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COMPLEX ENVELOPE SYSTEM

Membrane systems of plant cells

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[Plates 42–45]

The membrane system is made up of the nuclear envelopes, rough and smooth endoplasmic reticulum, Golgi apparatus and plasmalemma. Interconnexions between the various parts of the system are shown and these probably represent a flow of membrane from the endoplasmic reticulum through the Golgi apparatus to the plasmalemma.

Membrane fractions have been isolated from broken cells and their function in the synthesis of polysaccharides established. It has been shown that the matrix polysaccharides of the wall (pectic substances and hemicelluloses) are formed within the membranes and that the pattern of synthesis of these polymers changes during differentiation of the cells. Cellulose microfibrils are probably synthesized at the plasmalemma which is formed by incorporation of membrane bounded vesicles from the Golgi apparatus. Thus the assembly of the polymers takes place either when the membrane is within the cytoplasm or when it is incorporated as the plasmalemma of the cell.

1. Introduction

A study of plant cells at various stages of division and differentiation shows the relationship of the interchange of membranes between the various parts of the cells. In some instances a direct continuity between the different membranes can be seen. This account will attempt to trace these interrelationships. The central role of the endoplasmic reticulum in the dynamic movement, connexions and flow of membrane material will be considered.

The characteristic appearance and organization of the endoplasmic reticulum can be seen in sections of all higher plant material prepared for electron microscopy (Porter 1956; Porter & Machado 1960). Profiles of the endoplasmic reticulum in these sections represent both sheets of membrane and tubular arrays, they can be clearly seen in freeze-etched replicas of the cells (Northcote 1968*a*; Northcote & Lewis 1968). The membranes at certain stages of the cell cycle proliferate and this can be observed for instance from the two poles of the mitotic spindle at prophase and metaphase (Porter & Machado 1960; Burgess & Northcote 1968). The sheets of the endoplasmic reticulum encircle other organelles (Wooding & Northcote 1965*a*, *b*; Newcomb 1967; Roberts & Northcote 1970) and sometimes takes on a stacked appearance parallel to the plasmalemma near the periphery of the cell, and presumably the system is constantly moving, proliferating and breaking down within the cell (Burgess & Northcote 1968).

2. The endoplasmic reticulum and nuclear membrane

The nuclear envelope and the endoplasmic reticulum are very closely related (Porter & Machado 1960). There is a direct continuity of the outer nuclear membrane with endoplasmic reticulum so that the perinuclear space is in direct contact with the lumen of the endoplasmic reticulum and the chemical composition of the outer nuclear membrane must presumably be very similar to that of the membranes of the endoplasmic reticulum. Even more significant to the relationship is that the formation of the nuclear envelope which takes place at telophase, arises from the endoplasmic reticulum. Profiles of the reticulum system having penetrated into

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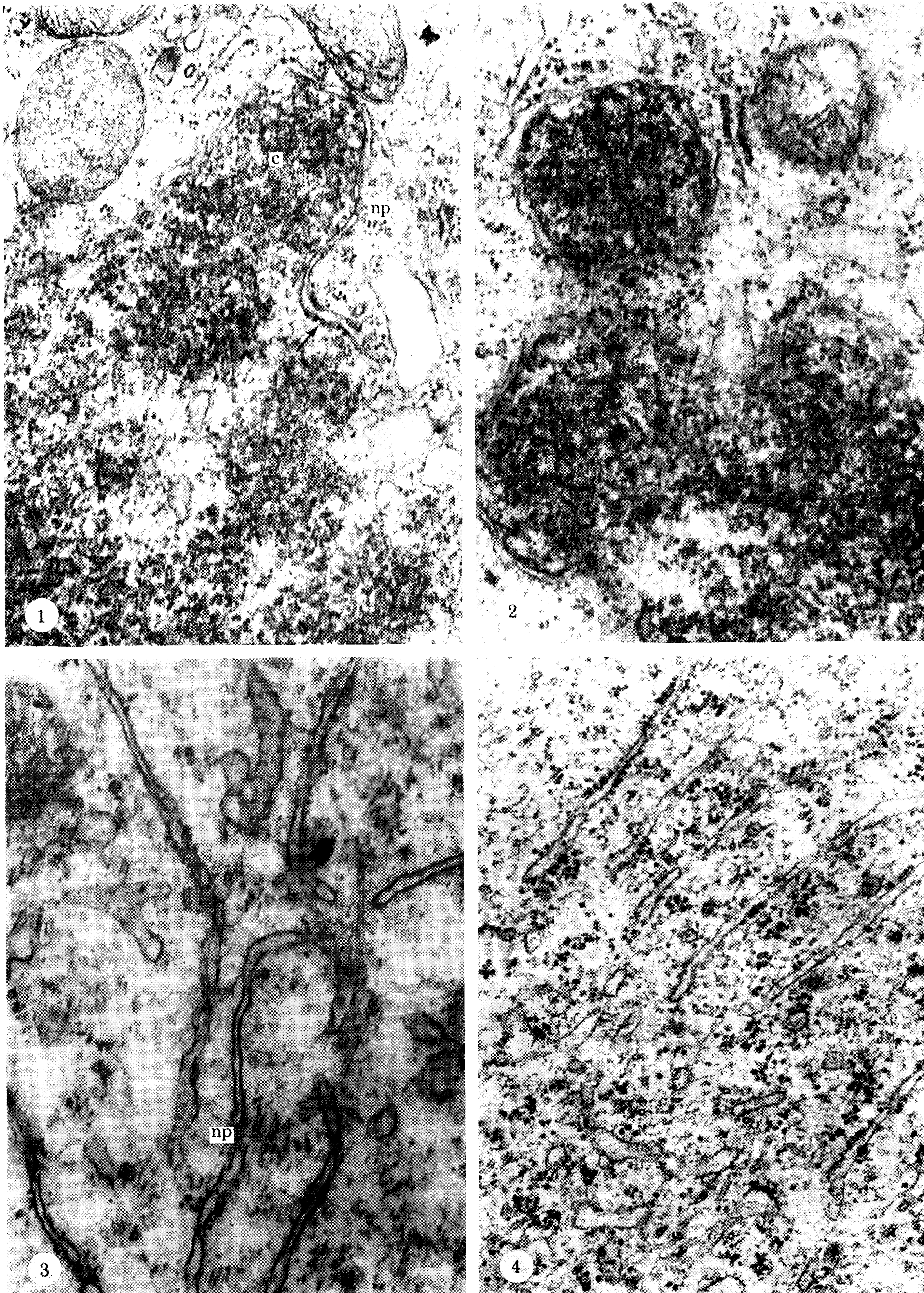
the nucleoplasm from the two mitotic poles (figures 4, 13) become closely applied to the chromosomes (figures 1, 2). The membrane on the inner surface next to the nucleoplasm loses its ribosomes and nuclear pores develop on the membranes as they become applied to the chromosomes (Roberts & Northcote 1971). The membrane portions fuse to become a complete nuclear envelope which surrounds the nucleoplasm as the chromosomes disperse (figure 5). At prophase when the nuclear envelope is broken away strands of the envelope can be detected in the cytoplasm, still carrying pores although they are indistinguishable from the general endoplasmic reticulum profiles of the cell in other respects (figure 3). After prophase they can no longer be recognized presumably because the pores are lost.

A particular problem that this method of formation and dispersion of the nuclear envelope makes apparent is that of the chemical nature of the inner and outer nuclear membranes and the possibility of any asymmetry or chemical difference between the two membranes. At its formation there is no apparent difference in the membranes of the endoplasmic reticulum that are applied to the chromosome. Both membranes as they trail away from the chromosome in the early stages of nuclear envelope formation, carry ribosomes (figure 1) and when the envelope disperses both sides take the appearance of a normal profile of the endoplasmic reticulum (figure 3). If there is a difference in chemical composition between the inner and outer membrane of the nuclear envelope then this is presumably reversible and takes place when the membrane of the endoplasmic reticulum is in close proximity to the chromatin. It is when the membrane is near the chromosomes that the nuclear pores are formed (Roberts & Northcote 1971).

The surface of the nucleus during interphase can be seen to be constantly undulating when it is viewed within a living cell by differential interference optics (Roberts & Northcote 1970, 1971). In fixed tissue large indentations lined by the nuclear envelope can be seen and these represent the undulation caught in a particular state by the fixation (figures 6, 7). The indentations are sometimes large enough to have within them cytoplasmic organelles such as mitochondria and endoplasmic reticulum and they nearly always contain microtubules which enter the indentation at the mouth and penetrate into it (figure 6). The membranes of the nucleus which line these indentations carry pores. Between the nucleus and cytoplasm there is a constant interchange of material (Goldstein 1964; Goldstein & Prescott 1967; Stevens 1967; Goldstein, Wise & Beeson 1973) and in a vacuolated plant cell the nucleus can be seen to be at the centre of a number of cytoplasmic strands along which there is continual cytoplasmic streaming both towards and away from the nucleus. The indentations serve to extend the surface contact between the nucleus and the cytoplasm. In addition the nucleus is moved about the cell and is not confined to any one position (Roberts & Northcote 1970, 1971).

The nuclear pores vary in their number and distribution pattern in different nuclei of the same plant and possibly at different stages of the same nucleus. It is probable therefore that the pores can be formed and reformed so that their organization and numbers can vary on the nuclear surface. In sycamore cell suspension culture cells the pore density is between 12 and $14/\mu m^2$ – that is, approximately 10 % of the nuclear surface. An average nucleus of diameter 15 μm carries about 9×10^3 pores.

In some plant cells, particularly those that are grown artificially in tissue culture and become tetraploid or of higher ploidy (Wright & Northcote 1973), the inner membrane of the nuclear envelope folds into the nucleoplasm to form a second type of indentation (figures 8, 9) (Roberts & Northcote 1971). These extend the perinuclear space into the nucleus and increase the surface



c, chromosome; ca, callose cone; cp, cell plate; cr, chromatin; er, endoplasmic reticulum; gv, Golgi vesicle; in, invagination of inner membrane of the nucleus; ms, mitotic spindle; ne, nuclear envelope; np, nuclear pore.

All the figures are of sycamore suspension callus cells except figures 10, 14 and 15.

FIGURE 1. Nuclear envelope reforming at telophase from profiles of the endoplasmic reticulum. In places (arrow) ribosomes are present on both membranes. A nuclear pore has formed where the endoplasmic reticulum is closely applied to the chromosome. (Magn. ×31000; Roberts & Northcote 1971.)

FIGURE 2. A stage in the formation of the nuclear envelope at telophase. The endoplasmic reticulum is closely applied to the chromosomes. (Magn. ×31000; Roberts & Northcote 1971.)

FIGURE 3. Fragments of the nuclear envelope found near the nucleoplasm at prophase. Pores are still present in the membranes. (Magn. ×27000; Roberts & Northcote 1971.)

FIGURE 4. Profiles of the endoplasmic reticulum invading the mitotic spindle during early telophase. Compare with figure 13. (Magn. ×25000.)

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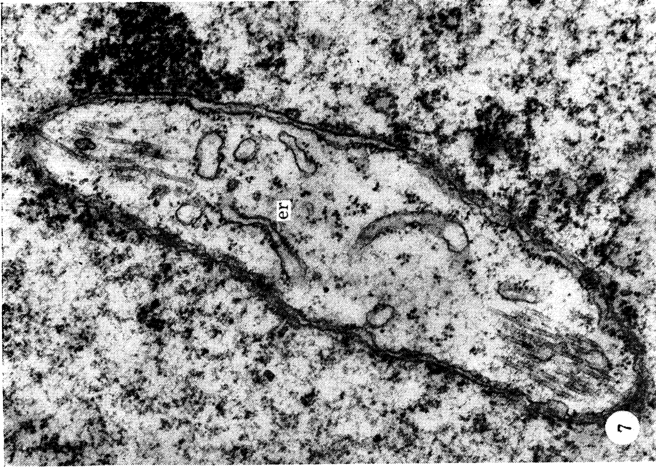

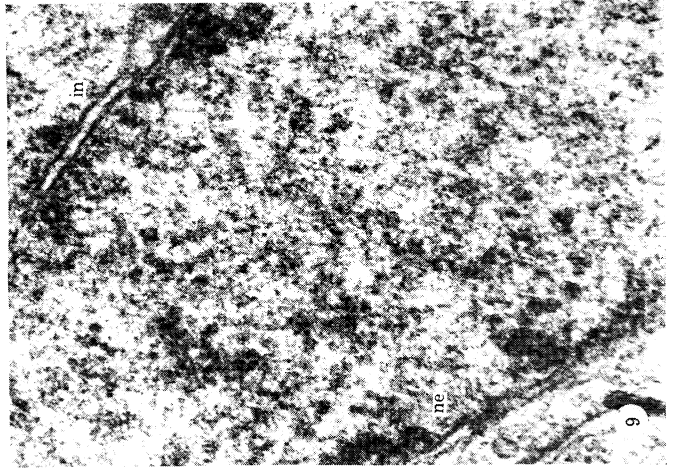

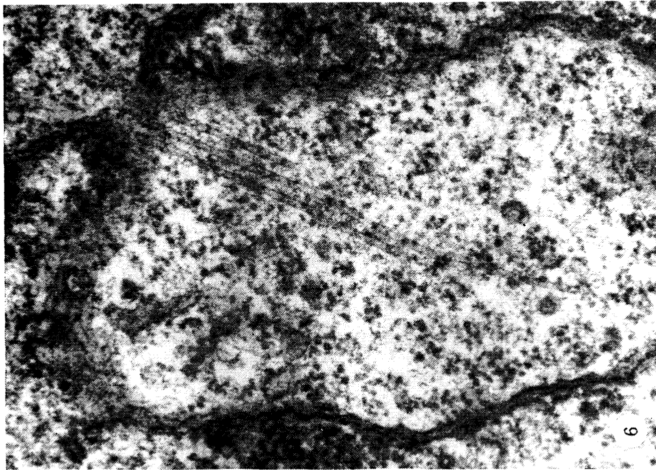

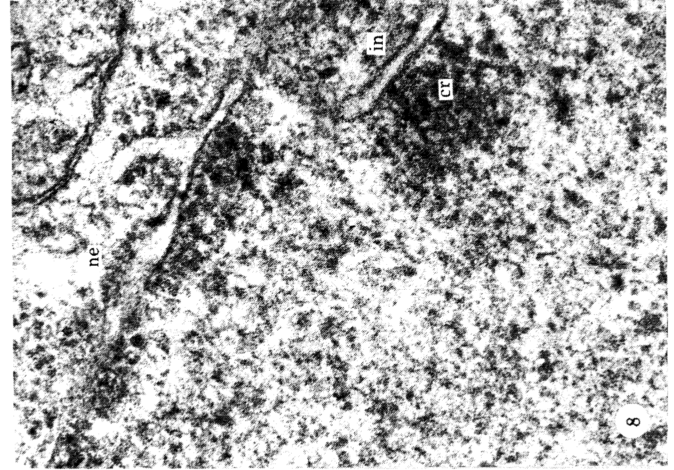

FIGURES 5–9. For description see opposite

area of the inner nuclear membrane. Since chromatin is associated with the nuclear membrane (Oppenheim & Wahrman 1973; Kay & Johnston 1973) these indentations extend the number of sites at which the chromatin can be organized within the nucleus although still associated with the membrane but not necessarily at its periphery.

