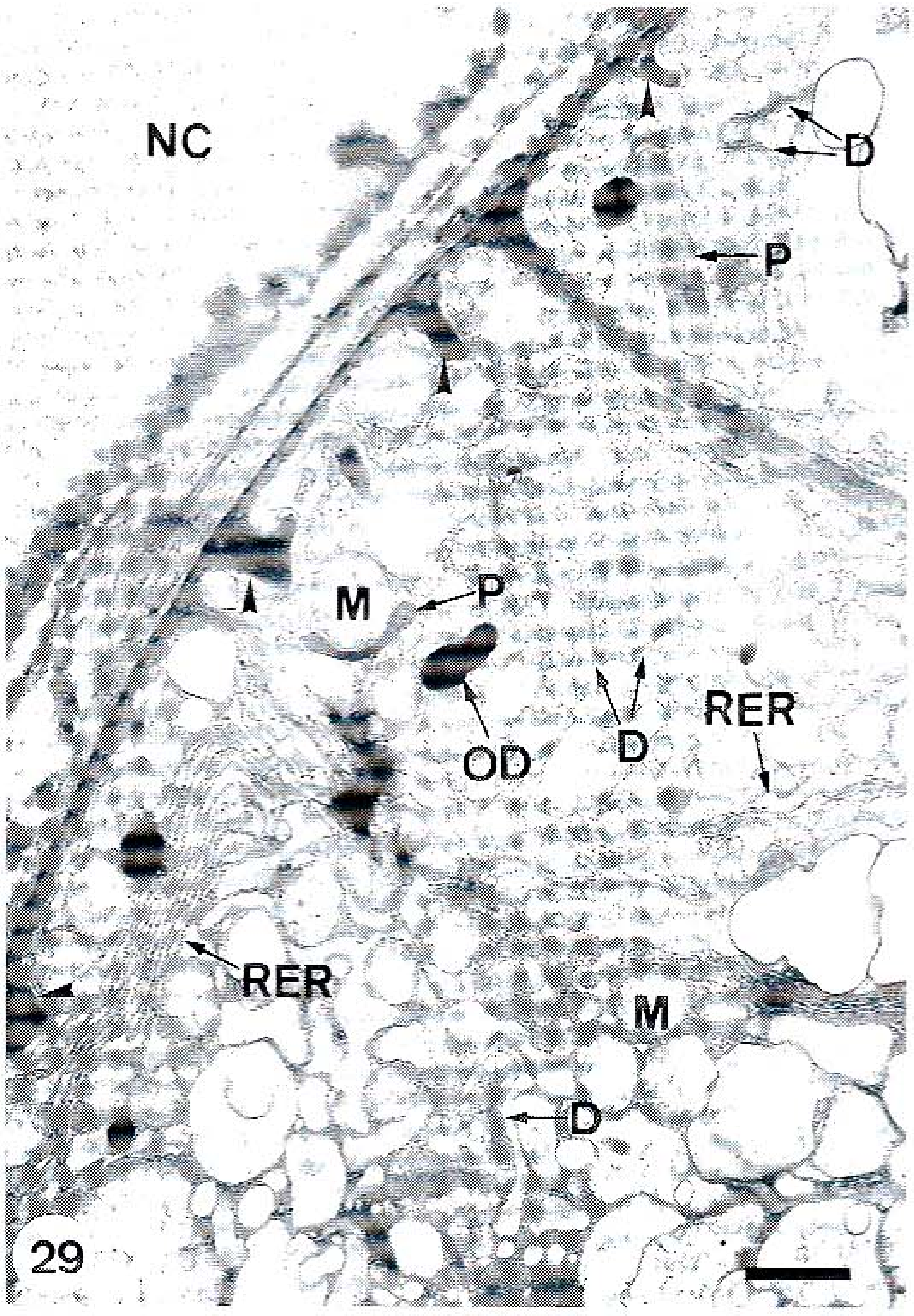
Fig. 24. Showing plastids, mitochondria, rough ER, dictyosomes and dictyosome vesicles. (bar=300 nm)

Fig. 25. Showing the ingrowth wall and its peripheral cytoplasm. (bar=300 nm)









Figs. 26-29. The antipodal cells.

Fig. 26. The longitudinal section. (bar=4 μm)

Fig. 27. Showing parallel stacked rough ER parallel to the cell wall and some regions showing cisternal dilations (▶). (bar=1 μm)

Fig. 28. Showing plastids, mitochondria, rough ER, dictyosomes and dictyosome vesicles. Note the electron dense particles (▶) between the plasma membranes and the cell wells. (bar=500 nm)

Fig. 29. Showing the ingrowth wall (▶) and some organelles. (bar=1 μm)

The egg

In most angiosperm species, the mature egg shows a complex organization characterized by distinct polarity (Willemse and van Went, 1984). The egg of *Arundo* is the same. In *Arundo, Zea* (Diboll and Larson, 1966), *Glycine* (Folsom and Peterson, 1984), *Arabidopsis* (Mansfield *et al.*, 1991) *Nicotiana* (Mogensen and Suthar, 1979), *Helianthus* (Newcomb, 1973; Yan *et al.*, 1991), *Capsella* (Schulz and Jensen, 1968b), *Brassica* (Sumner and van Caeseele, 1989), *Ornithogalum* (Tilton, 1981; Tilton and Lersten, 1981) and *Triticum* (You and Jensen, 1985), the polarity is established before fertilization in the egg. Except for grasses *Arundo, Zea* and *Triticum,* the large nucleus of the egg in the others is situated at the chalazal end of the cell and surrounded by the majority of the cytoplasm, whereas a large vacuole is situated at the micropylar end of the cell. Before pollination, the nuclear position is central in *Arundo* and *Triticum,* that is central and slightly toward the chalazal end in *Zea.* In *Arundo, Zea* and *Triticum,* the cytoplasm distribution is perinuclear and many vacuoles are distributed at the chalazal half. After pollination, the cytoplasm of *Arundo* is distributed at micropylar half; in other words, the polarity of the egg shows a considerable increase. There are few reports describing this condition. The egg is no characteristic distribution of organelles in grass *Stipa* (Maze and Lin, 1975).

In many angiosperm species, including *Arundo,* the egg is only partially surrounded by a cell wall at the micropylar end that the cell wall is the thickest at the micropylar end, and becomes thinner and thinner gradually toward the chalazal end. Its chalazal end is limited by a plasma membrane. Some species are different from this condition. In *Epidendrum* (Cocucci and Jensen, 1969) and *Bellis* (Engel and Petersen, 1977), the wall is more complete. In *Capsella,* the expanded areas of the cell wall appear to be either electron translucent or containing an electron-dense substance (Schulz and Jensen, 1968b). In *Ornithogalum,* the chalazal wall material may be present not as a continuous, but rather as disjunct islands of wall materials (Tilton, 1981). In *Glycine,* the egg contains expanded wall areas at the chalazal end (Folsom and Peterson, 1984). In *Brassica,* the chalazal wall between the egg and the central cell consists of electron-transparent expanded region of cell wall alternating with deposits of electron-opaque materials (Sumner and van Caeseele, 1989). In *Arabidopsis,* the plasma membranes between the egg and the central cell are separated by wide gaps that contain a small mass of electron dense materials (Mansfield *et al.*, 1991). *Arundo* also has electron dense materials, but it appears different with *Arabidopsis.*

The cytoplasm of the egg of *Arundo* before pollination appears very similar with that of *Zea* (Diboll and Larson, 1966) and *Triticum* (You and Jensen, 1985). Mitochondria and ribosomes are abundant, but ER and dictyosomes are scarce. The distribution of dictyosomes is at the periphery of the cell. Plastids usually contain starch and are less abundant than mitochondria.

Mansfield *et al.* (1991) suggested that the egg may serve other roles in certain species, e. g., as a sink for carbohydrate prior to fertilization, indicated by the presence of starch in proplastid (Sumner and van Caeseele, 1989), providing a source of nutrients during fertilization and early embryo development. We agree this repect, because the quantities of oil drops and starch increase after pollination. The egg of *Arundo* appears to be a sink for oil and carbohydrate. They may be from the central cell or the synergid cells.