The continuity of the perinuclear space with the endoplasmic reticulum provides a major transport connexion between the nucleus and the cytoplasm and this can be extended because of the association of the endoplasmic reticulum around other organelles within the cell and by the passage of the endoplasmic reticulum through plasmodesmata whereby the endoplasmic reticulum system of one cell can be connected with adjacent cells.

3. The endoplasmic reticulum

The encircling of organelles by the endoplasmic reticulum seems to have two functions. An obvious feature of such an organization is that it provides a directed, channelled route for the movement of material within the lumen of the endoplasmic reticulum to and from the organelle (Wooding & Northcote 1965*a*). Part of the transport probably takes place by diffusion or active transport across the closely applied membrane of the endoplasmic reticulum which is directly adjacent to the membrane of the organelle. It is significant that this membrane of the endoplasmic reticulum usually carries no ribosomes. A similar feature of the endoplasmic reticulum can be seen when it is closely positioned against the plasmalemma during the early stages of sieve-plate formation (Northcote & Wooding 1968 (figure 10)). That some transport can take place from organelles via the endoplasmic reticulum is apparent from a study of the resin canal cells of pine (Wooding & Northcote 1965*c*). In these cells material similar in appearance to that arising in the plastid can be found in the lumen of the endoplasmic reticulum surrounding the plastid and also in the endoplasmic reticulum some distance away from the plastid and at the reticulum profiles adjacent to the wall next to the resin duct. The material within the resin duct resembles that found in the plastid and the endoplasmic reticulum and it can be inferred that transport to the duct from the plastid has taken place through the lumen of the endoplasmic reticulum system.

A second function of the endoplasmic reticulum when it enfolds a cellular organelle can be deduced from the appearance of a cell during its differentiation into a phloem sieve tube (Northcote & Wooding 1966). The contents of the cell are broken down progressively and in an organized manner to give the fully differentiated functional unit. During the various stages of breakdown some of the organelles such as the plastids become transiently encircled by the endoplasmic

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Description of plate 43

Figure 5. The nuclear envelope almost completely formed at late telophase. (Magn. × 14000.)

Figure 6. Oblique section through a nuclear invagination. Groups of microtubules are present within it. (Magn. × 37500; Roberts & Northcote 1971.)

Figure 7. Section showing a group of parallel microtubules at the opening of a nuclear invagination. (Magn. × 20000; Roberts & Northcote 1971.)

Figure 8. Profile of an invagination of the inner nuclear membrane. Chromatin is seen in association with the membrane surface. (Magn. × 61000; Roberts & Northcote 1971.)

Figure 9. Profile of an invagination of the inner nuclear membrane within the nucleoplasm. (Magn. × 47500; Roberts & Northcote 1971.)

reticulum which presumably then protects the organelle from any more general autolytic activity which is destroying the other organization within the cell.

Because the endoplasmic reticulum carries ribosomes it is associated with protein synthesis. Certain proteins occur within the cell as important organized structures. These can be identified as microtubules, phloem protein fibrils or even as crystals within membrane bounded microbodies (figure 12). At some stage in the development of each of these the endoplasmic reticulum is found in a characteristic form very close to the assemblage of the protein structure. Phloem protein is present quite early in the development of the sieve tubes, as bundles of fibrils called slime bodies. These are found in association with profiles of the endoplasmic reticulum although the slime bodies are not limited by a unit membrane.

In plant cells the distribution of microtubules during mitosis occurs at definite positions, just before and during the cycle (Pickett-Heaps & Northcote 1966*a*, *b*). It is possible to investigate these sites by using cells which have been brought into a synchrony of division (Burgess & Northcote 1968). If the locations are examined just before the stage at which the microtubules are assembled then profiles of smooth endoplasmic reticulum are found. Within the mitotic spindle even after assembly, the microtubules can be seen with profiles of endoplasmic reticulum applied very close to them over an extensive length (Pickett-Heaps & Northcote 1966*a*). It is possible that the endoplasmic reticulum is responsible for the transport of the subunits of the microtubule or that it contributes to the right conditions, such as the ionic concentrations at the site, for the assembly of the subunits.

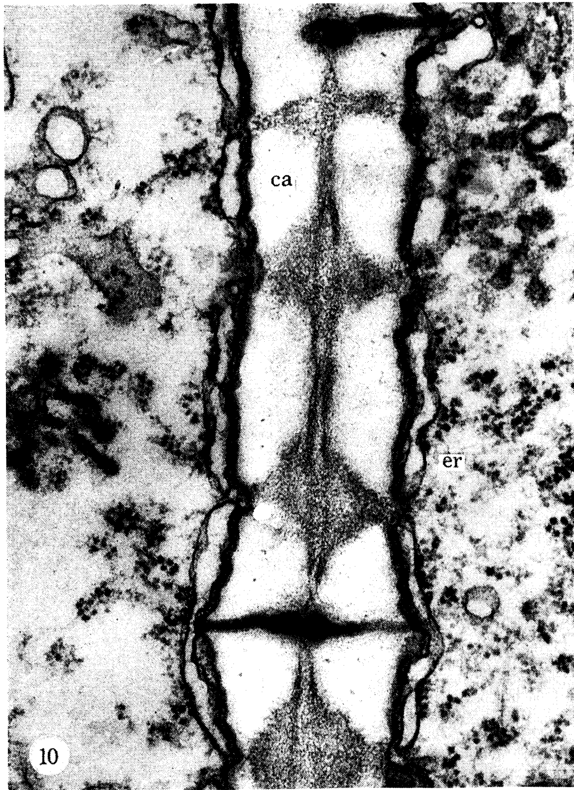
4. The endoplasmic reticulum, Golgi apparatus and plasmalemma

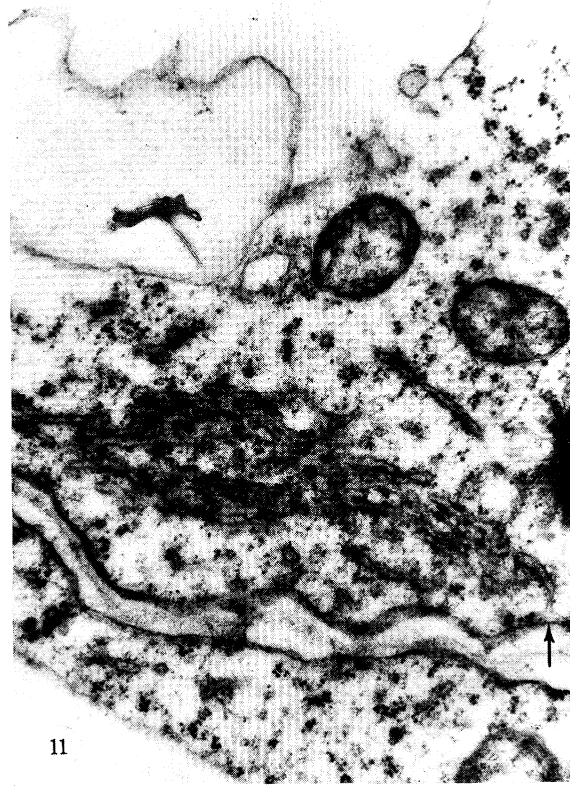
4.1. *The membrane system*

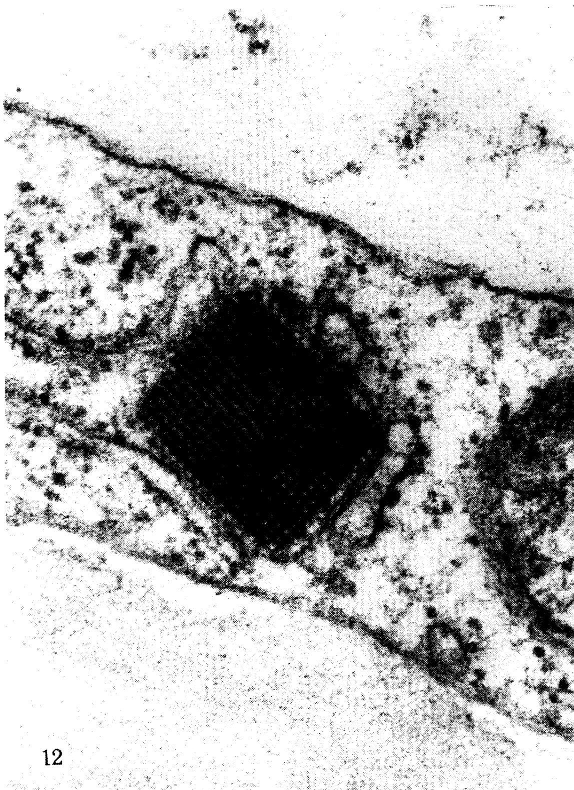
The relationship of the Golgi apparatus and the endoplasmic reticulum is not clear but the evidence from animal tissues (Caro & Palade 1964; Jamieson & Palade 1967*a*, *b*, 1968*a*, *b*, 1971*a*, *b*) and the general location of the membranes with respect to the Golgi apparatus, especially in some algal cells (figure 15) makes it possible that the Golgi apparatus is formed from membrane shuttled in vesicles from the endoplasmic reticulum to the forming face of the organelle (Northcote 1970; Dauwalder, Whaley & Kephart 1972). Since the Golgi apparatus is also degraded at the opposite face, the apparatus is envisaged as being in a dynamic state with a rate of formation, in some instances, of about 20 min for the complete organelle and each cisternae being formed and reformed about every 2 min (Neutra & Leblond 1966; Brown 1969).

These ideas suggest that there is a flow of membrane from the endoplasmic reticulum through the Golgi apparatus to the plasmalemma. This hypothesis is extremely important for the theories of membrane synthesis, and also for the concepts of the mechanisms for the synthesis and transport of materials such as polysaccharides and glycoproteins which are exported outside the cell (Northcote 1972).

At telophase in a plant cell the new cell wall dividing the two daughter cells arises as a cell plate. This plate appears as a disk of material at the centre of the mitotic spindle and it grows outwards towards the mother cell wall by the incorporation of vesicles at its edge (Pickett-Heaps & Northcote 1966*a*) (figures 16, 17). The vesicles are brought into position by microtubules (figure 16) and the vesicles fuse so that the material inside them is confined by a membrane on the surface of the disk. The surface membrane of the disk becomes the new







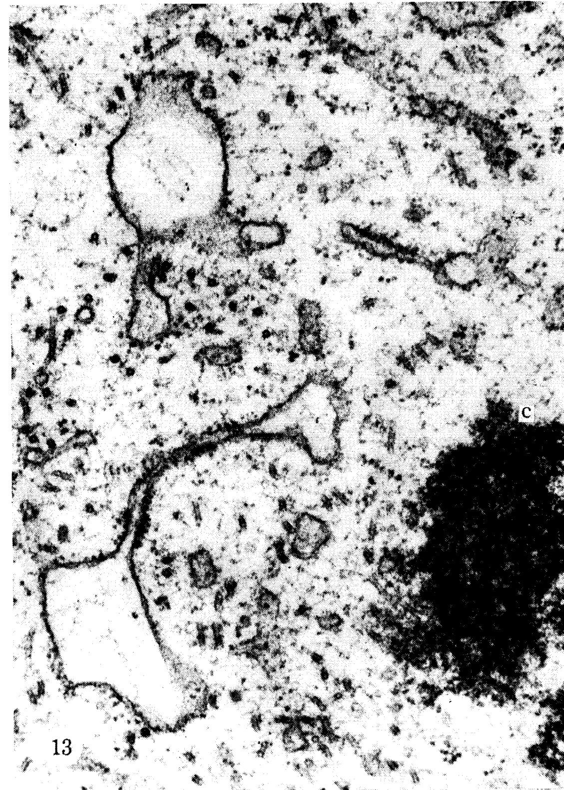


FIGURE 10. An early stage in the development of the sieve plate in the phloem of a stem of sycamore seedlings. The profiles of the endoplasmic reticulum over the cones of callose deposited in the wall at the plasmadesmata can be seen. (Magn. $\times$ 41 000; Northcote & Wooding 1968.)

FIGURE 11. A region just behind the growing edge of the cell plate. Profiles of endoplasmic reticulum in a characteristic array can be seen near the cell plate. A tubular profile (arrow) is closely applied to the plasmalemma. (Magn. $\times$ 30 000; Roberts & Northcote 1970.)

FIGURE 12. A crystal containing microbody. The close association of the organelle with profiles of the endoplasmic reticulum can be seen. (Magn. $\times$ 50 000; Roberts & Northcote 1970.)

FIGURE 13. Section through the mitotic spindle at metaphase. Profiles of the endoplasmic reticulum have penetrated the mitotic spindle. The section is approximately at right angles to that shown in figure 4. (Magn. $\times$ 22 000.)