The synergid cells

In a number of species, including *Arundo*, *Hordeum* (Cass and Jensen, 1970), *Paspalum* (Chao, 1971), *Gossypium* (Jensen, 1965a), *Stipa* (Maze and Lin, 1975), *Nicotiana* (Mogensen and Suthar, 1979), *Brassica* (Sumner and van Caeseele, 1989), *Spinacia* (Wilms, 1981) and *Helianthus* (Yan *et al.*, 1991), one of the two synergid cells degenerates before fertilization. The degeneration results in a decreased volume of the synergid cell, disappearance of the vacuole, and an increased stainability and density of the cytoplasm (Willemse and van Went, 1984). In other species as *Zea* (Diboll, 1968), *Glycine* (Folsom and Peterson, 1984), *Arabidopsis* (Mansfields *et al.*, 1991), and *Capsella* (Schulz and Jensen, 1968a), two synergid cells remain healthy until the moment of pollen tube penetrating into the embryo sac. The two synergid cells show similar degeneration in *Eustachys* (Aulbach-Smith and Herr, 1984) and *Triticum* (You and Jensen, 1985). Mogensen (1984) showed that the synergid degeneration occurs in various patterns in *Hordeum*.

The polarity of the synergid cells in *Arundo* appears different with other angiosperms, including *Glycine* (Folsom and Peterson, 1984), *Gossypium* (Jensen, 1965a), *Arabidopsis* (Mansfields *et al.*, 1991), *Nicotiana* (Mogensen and Suthar, 1979), *Helianthus* (Newcomb, 1973; Yan *et al.*, 1991), *Capsella* (Schulz and Jensen, 1968a) and *Ornithogalum* (Tilton, 1981; Tilton and Larsten, 1981) that a single large vacuole occurs at the chalazal end, and the nucleus and the majority of the cytoplasm distribute at the micropylar end. In *Brassica* (Sumner and van Caeseele, 1989), the vacuoles are uniformly distributed and never become a predominant component of the mature synergid cell. The numerous vacuoles increase in volume toward the chalazal end of the synergid cell in grasses *Zea* (Diboll and Larson, 1966) and *Stipa* (Maze and Lin, 1975), but the vacuoles are uniformly distributed in *Arundo*.

The cytoplasm degeneration of the synergid cell in *Arundo* is similar with *Brassica* (Sumner and van Caeseele, 1989), *Aquilegia* (Vijayaraghavan *et al.*, 1972) and *Helianthus* (Yan *et al.*, 1991). The two synergid cells appear similar before pollination and gradually different after pollination. Finally, the degenerated synergid cell is almost filled with the electron dense materials; however, some regions appear electron transparency. Maze and Lin (1975) considered that these electron transparent areas are the remains of small vacuoles in *Stipa*.

After pollination, one of two synergid cells in *Arundo* retains its original constitution which is the persistent synergid cell. The cytoplasm of the persistent synergid cell is rich in organelles, especially in mitochondria, dictyosomes and ER. In *Arundo*, there is a tendency for a high concentration of mitochondria to accumulate near the filiform apparatus, which has also been shown to be the case in *Zea* (Diboll, 1968), *Gossypium* (Jensen, 1965a), *Capsella* (Schulz and Jensen, 1968a) and *Arabidopsis* (Mansfields *et al.*, 1991). In contrast to this case, in some species including *Quercus* (Mogensen, 1972; 1973; 1975), *Brassica* (Sumner and van Caeseele, 1989) and *Ornithogalum* (Tilton, 1981), the mitochondria are uniformly distributed. The numerous dictyosomes, which are active in vesicle production, are found close to the filiform apparatus in *Arundo*, *Zea*, *Arabidopsis*, *Ornithogalum* and *Helianthus* (Yan *et al.*, 1991). In *Arundo*, ER is present as dilated vesicles and similar with *Zea* (Diboll and Larson, 1966), but parallel stacked cisternae in *Capsella*, *Brassica* and *Arabidopsis*. The distribution of ER in *Arundo* is uniform, but large accumulation adjacent to the filiform apparatus in *Gossypium* and *Arabidopsis*.

The plastids of the synergid cells in *Arundo* do not contain starch and the same case is in *Ornithogalum* (Tilton, 1981) and *Zea* (Diboll, 1968; Diboll and Larson, 1966). In contrast to this case, the starch-containing plastids are present in *Stipa* (Maze and Lin, 1975), *Gossypium* (Jensen, 1965a), *Arabidopsis* (Mansfields *et al.*, 1991) and *Brassica* (Sumner and van Caeseele, 1989).