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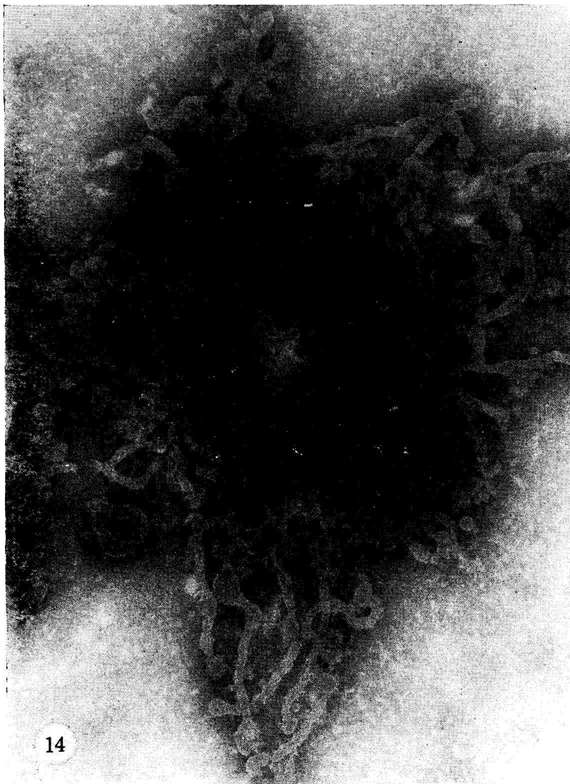
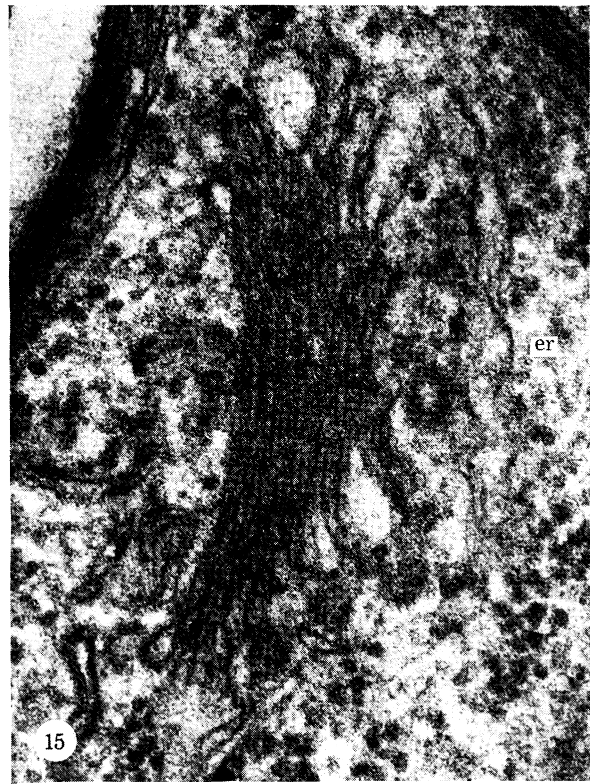
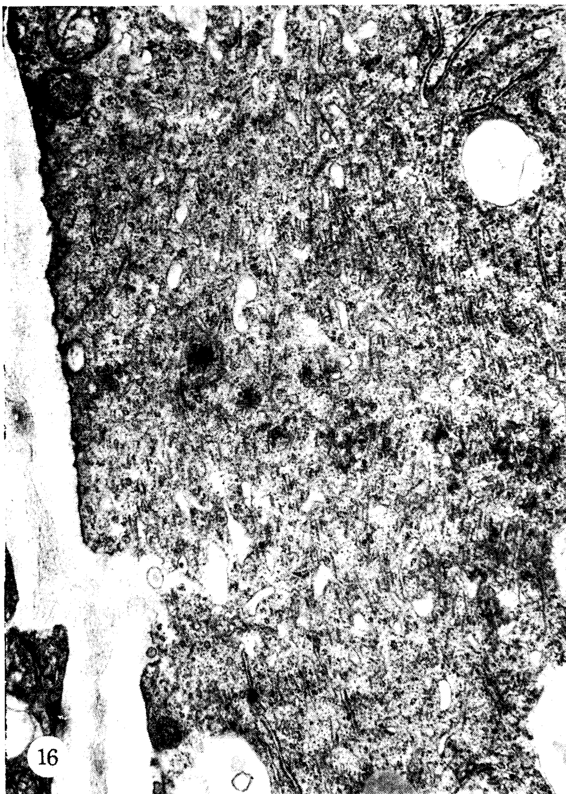






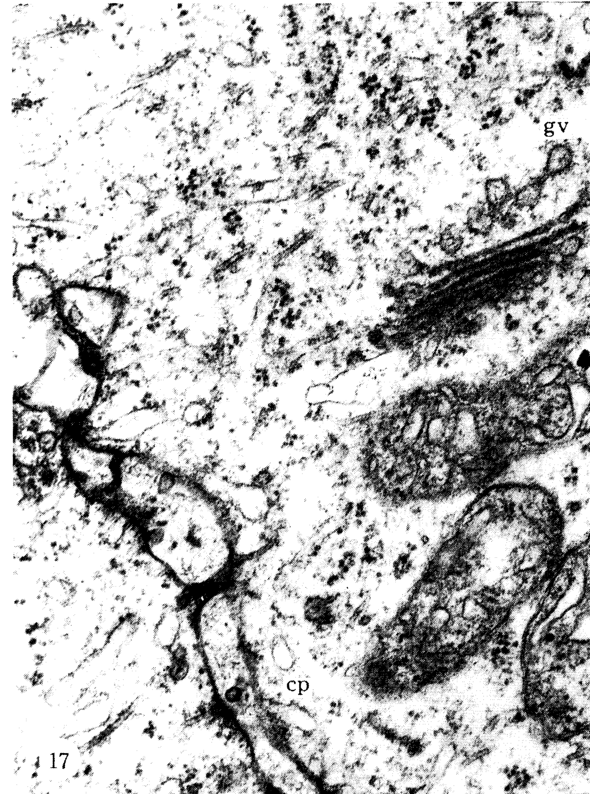


FIGURE 14. A Golgi body isolated by centrifugation of a homogenate of maize shoot tissue. The homogenate was made in the presence of 0.1 M glutaraldehyde. (Magn. ×39000; Bowles & Northcote 1972.)

FIGURE 15. A Golgi apparatus in the coenocytic cell of *Hydrodictium africanum*. The presence of a profile of the endoplasmic reticulum overlying the Golgi bodies is nearly always seen in these cells. (Magn. ×75000.)

FIGURE 16. A section at the outer edge of a growing cell plate. Vesicles are aligned at the site of the formation of the plate. (Magn. ×14000.)

FIGURE 17. The organization of the cytoplasm near the developing cell plate. Vesicles with a dense core can be seen at the cell plate and at the Golgi apparatus. (Magn. ×22000.)

plasmalemma of each daughter cell at the new wall (figure 17). In part the cell plate is derived from the Golgi apparatus (Whaley, Dauwalder & Kephart 1966; Hepler & Newcomb 1967) from vesicles which have a characteristic appearance both at the cell plate and before they are liberated from the Golgi cisternae (Roberts & Northcote 1970) (figure 17). The new plasmalemma is therefore formed as a consequence of the membrane production and modification which occurs at the Golgi apparatus. Not all the vesicles which can be seen at the site of cell plate formation can be identified as being pinched off from the Golgi apparatus and it is possible that a direct contribution from the endoplasmic reticulum may occur. The endoplasmic reticulum is found in layers near the developing cell plate and may in places be closely applied to the new plasmalemma surface (Roberts & Northcote 1970) (figure 11).

4.2. *Plasmodesmata*

At the stage of cell plate formation plasmodesmata are formed. These are said to arise as profiles of tubular endoplasmic reticulum which are caught across the developing cell plate during its construction by the fusion of the vesicles (Porter & Machado 1960; Hepler & Newcomb 1967). There is also a possibility that microtubules may be involved (Robards 1968). Some plasmodesmata may be produced at a later stage in cell wall formation (Burgess 1972). The plasmodesmata are lined by the plasmalemma and within them the endoplasmic reticulum passes through the developing cell plate or wall (Northcote & Wooding 1966; Burgess 1971) and it is very close or even pressed against the plasmalemma. Thus at these positions as well as at the other sites where the endoplasmic reticulum is brought into close proximity with the developing or fully formed plasmalemma there is no fusion of these membranes. The plasmodesmata provide a connexion between adjacent cells and since during growth of the wall some may be grown over and others may be formed and modified, they can be concentrated in certain areas of the wall as pit fields and even confined to certain walls of the cells. Connexions between rows of contiguous cells can be made with few connexions to other adjacent cells. In this way an important and sometimes directed transport system is established between the cells of a tissue with connexions between the endoplasmic reticulum system of each cell (Juniper & Barlow 1969; Juniper & French 1973).

4.3. *Sites of polysaccharide synthesis*

The membrane system of the endoplasmic reticulum, Golgi bodies and plasmalemma is responsible for the transport and synthesis of cell wall material and other exportable polysaccharide substances from the cell (Northcote 1972). This can be clearly seen by radioautographic studies on rapidly growing tissue when radioactive glucose can be seen to be incorporated into the material of the Golgi cisternae and vesicles and subsequently it can be chased by incubation with non-radioactive glucose into the wall outside the plasmalemma. Since the radioactive material detected can be isolated it can be analysed, and it has been shown to be polysaccharide and resemble wall material (Northcote & Pickett-Heaps 1966). Similar results show that the Golgi vesicles give rise to some of the wall material in secondarily thickened walls (Wooding 1968; Northcote & Wooding 1966, 1968). Direct observations on the production of scales which are deposited as a skeletal layer on the outside of some algae have shown that these are formed and assembled within the Golgi apparatus and are deposited outside the cell via a Golgi vesicle (Manton 1966, 1967). These scales are in part made up of polysaccharides (Green & Jennings 1967; Brown *et al.* 1970). The Golgi apparatus has also been shown to take

part in the formation of the cell plate at telophase (see §4.1) (figures 16, 17). There is therefore considerable evidence that the Golgi apparatus is involved in the transport mechanism for exporting polysaccharide out of the cell. In addition, the evidence also suggests that it takes part in the synthesis of the material which it transports. The enzymes for polysaccharide synthesis are known to be membrane bound (Hassid 1967). These enzymes carried within the membrane system will also be exported to the outside of the cell at the plasmalemma when the vesicles fuse with and extend the plasmalemma at the cell surface. This transfer of the enzymes is especially relevant for the theories about the site of cellulose synthesis and its relationship to the sites of synthesis of the other polysaccharides of the wall (Northcote 1973).

The plasmalemma is continually being formed by incorporation of vesicles from the Golgi apparatus even when the surface area of the cell is not increasing, although the wall is growing in thickness. Therefore some of the plasmalemma must at this time be broken down either by disaggregation or by transfer back into the cytoplasm of intact membrane.

Although the radioautographic evidence shows clearly the function of the Golgi apparatus in cell wall assembly no indication of the role of the endoplasmic reticulum is given by this type of investigation. However, many direct observations on tissue where it is known that cell-wall synthesis is occurring have shown characteristic organizations and distribution patterns of the endoplasmic reticulum which suggest that it has a distinct role in the wall formation (Northcote 1968*b*). For instance, the distribution of the endoplasmic reticulum during cell plate formation has already been mentioned (§4.1). It has also been observed that the endoplasmic reticulum is very important for the synthesis of callose in the sieve plate of phloem (Northcote & Wooding 1966, 1968) and that it is distributed in a definite pattern with respect to the secondary thickening of xylem vessels of rapidly growing wheat roots (Pickett-Heaps & Northcote 1966*c*).

The function of the endoplasmic reticulum during sieve plate formation is particularly significant because the pores seem to be formed at sites marked out by the distribution of the endoplasmic reticulum along the developing sieve plate (figure 10). At these sites callose is deposited and it is then subsequently removed during the formation of the pore. Callose can be deposited much later at these same sites in the mature phloem sieve tubes, within the wall of the fully formed sieve plate at the pores (Northcote & Wooding 1966). At this later time no organized endoplasmic reticulum or Golgi system is present within the sieve tube so that it is reasonable to suppose that the full complement of enzymes necessary for the synthesis of callose are either present within the wall or at the plasmalemma and that their presence at these situations is associated with the earlier endoplasmic reticulum distribution during the initial stages of the sieve plate formation.

More direct evidence for the function of the endoplasmic reticulum and the Golgi apparatus in cell-wall formation is obtained by isolating the various parts of the membrane system, separately from broken cells (Harris & Northcote 1971; Bowles & Northcote 1972) (figure 14). The membranes are isolated from maize and pea roots at definite stages of differentiation when polysaccharides of known composition are formed by the cells (Harris & Northcote 1970). The polysaccharides that were synthesized just before the isolation of the membranes are made radioactive by incubating the tissue with radioactive glucose. These experiments show that the endoplasmic reticulum and the Golgi apparatus contain polysaccharide material (hemicellulose and pectic substances) characteristic of the type of cell wall or other substance exported by the cell at the time of the isolation of the membranes (tables 1–3). The only polysaccharide not found within the membrane system but which is deposited in the wall in large amounts (table 1)

is cellulose (tables 2, 3). In the experiments the membranes are isolated either as intact Golgi bodies and closed membrane bounded sacs of rough endoplasmic reticulum, or as closed smooth vesicles, so that the contents remain within the isolated membrane system. If cellulose is synthesized to a great extent at the plasmalemma surface then it would not be isolated within a membrane fraction even though a rapid synthesis of cellulose into the wall was occurring.

Table 1. Relative amounts of radioactivity incorporated from D-[U-^{14}C]glucose into the polysaccharide components of the wall fractions from maize-root tissue

sugar	radioactivity (%)		
	whole roots	root-cap tissue	older tissue
galacturonic acid	2.6	7.8	2.7
glucuronic acid	1.2	1.3	0.8
galactose	7.0	17.4	6.9
glucose	63.8	38.3	62.5
mannose	1.2	2.5	1.8
arabinose	7.2	12.5	8.8
xylose	15.7	13.5	15.6
fucose	0.9	4.9	0.4
ribose + rhamnose	2.7	1.2	0.7
total count/min	720 300	130 500	18 200

Table 2. Relative amounts of radioactivity incorporated from D-[U-^{14}C]glucose into the polysaccharide components of the dictyosome fractions from maize-root tissue

sugar	radioactivity (%)		
	whole roots	root-cap tissue	older tissue
galacturonic acid	14.0	11.6	10.3
glucuronic acid	1.9	4.7	1.6
galactose	26.6	34.1	21.5
glucose	6.6	6.8	3.95
mannose	3.5	1.8	1.0
arabinose	22.3	14.7	19.8
xylose	20.1	18.5	41.4
fucose	2.8	6.2	0.2
ribose + rhamnose	1.7	1.7	—
total count/min	4500	1100	790

Table 3. Relative amounts of radioactivity incorporated from D-[U-^{14}C]glucose into the polysaccharide components of the microsome fractions from maize-root tissue

sugar	radioactivity (%)		
	whole root	root-cap tissues	older tissue
galacturonic acid	7.5	11.2	5.2
glucuronic acid	1.7	1.6	1.2
galactose	24.1	31.4	21.2
glucose	4.0	7.3	8.5
mannose	3.1	5.0	3.4
arabinose	23.0	22.4	20.4
xylose	31.0	16.4	38.8
fucose	1.9	4.5	1.1
total count/min	89 000	68 000	26 000

Thus the direct evidence provided by the isolation of the membranes from higher plants indicates that both the endoplasmic reticulum and the Golgi apparatus are involved in the synthesis of pectic substances, hemicellulose and root-cap slime but that these membrane fractions are not active in cellulose synthesis, which is carried out at the plasmalemma surface. However, the potential enzymic activity for cellulose synthesis, like the active enzymes responsible for the

TABLE 4. AMOUNTS OF THE THREE MEMBRANE FRACTIONS ISOLATED FROM MAIZE ROOTS, AND THE RELATIVE SPECIFIC RADIOACTIVITIES OF THE RADIOACTIVITY INCORPORATED FROM D-[U-^{14}C]-GLUCOSE INTO THE POLYSACCHARIDE COMPONENTS OF THE MEMBRANE FRACTIONS

	lipid extracted from membrane fractions of maize roots		average relative amounts of the different membrane fractions	relative specific radioactivities of the polysaccharide components
	μg/11 g fresh roots	μg/15 g fresh roots		
dictyosomes	80	264	1	6.0
microsomes	4001	6950	40	2.9

synthesis of hemicellulose and pectin, could have been present within the endoplasmic reticulum–Golgi apparatus system since the plasmalemma is derived in part by a direct contribution of membrane from the cytoplasmic part of the membrane system. The difference being that the enzymes responsible for cellulose synthesis only become fully active when the membrane is incorporated at the cell surface. Brown and his colleagues (Brown, Herth, Franke & Romanovicz 1973) have suggested that in an alga the enzymes which synthesize a cellulose-like polymer, a glucan that contains β 1 → 4 glucose links, are present in the Golgi apparatus. The alga, *Pleurochrysis scherffelii*, forms scales which are exported to the external surface of the cells and the scales which contain the cellulose are assembled within the Golgi apparatus.

If the amount of the membrane fractions isolated from a given weight of maize tissues is estimated as a quantity of lipid it is shown that the polysaccharides (hemicelluloses and pectic substances) are concentrated in the Golgi apparatus relative to the polysaccharides in the endoplasmic reticulum (table 4) (Bowles & Northcote 1972). The Golgi apparatus can therefore be considered as an important localized focal point in the synthetic and transport system of polysaccharides and one at which some control of the processes may be operated.

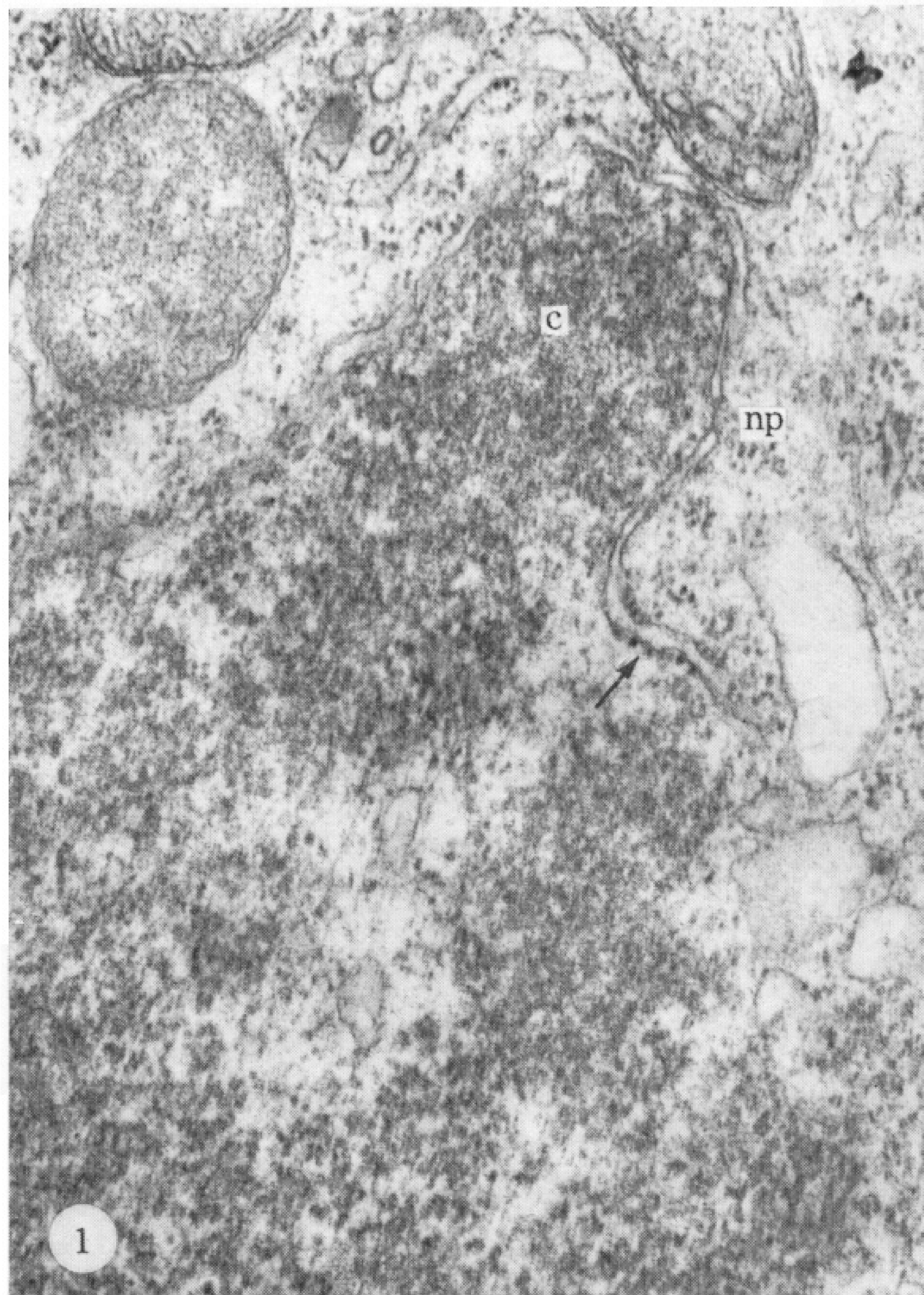
Whether there is a direct contribution from the endoplasmic reticulum to the wall or whether all the material present in the endoplasmic reticulum has to be modified by passage through the Golgi apparatus is not yet established. Transfer of material to the Golgi apparatus may be necessary for several reasons. It may be that additional synthesis has to take place by reactions that occur only in this part of the system; the material may have to be assembled in a definite manner before export or it may have to be concentrated and covered with the different modified membrane of the Golgi vesicle. The endoplasmic reticulum can be very close to the cell membrane and not fuse with it. On the other hand, the Golgi vesicles do fuse with the plasmalemma and this is probably due in part to the chemical similarity of the membranes at the dispersing face of the Golgi apparatus to that of the plasmalemma. The similarities of the membranes of the exported vesicles of the Golgi apparatus and the plasmalemma and the differences of these from the membranes of the forming face of the Golgi body and the endoplasmic reticulum has been indicated by microscopic observations and chemical analysis (Keenan & Morré 1970; Grove, Bracker & Morré 1968; Hereward & Northcote 1972). The mechanism of vesicle fusion and membrane extension is not clear but it seems likely that in addition to a similarity in

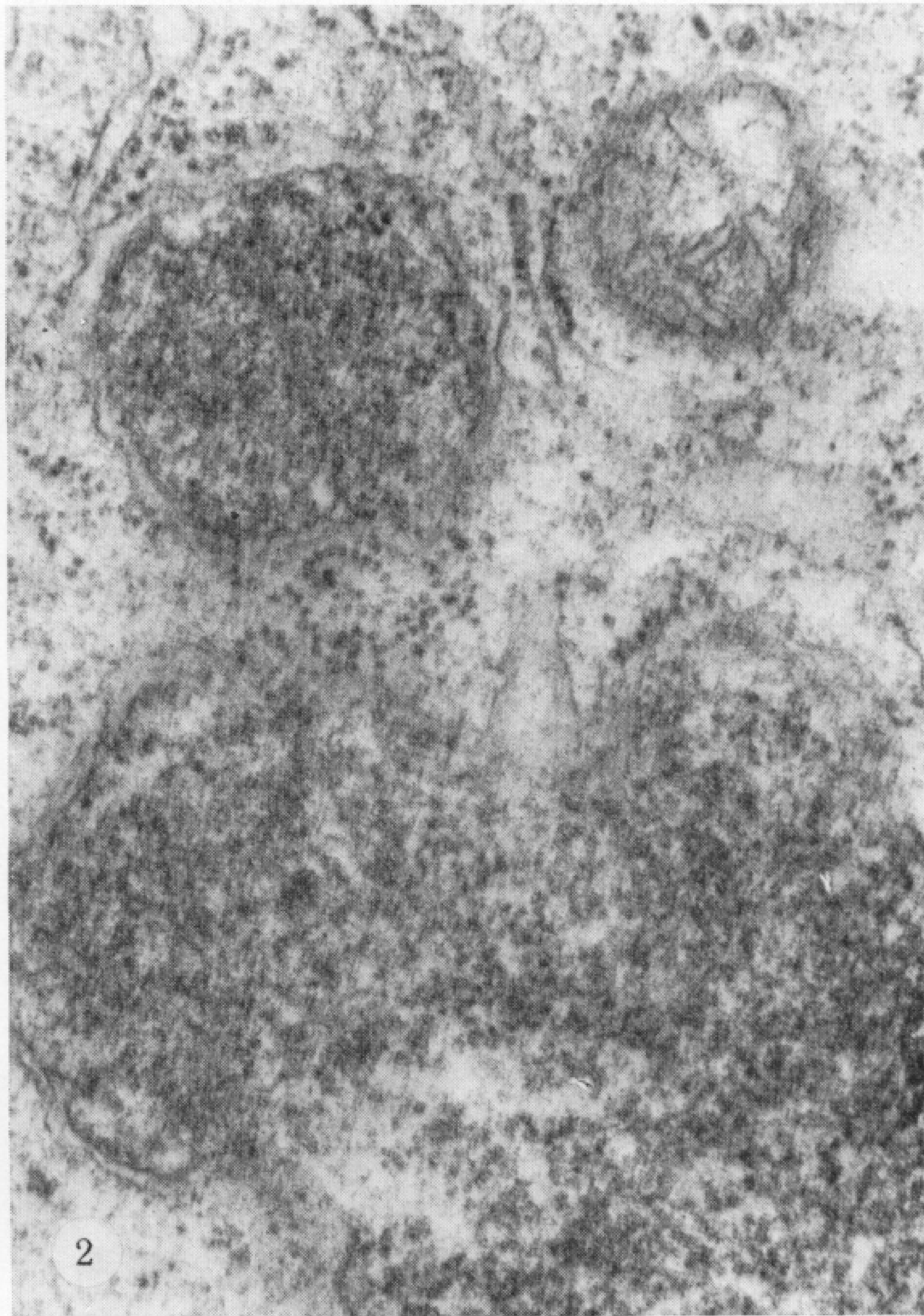
chemical composition the sites of fusion may be marked by particlar substructures at the plasmalemma and on the vesicle (Palade & Bruns 1968; Northcote 1969; Satir, Schooley & Satir 1973; Lagunoff 1973). This indicates that a definite position and process is needed for the fusion.

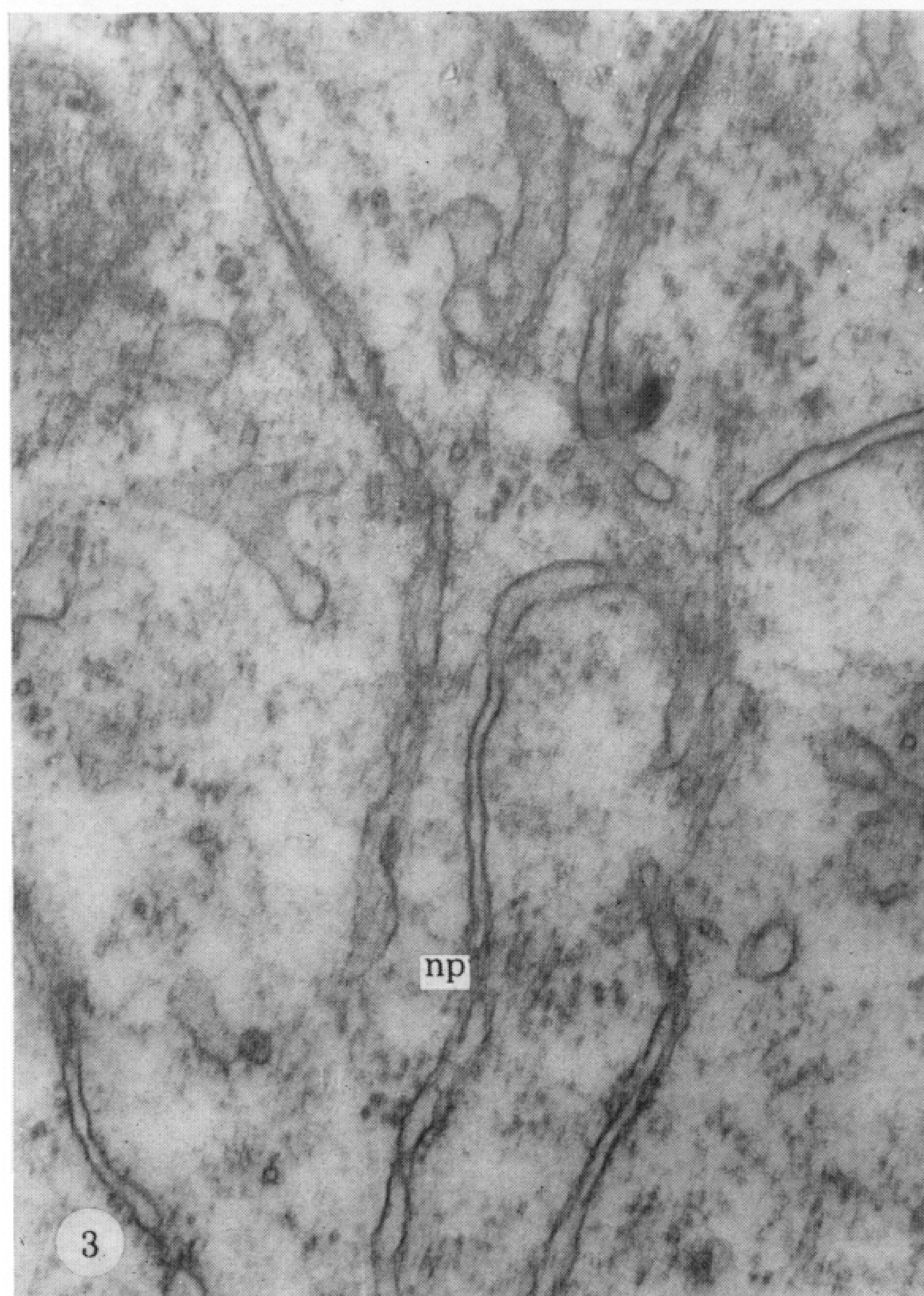
References (Northcote)