In most species, including *Arundo*, the filiform apparatus forms a broad layer of long, irregular finger-like wall projections extending into the cytoplasm. In contrast to this case, in *Nicotiana* (Mogensen and Suthar, 1979), the filiform apparatus does not possess these finger-like wall projections. Instead, large cell wall proliferations occur on the lateral synergid walls just chalazal to the apical pocket region. The synergid cells of sunflower have neither finger-like wall projections on their filiform apparatus nor lateral cell wall projections (Newcomb and Steeves, 1971; Yan *et al.*, 1991). In some danthonioid grasses, the synergid cells with a haustorial projection, which extends through the micropyle to lie between the ovule and ovary wall (Philipson and Conner, 1984).

The central cell

In *Arundo*, the polar nuclei are partially fused before fertilization, which is also the same case in *Zea* (Diboll and Larson, 1966), *Glycine* (Folsom and Peterson, 1984), *Stipa* (Maze and Lin, 1975) and *Triticum* (You and Jensen, 1985). In contrast to this case, the polar nuclei are completely fused before fertilization in *Arabidopsis* (Mansfield *et al.*, 1991), *Helianthus* (Newcomb, 1973; Yan *et al.*, 1991), *Capsella* (Schulz and Jensen, 1973) and *Ornithogalum* (Tilton and Lersten, 1981).

The central cell of most species, including *Arundo*, has a complex organized cytoplasm which is rich in organelles. The rough ER, mitochondria and plastids are abundant, ribosome concentration is high, and dictyosomes are numerous and active in vesicle production. In contrast to this case, the numbers of mitochondria and dictyosomes are low, and the ER is poorly developed in *Petunia* (van Went, 1970).

In *Arundo*, *Triticum* (You and Jensen, 1985), *Capsella* (Schulz and Jensen, 1973), *Gossypium* (Jensen, 1965b), *Spinacia* (Wilms, 1981) and *Helianthus* (Yan *et al.*, 1991), plastids with starch grains are present in the cytoplasm of the central cell. The starch-containing plastids are abundant in *Glycine* (Folsom and Peterson, 1984) *Arabidopsis* (Mansfield *et al.*, 1991) and *Nicotiana* (Sehgal and Gifford, 1979). The plastids in most central cell are less-differentiated, but *Capsella* and *Arabidopsis* have well-developed chloroplasts.

As in *Triticum* (You and Jensen, 1985) and *Arabidopsis* (Mansfield *et al.*, 1991), the polar nuclei of *Arundo* become irregular and nuclear membranes form some lobed edges before fertilization. The polar nuclei of *Spinacia* also form long protrusion (Wilms, 1981). This feature may be prepared for fertilization.

A structural characteristic of the central cell in *Arundo* is the wall ingrowth adjacent to the nucellus. The degree of the wall ingrowth seems to be homogeneous from the chalazal end to the micropylar end. In contrast to *Arundo*, these ingrowth walls occur at the micropylar end of the central cell in close association with the egg apparatus in *Zea* (Diboll and Larson, 1966), *Glycine* (Folsom and Peterson, 1984), *Helianthus* (Newcomb and Steeves, 1971, *Capsella* (Schulz and Jensen, 1973) and *Spinacia* (Wilms, 1981). The central cell of *Arabidopsis* (Mansfield *et al.*, 1991) is the absence of ingrowth walls. The central cell of *Arundo* can be called transfer cell because of these ingrowth walls (Pate and Gunning, 1972). Newcomb and Steeves (1971) suggested that the ingrowth walls of the central cell play an important role in the absorption of metabolites from the surrounding tissues. In *Helianthus*, the lipid bodies increase in size and number gradually as the central cell matures. The quantities of oil drops and starch in *Arundo* increase after pollination. In *Arundo* and *Glycine* (Folsom and Peterson, 1984), mitochondria and rough ER are closely associated with the wall ingrowth. Folsom and Peterson (1984) suggested that they are sites of intense metabolic activity.