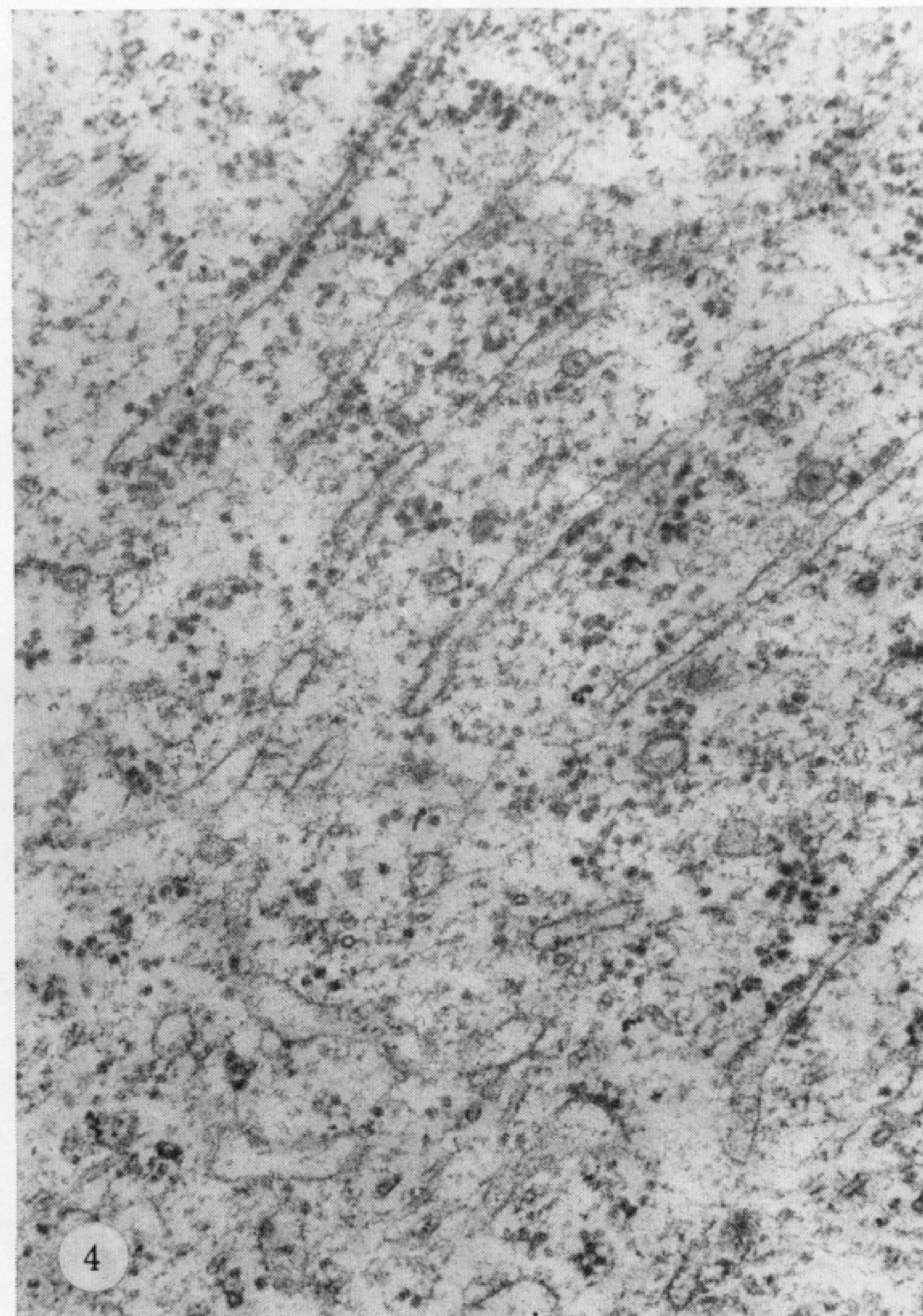
Bowles, D. J. & Northcote, D. H. 1972 *Biochem. J.* **130**, 1133–1145.
Brown, R. M. 1969 *J. Cell Biol.* **41**, 109–123.
Brown, R. M., Franke, W. W., Kleinig, H., Falk, H. & Sitte, P. 1970 *J. Cell Biol.* **45**, 246–271.
Brown, R. M., Herth, W., Franke, W. W. & Romanovicz, D. 1973 In *Biogenesis of plant cell wall polysaccharides*. London: Academic Press.
Burgess, J. 1971 *Protoplasma* **73**, 83–95.
Burgess, J. 1972 *Protoplasma* **74**, 449–458.
Burgess, J. & Northcote, D. H. 1968 *Planta* **80**, 1–14.
Caro, L. G. & Palade, G. E. 1964 *J. Cell Biol.* **20**, 473–495.
Dauwalder, M., Whaley, W. G. & Kephart, J. E. 1972 *Sub-Cell. Biochem.* **1**, 225–275.
Goldstein, L. 1964 In *The nuclear membrane and nucleocytoplasmic interchange*. Protoplasmatologia, p. 51.
Goldstein, L. & Prescott, D. M. 1967 In *The control of nuclear activity* (ed. L. Goldstein), p. 273. New Jersey: Prentice-Hall.
Goldstein, L., Wise, G. E. & Beeson, M. 1973 *Expl Cell Res.* **76**, 281–288.
Green, J. C. & Jennings, D. H. 1967 *J. expl Bot.* **18**, 359–370.
Grove, S. N., Bracker, C. E. & Morré, D. J. 1968 *Science, N.Y.* **161**, 171–173.
Harris, P. J. & Northcote, D. H. 1970 *Biochem. J.* **120**, 479–491.
Harris, P. J. & Northcote, D. H. 1971 *Biochim. biophys. Acta* **237**, 56–64.
Hassid, W. Z. 1967 *A. Rev. Pl. Physiol.* **18**, 253–280.
Hepler, P. K. & Newcomb, E. H. 1967 *J. ultrastruct. Res.* **19**, 498–513.
Hereward, F. V. & Northcote, D. H. 1972 *Expl Cell Res.* **70**, 73–80.
Jamieson, J. D. & Palade, G. E. 1967*a* *J. Cell Biol.* **34**, 577–596.
Jamieson, J. D. & Palade, G. E. 1967*b* *J. Cell Biol.* **34**, 597–615.
Jamieson, J. D. & Palade, G. E. 1968*a* *J. Cell Biol.* **39**, 580–588.
Jamieson, J. D. & Palade, G. E. 1968*b* *J. Cell Biol.* **39**, 589–603.
Jamieson, J. D. & Palade, G. E. 1971*a* *J. Cell Biol.* **48**, 503–522.
Jamieson, J. D. & Palade, G. E. 1971*b* *J. Cell Biol.* **50**, 135–158.
Juniper, B. E. & Barlow, P. W. 1969 *Planta* **89**, 352–360.
Juniper, B. E. & French, A. 1973 *Planta* **109**, 211–224.
Kay, R. R. & Johnston, I. R. 1973 *Sub-cell. Biochem.* **2**, 127–166.
Keenan, T. W. & Morré, D. J. 1970 *Biochemistry* **9**, 19–25.
Lagunoff, D. 1973 *J. Cell Biol.* **57**, 252–259.
Manton, I. 1966 *J. Cell Sci.* **1**, 375–380.
Manton, I. 1967 *J. Cell Sci.* **2**, 411–418.
Neutra, M. & Leblond, C. P. 1966 *J. Cell Biol.* **30**, 119–136.
Newcomb, E. H. 1967 *J. Cell Biol.* **33**, 143–163.
Northcote, D. H. 1968*a* *Br. Med. Bull.* **24**, 107–112.
Northcote, D. H. 1968*b* In *Plant cell organelles* (ed. J. B. Pridham), pp. 179–197. London: Academic Press.
Northcote, D. H. 1969 *Proc. R. Soc. Lond.* B **173**, 21–30.
Northcote, D. H. 1970 *Endeavour* **30**, 26–33.
Northcote, D. H. 1972 *A. Rev. Pl. Physiol.* **23**, 113–132.
Northcote, D. H. 1973 In *Cell biology in medicine* (ed. by E. E. Bittar), pp. 197–214. London: John Wiley.
Northcote, D. H. & Lewis, D. R. 1968 *J. Cell Sci.* **3**, 199–206.
Northcote, D. H. & Pickett-Heaps, J. D. 1966 *Biochem. J.* **98**, 159–167.
Northcote, D. H. & Wooding, F. B. P. 1966 *Proc. R. Soc. Lond.* B **163**, 524–537.
Northcote, D. H. & Wooding, F. B. P. 1968 *Sci. Prog. Oxf.* **56**, 35–58.
Oppenheim, A. & Wahrman, J. 1973 *Expl Cell Res.* **79**, 287–294.
Palade, G. E. & Bruns, R. R. 1968 *J. Cell Biol.* **37**, 633–649.
Pickett-Heaps, J. D. & Northcote, D. H. 1966*a* *J. Cell Sci.* **1**, 109–120.
Pickett-Heaps, J. D. & Northcote, D. H. 1966*b* *J. Cell Sci.* **1**, 121–128.
Pickett-Heaps, J. D. & Northcote, D. H. 1966*c* *J. expl Bot.* **17**, 20–26.
Porter, K. R. 1956 *The Harvey Lectures*, pp. 175–228.
Porter, K. R. & Machado, R. D. 1960 *J. biophys. biochem. Cytol.* **7**, 167–180.
Robards, A. W. 1968 *Planta* **82**, 200–210.

Roberts, K. & Northcote, D. H. 1970 *J. Cell Sci.* **6**, 299–321.
Roberts, K. & Northcote, D. H. 1971 *Microscopica Acta* **71**, 102–120.
Satir, B., Schooley, C. & Satir, P. 1973 *J. Cell Biol.* **56**, 153–176.
Stevens, A. R. 1967 In *The control of nuclear activity* (ed. L. Goldstein), p. 189. New Jersey: Prentice-Hall.
Whaley, W. G., Dauwalder, M. & Kephart, J. E. 1966 *J. ultrastruct. Res.* **15**, 169–180.
Wooding, F. B. P. 1968 *J. Cell Sci.* **3**, 71–80.
Wooding, F. B. P. & Northcote, D. H. 1965*a* *J. Cell Biol.* **24**, 117–128.
Wooding, F. B. P. & Northcote, D. H. 1965*b* *Am. J. Bot.* **52**, 526–531.
Wooding, F. B. P. & Northcote, D. H. 1965*c* *J. ultrastruct. Res.* **13**, 233–244.
Wright, K. & Northcote, D. H. 1973 *J. Cell Sci.* **12**, 37–53.









c, chromosome; ca, callose cone; cp, cell plate; cr, chromatin; er, endoplasmic reticulum; gv, Golgi vesicle; in, invagination of inner membrane of the nucleus; ms, mitotic spindle; ne, nuclear envelope; np, nuclear pore.

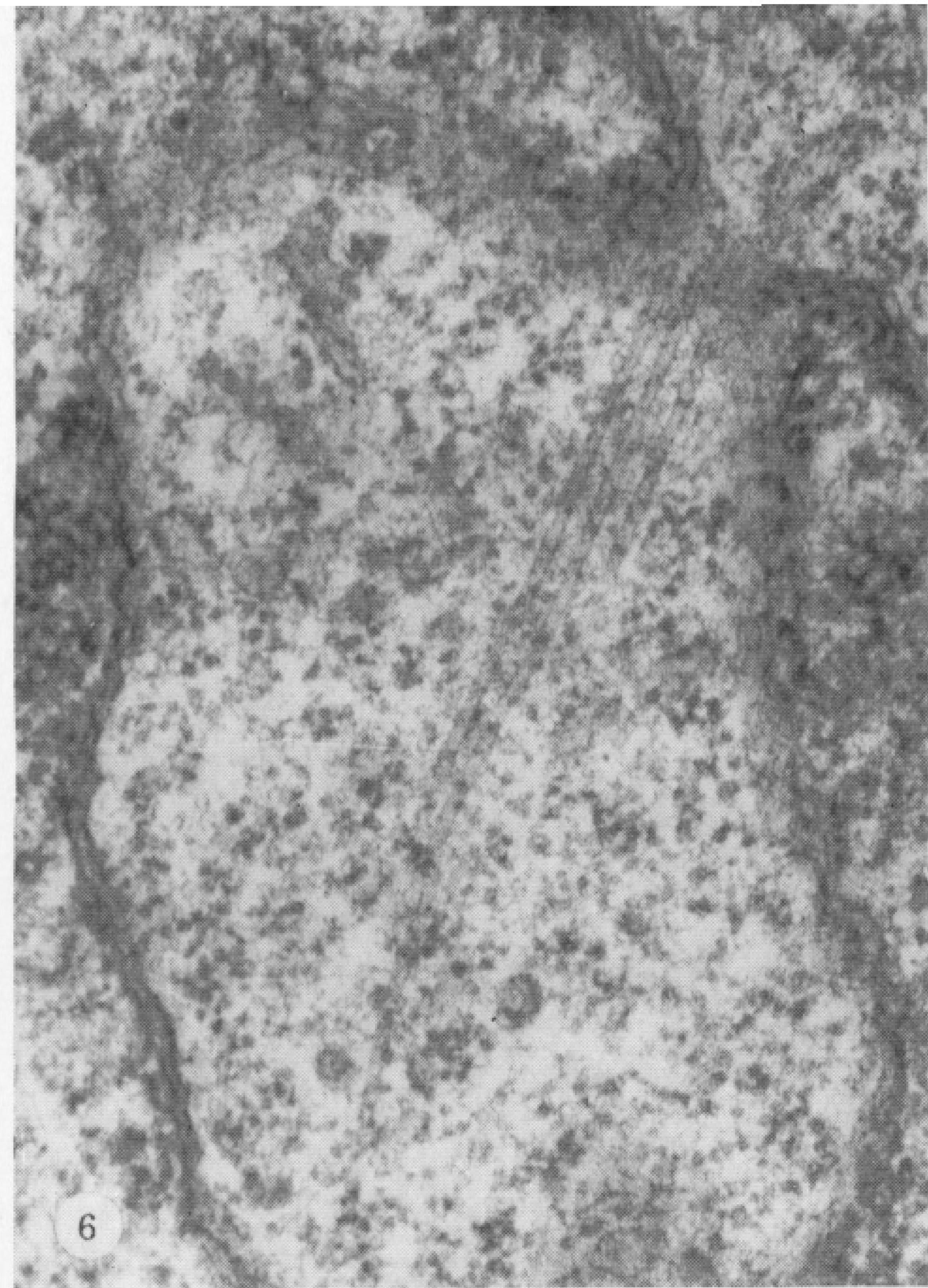
All the figures are of sycamore suspension callus cells except figures 10, 14 and 15.

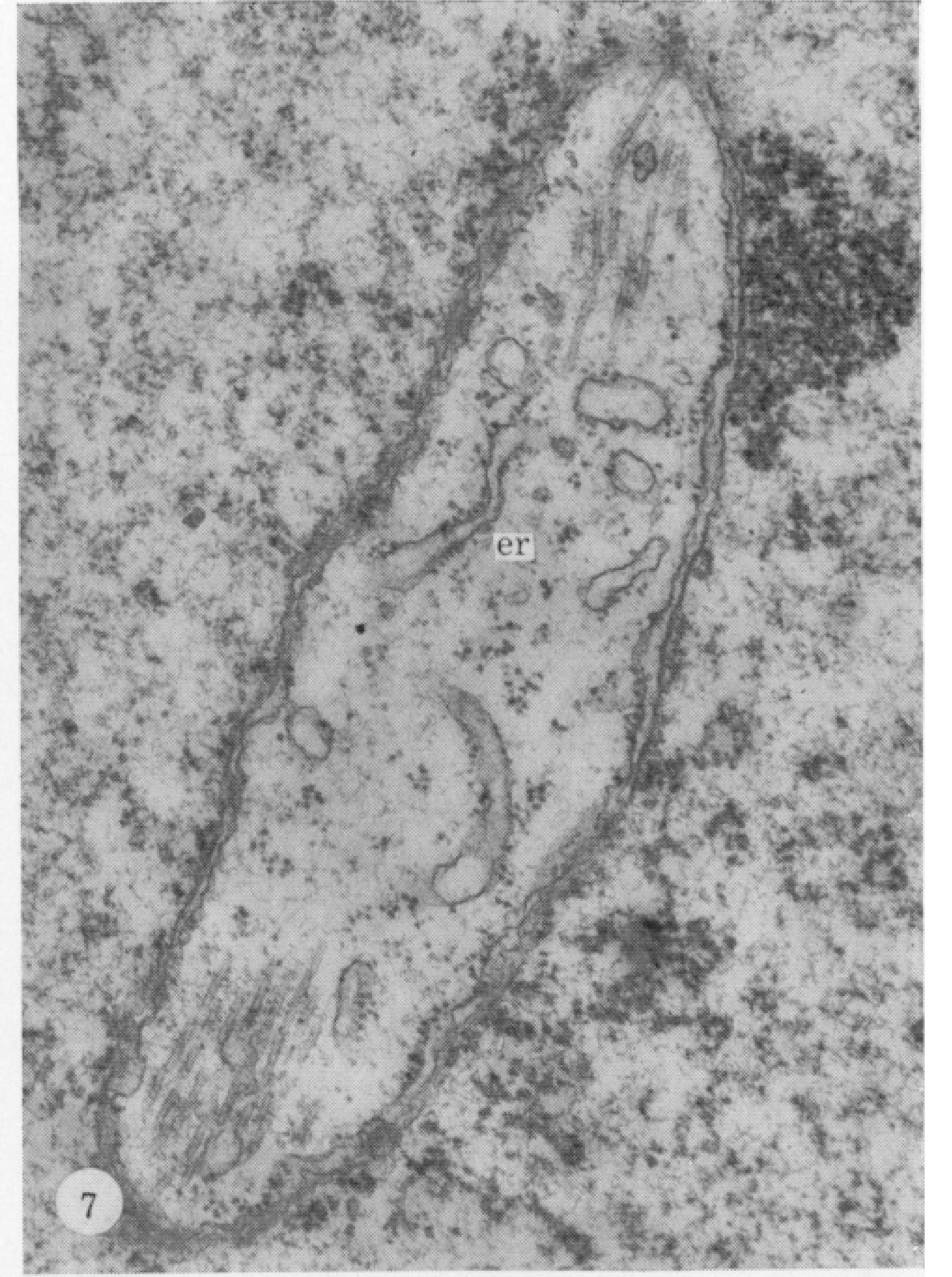
FIGURE 1. Nuclear envelope reforming at telophase from profiles of the endoplasmic reticulum. In places (arrow) ribosomes are present on both membranes. A nuclear pore has formed where the endoplasmic reticulum is closely applied to the chromosome. (Magn. × 31000; Roberts & Northcote 1971.)

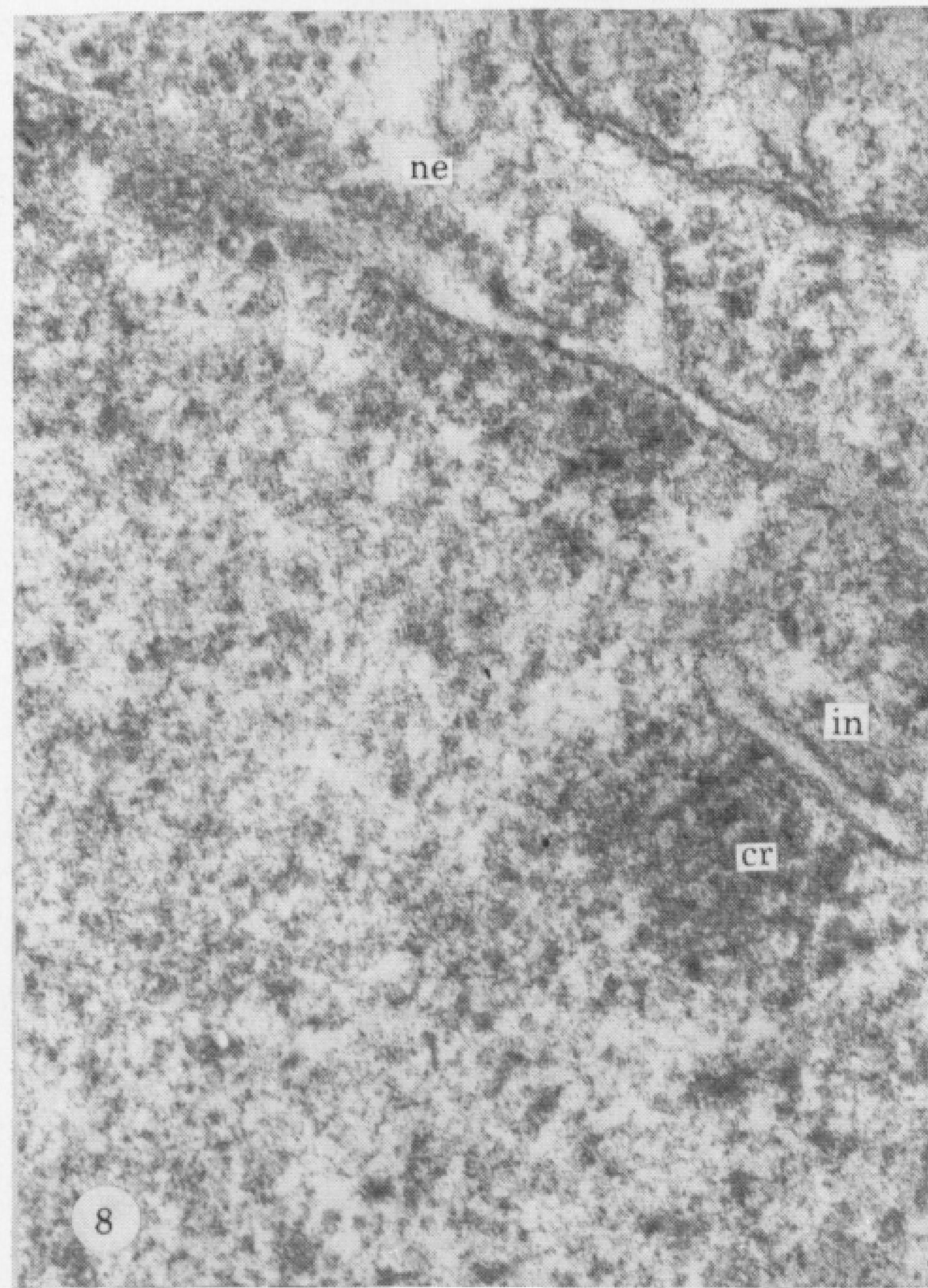
FIGURE 2. A stage in the formation of the nuclear envelope at telophase. The endoplasmic reticulum is closely applied to the chromosomes. (Magn. × 31000; Roberts & Northcote 1971.)

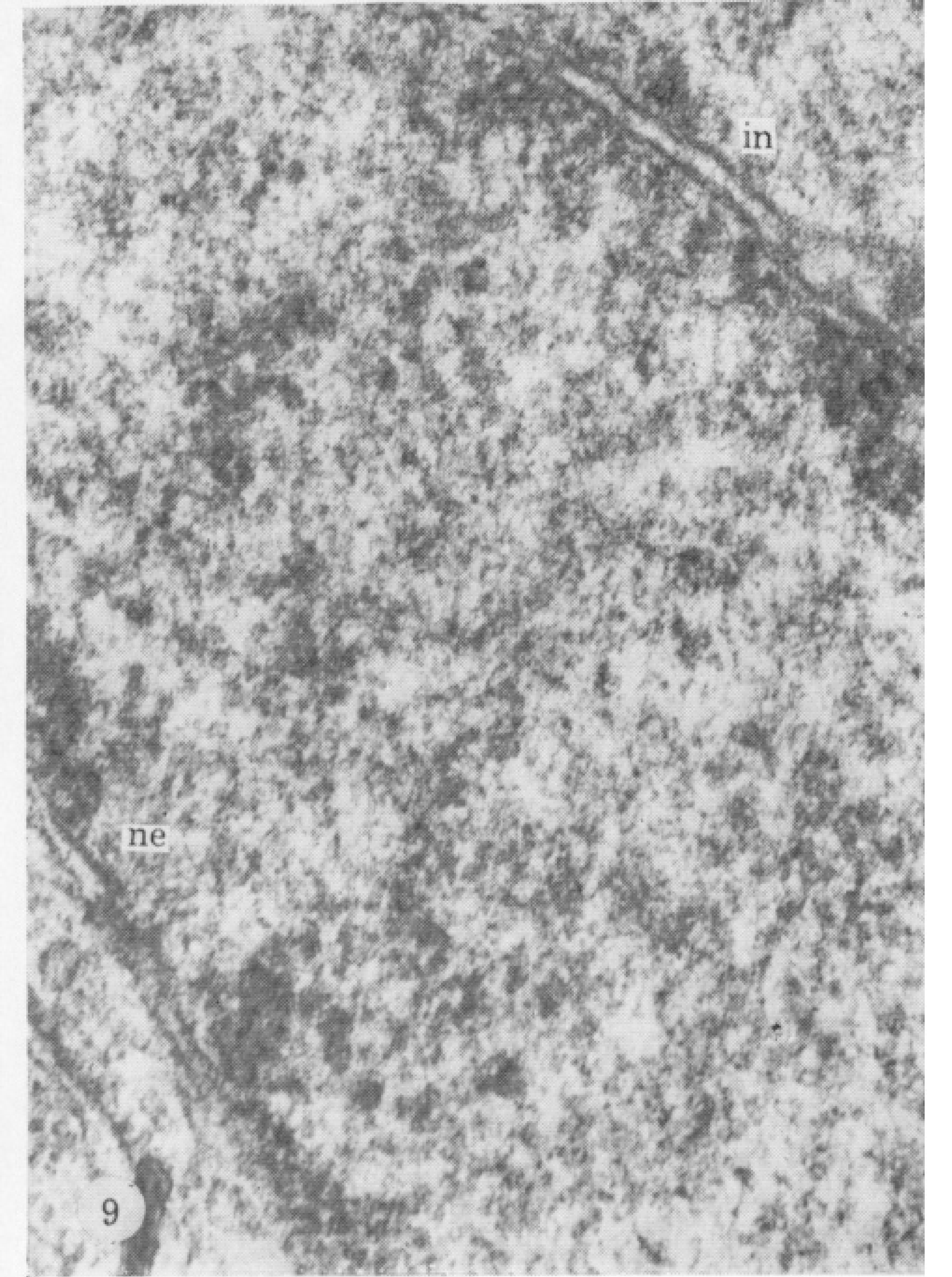
FIGURE 3. Fragments of the nuclear envelope found near the nucleoplasm at prophase. Pores are still present in the membranes. (Magn. × 27000; Roberts & Northcote 1971.)

FIGURE 4. Profiles of the endoplasmic reticulum invading the mitotic spindle during early telophase. Compare with figure 13. (Magn. × 25000.)