The antipodal cells

In many dicotyledons, the antipodal cells degenerate before or during maturation of the embryo sac. But in grasses, including *Arundo*, *Zea* (Diboll and Larson, 1966), *Stipa* (Maze and Lin, 1975) and *Triticum* (You and Jensen, 1985), the antipodal cells are very active at mature which the cytoplasm contains a large amount of ER and ribosomes. In *Arundo*, some ER is present in parallel stacked cisternae and some shows cisternal dilations before pollination. After pollination, most of ER is present in parallel stacked cisternae and arranges parallel with the cell wall, that is the same with the mature antipodal cells of *Zea*, *Stipa* and *Triticum*. Brink and Cooper (1944) suggested that the antipodal cells are most active about the time of fertilization based on studies of hybrids of barley and rye. They postulated that normal activity is essential for endosperm development. The antipodal cells of *Arundo*, *Zea* and *Triticum* are no polarity, but some antipodal groups of *Stipa* show some polarization in the cells which are contiguous to the central cell to have a greater amount of ER.

The plastids of the antipodal cells in *Arundo* are uniformly distributed and without starch, as in *Stipa* (Maze and Lin, 1975) and *Triticum* (You and Jensen, 1985), but some plastids with small starch grains are present in *Zea* (Diboll and Larson, 1966). Oil drops are few in *Arundo* and *Zea*. A special feature in the antipodal cells of *Arundo* is that some dense-staining particles are present between the plasma membranes and the cell walls. There are few reports to describe this feature.

In most grasses, including *Arundo*, the cell walls are complete between the antipodal cells, but the cell walls are absent in parts in *Zea* (Diboll and Larson, 1966) forming a syncytium.

The antipodal cells of *Arundo* can be called transfer cell because their cell walls adjacent to the nucellus are tending to be papillate and they contain an extensive system of rough ER (Pate and Gunning, 1972). The same condition is found in *Zea* (Diboll and Larson, 1966), *Stipa* (Maze and Lin, 1975), *Helianthus* (Newcomb, 1973) and *Spinacia* (Wilms, 1981).

In many species, including *Arundo*, some plasmodesmata can be seen between antipodal cells and between antipodal cells and central cell, but not between any antipodal cell and nucellar cells. But in *Capsella* (Schulz and Jensen, 1971), *Helianthus* (Newcomb, 1973) and *Arabidopsis* (Mansfield *et al.*, 1991), there are some plasmodesmata between antipodal cells and nucellar cells.

The main function of the antipodal cells in *Arundo* as Greenham and Chapman (1990) suggested for grasses is that they may be involved in the transfer of nutrients and serve as a pathway from the nucellus to the central cell because their transfer cell-like walls and many plasmodesmata are present between antipodal cells and central cell. Apart from the transfer of nutrients, they mays also have a secretory function because of the presence of extensive rough ER and abundant ribosomes.

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臺灣蘆竹受精前胚囊之微細構造

簡 萬 能

摘 要

臺灣蘆竹 (*Arundo formosana* Hack.)成熟之胚囊含有一位於珠孔端之卵器（由一個卵細胞和兩個助細胞組成)，中間位置爲具兩個大極核之中央細胞和於合點端有8至18個反足細胞羣。卵器於珠孔端有細胞壁，而於合點端僅有細胞膜包圍著。卵細胞之細胞質含有很多粒線體，含澱粉之顆粒與油滴。兩個助細胞頗爲類似且其內含物分佈有明顯之極性；粒線體分佈於珠孔端且圍繞著絲狀器；顆粒體分佈於合點端，而高基氏體和膨大內質網囊胞很多。中央細胞有組成複雜之細胞質且富含胞器；兩個極核部分癒合，而中央細胞與珠心細胞接壤處有很多內凸之細胞壁。反足細胞含大量之內質網和核醣體。原生質絲存在於胚囊細胞間之細胞壁，而在胚囊細胞與珠心細胞間之細胞壁則無。受粉後，卵之極性增加。宿存助細胞維持原有構造，而瓦解助細胞則瓦解且充滿於電子顯微鏡下呈濃密之物質。中央細胞內之高基氏體數目和油滴與澱粉數量皆增加。反足細胞內大部分粗質內質網成爲平行細胞壁排列；於細胞膜與細胞壁間有許多染色濃之小顆粒；反足細胞與珠心細胞接壤處亦有內凸之細胞壁。