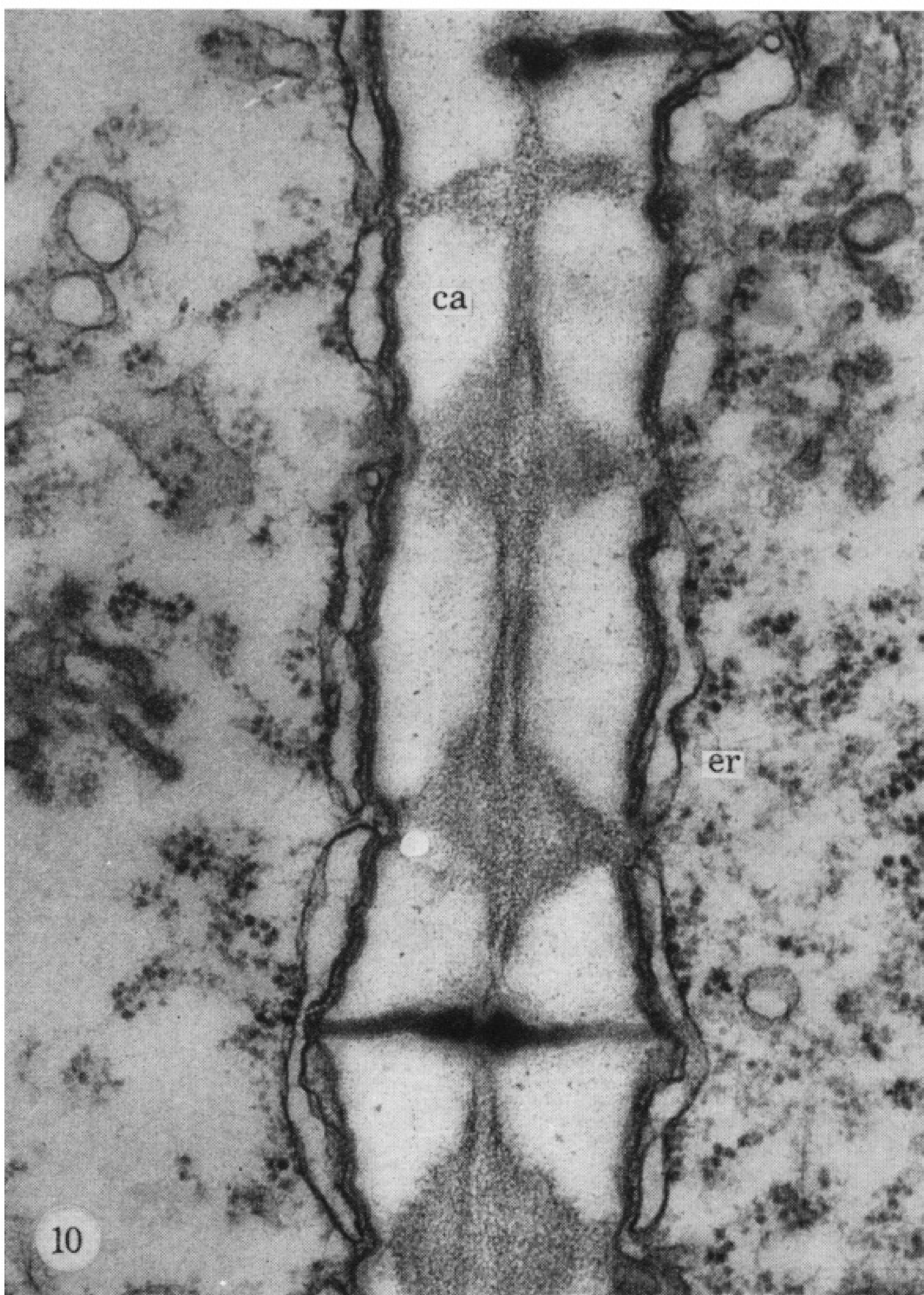


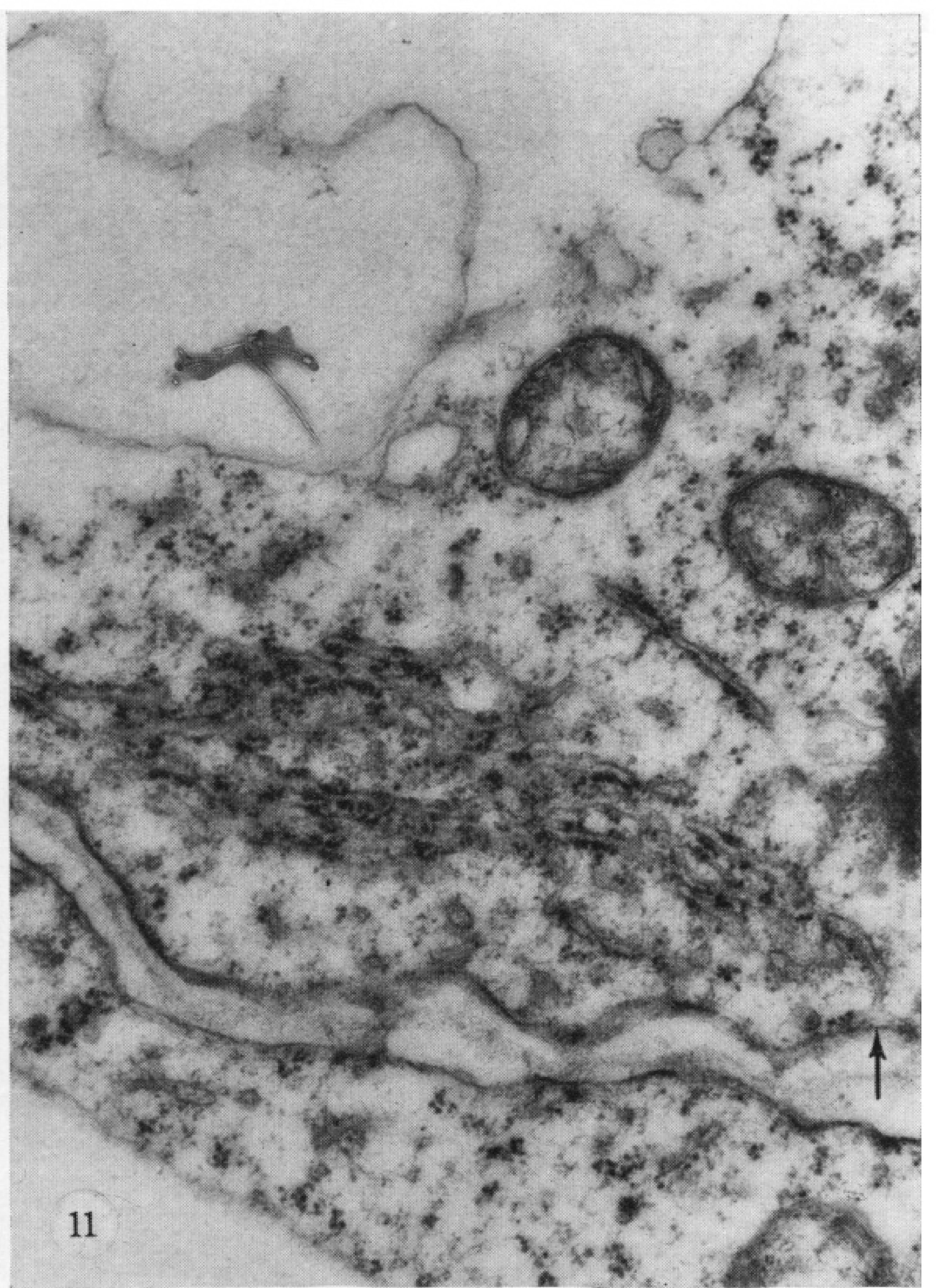


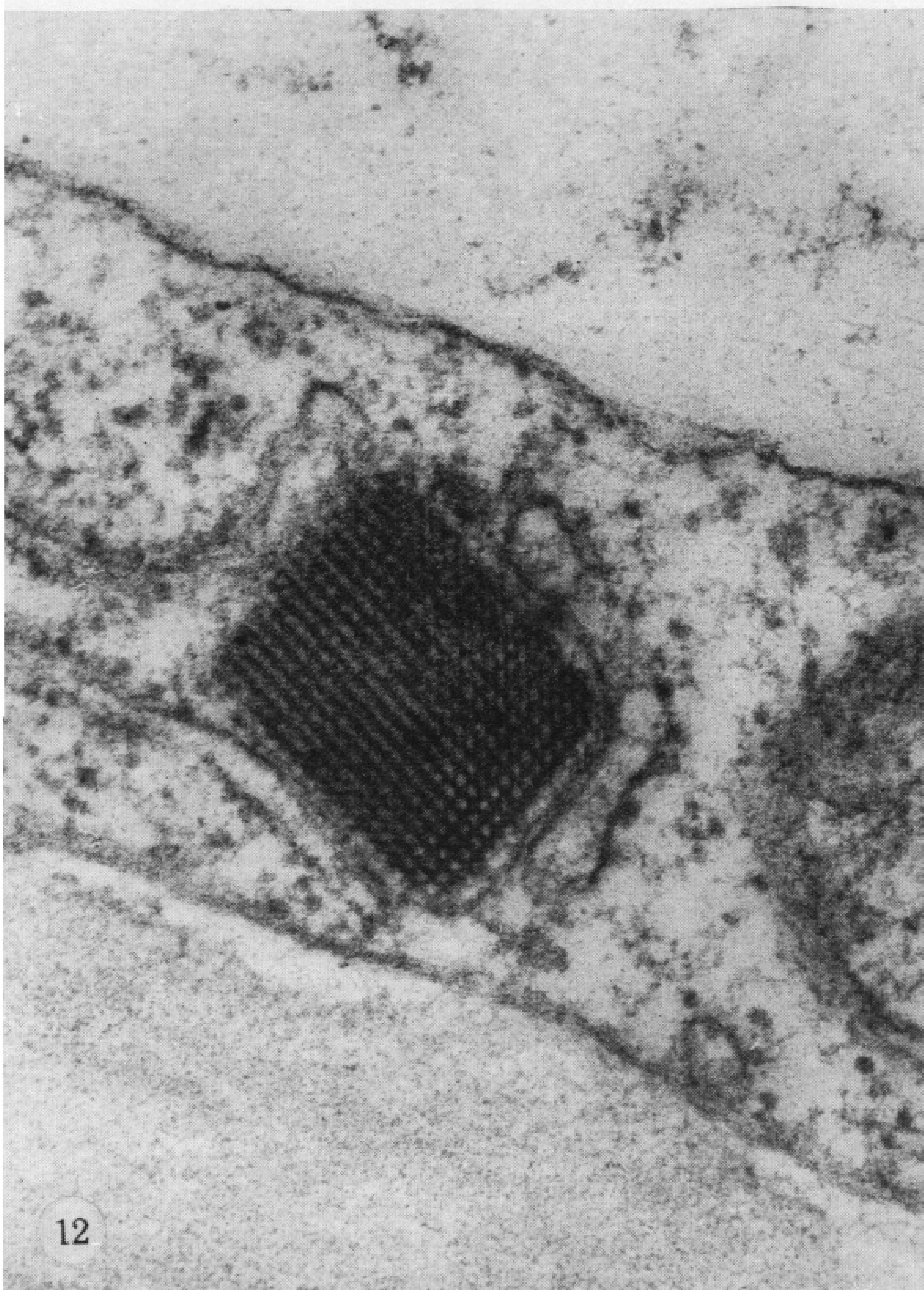




FIGURES 5–9. For description see opposite







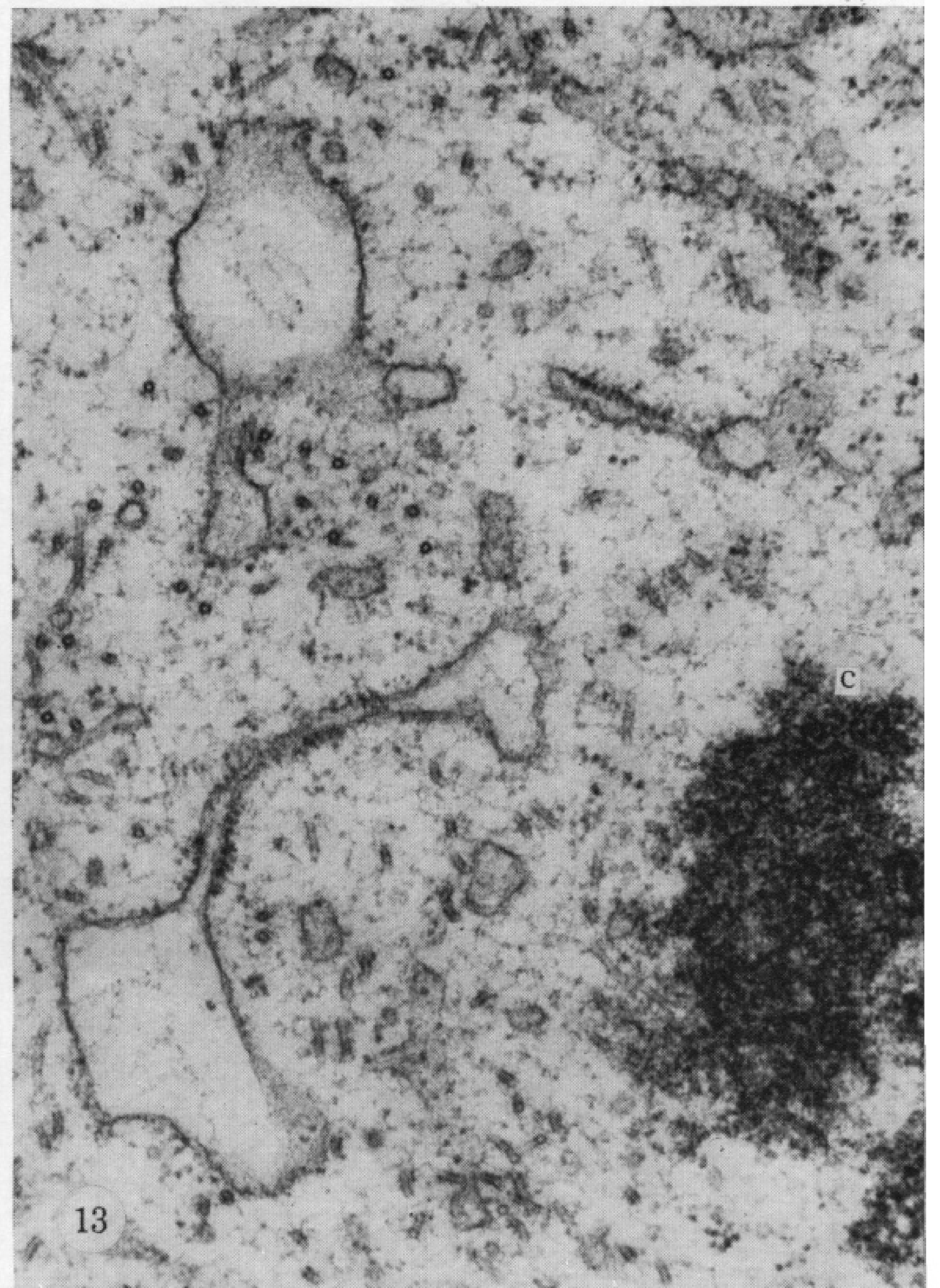
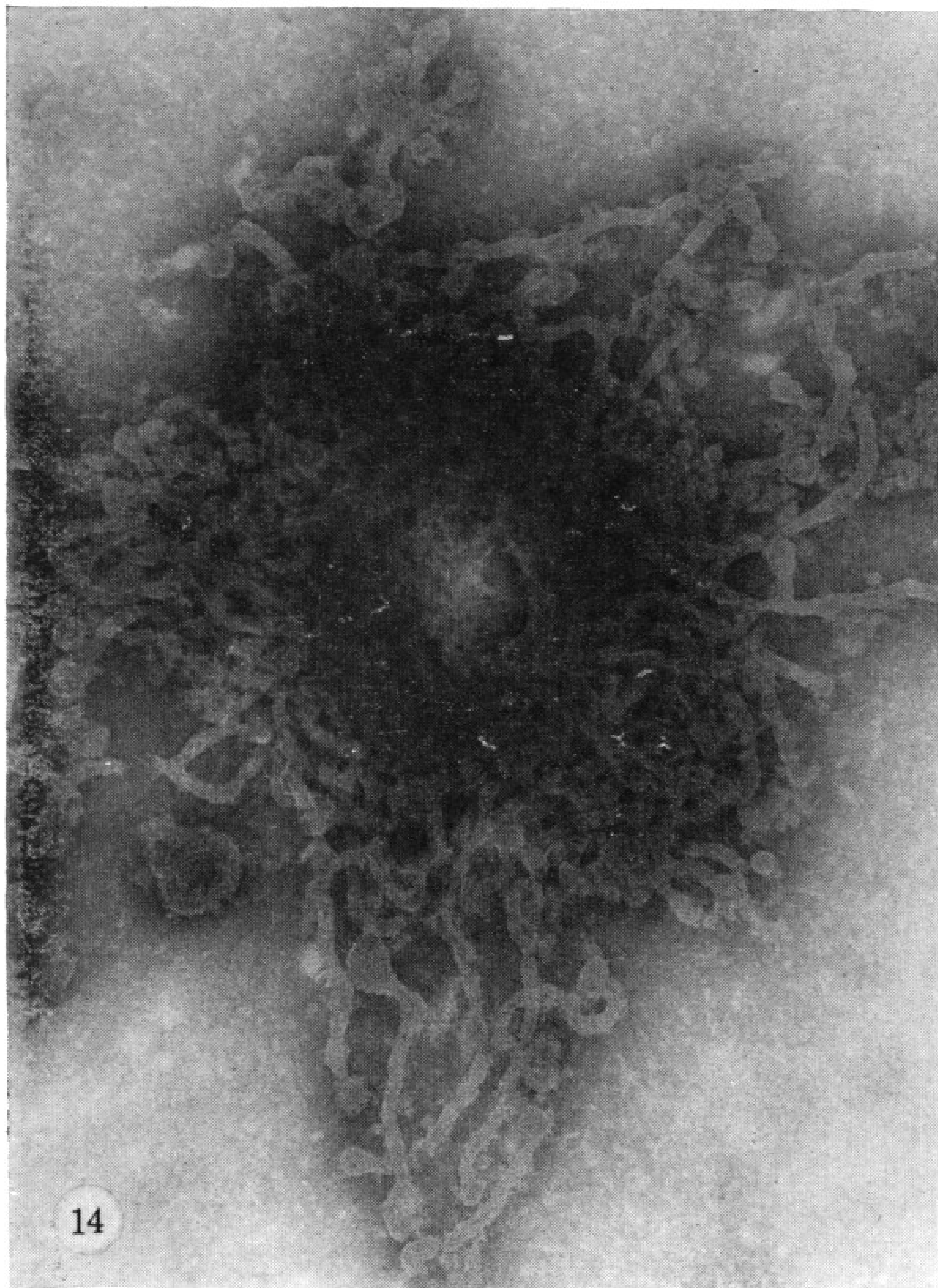


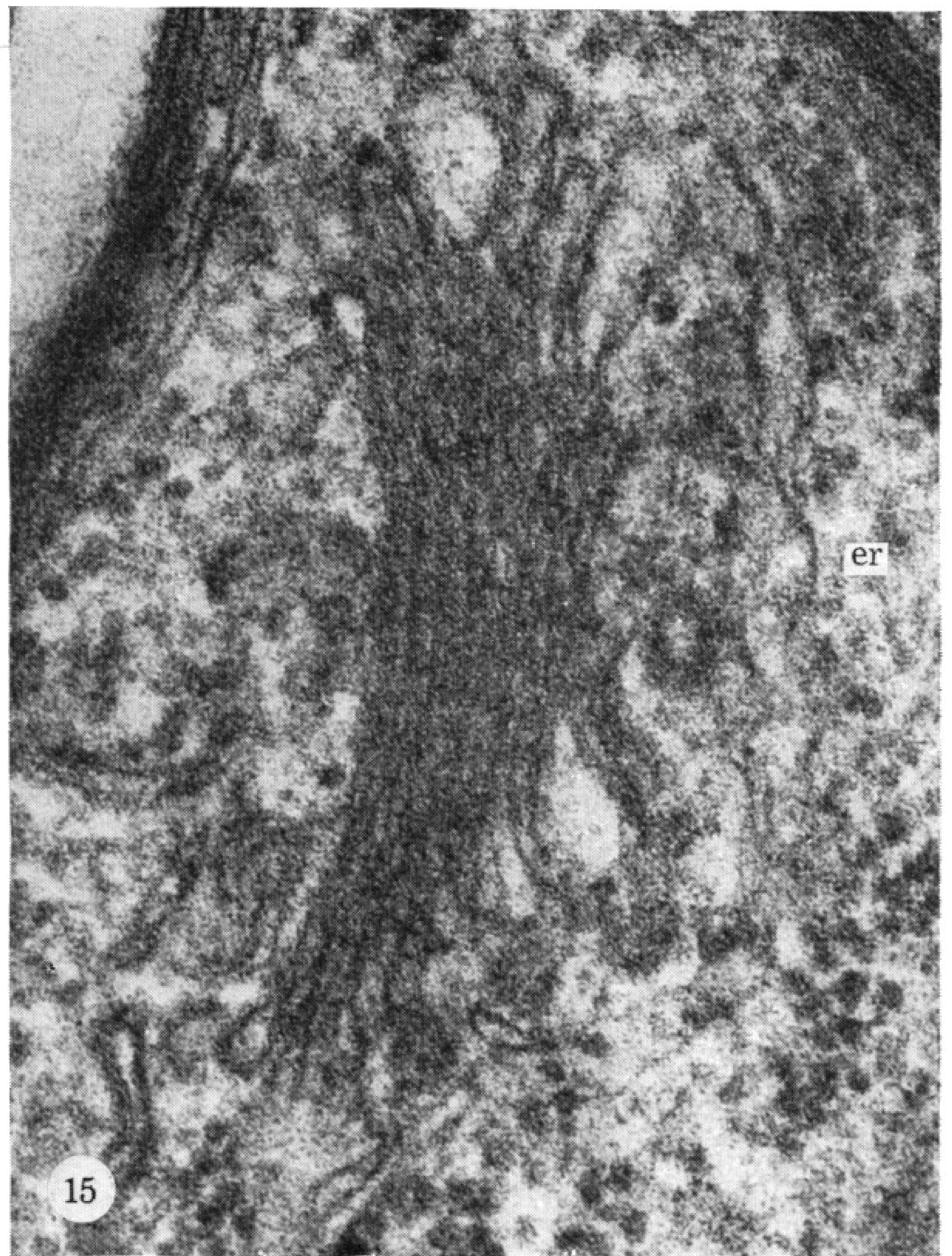
FIGURE 10. An early stage in the development of the sieve plate in the phloem of a stem of sycamore seedlings. The profiles of the endoplasmic reticulum over the cones of callose deposited in the wall at the plasmadesmata can be seen. (Magn. ×41000; Northcote & Wooding 1968.)

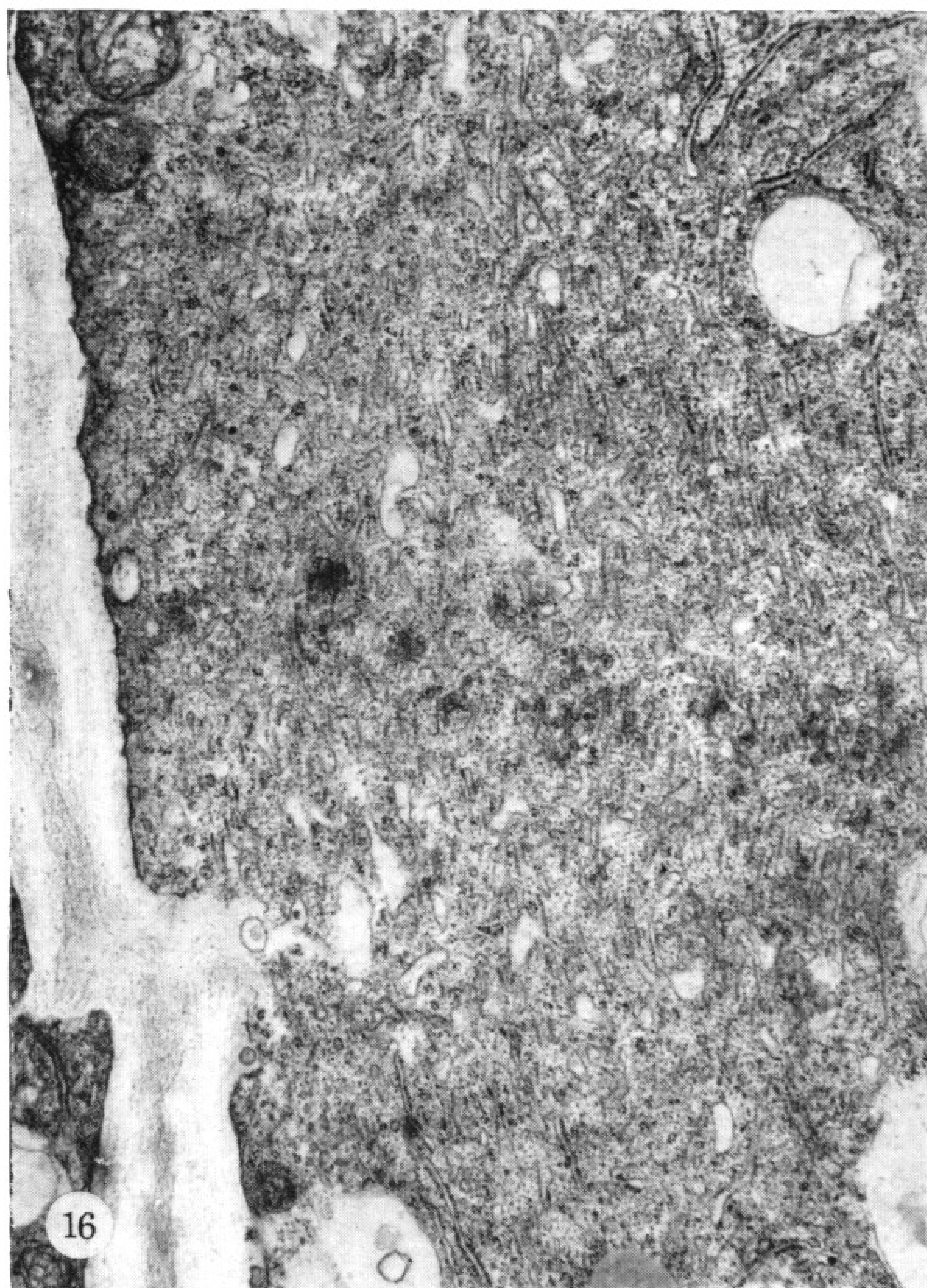
FIGURE 11. A region just behind the growing edge of the cell plate. Profiles of endoplasmic reticulum in a characteristic array can be seen near the cell plate. A tubular profile (arrow) is closely applied to the plasmalemma. (Magn. ×30000; Roberts & Northcote 1970.)

FIGURE 12. A crystal containing microbody. The close association of the organelle with profiles of the endoplasmic reticulum can be seen. (Magn. ×50000; Roberts & Northcote 1970.)

FIGURE 13. Section through the mitotic spindle at metaphase. Profiles of the endoplasmic reticulum have penetrated the mitotic spindle. The section is approximately at right angles to that shown in figure 4. (Magn. ×22000.)







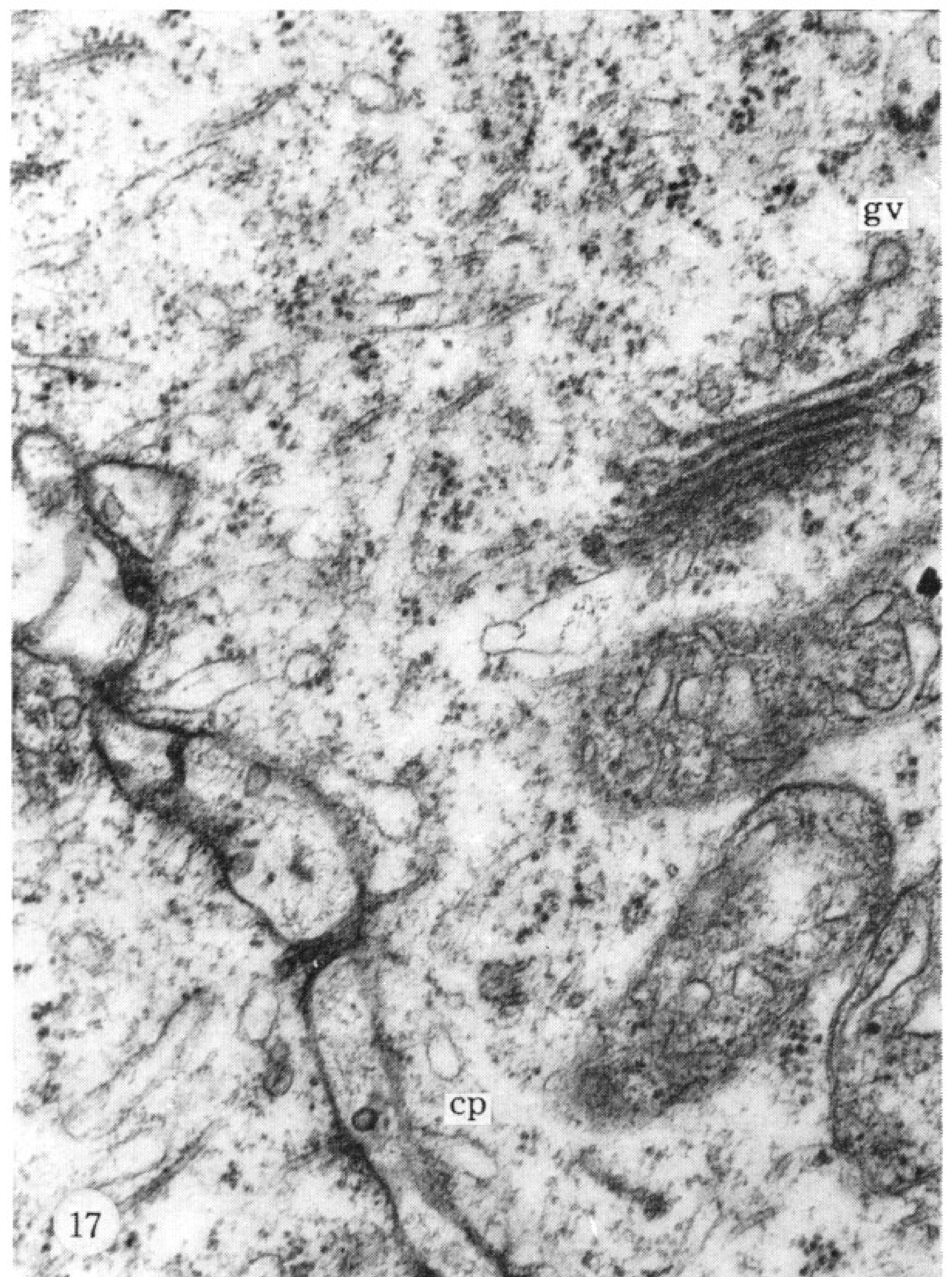


FIGURE 14. A Golgi body isolated by centrifugation of a homogenate of maize shoot tissue. The homogenate was made in the presence of 0.1 M glutaraldehyde. (Magn. ×39000; Bowles & Northcote 1972.)

FIGURE 15. A Golgi apparatus in the coenocytic cell of *Hydrodictium africanum*. The presence of a profile of the endoplasmic reticulum overlying the Golgi bodies is nearly always seen in these cells. (Magn. ×75000.)

FIGURE 16. A section at the outer edge of a growing cell plate. Vesicles are aligned at the site of the formation of the plate. (Magn. ×14000.)

FIGURE 17. The organization of the cytoplasm near the developing cell plate. Vesicles with a dense core can be seen at the cell plate and at the Golgi apparatus. (Magn. ×22000.)