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Nuclear pores at prophase of meiosis in plants

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[Plates 34–35]

Nuclear pores have been studied with the electron microscope in thin sections of pollen mother cells at early- to mid-meiotic prophase (*a*) in respect of distribution, (*b*) in relation to fine structure in the pore complex in the following plants: *Fritillaria lanceolata*, *Phaedranassa viridiflora*, *Tulbaghia violacea*, an F_1 hybrid of *Allium fisultosum* × *Allium cepa* and the lily var. 'Formobel'. In all plants from leptotene to pachytene, the pores were irregularly spread over the envelope in random clusters of variable size encircled by areas in which they did not occur. Further proof was obtained from the lily for the premise that pores are not formed in regions of the envelope to which the nucleolus is adpressed at leptotene. The fine structure of the pore complex observed supports a model which proposes that annuli are composed of three rings of eight granular subunits. Most pores contained a central granule ranging from 25 to 30 nm in diameter composed of amorphous substance and filaments about 3 nm wide, apparently continuous with filaments of similar dimensions in the symmetrical annular subunits that encircle the orifice at both the nuclear and cytoplasmic sides of the pore. The pore complex and central granule were relatively more stable to osmotic shock than the ribosomal region of the nucleolus. Recent ideas concerning the role of the annulus and central granule in nucleocytoplasmic transfer of ribonucleoprotein and assembly of polyribosomes are discussed.

Introduction

Several important problems concerning nuclear pores and the structure of the pore complex remain quite unresolved. Among these are (1) the factors reponsible for the regulation of their distribution in nuclear envelopes, (2) the question as to whether the annulus and associated central granule are in some way involved in opening and closing the pore and (3) whether the pore complex plays a major role in the assembly of ribosomes or ribosomal aggregates? The earlier literature concerned with these problems has been discussed in a number of recent papers (Stevens & Andre 1969; Kessel 1969; Franke 1970*a*; Franke & Scheer 1970*a*, *b*; Roberts & Northcote 1971; La Cour & Wells 1972).

The present observations at meiotic prophase in pollen mother cells (p.m.c.) of some monocotyledonous plants have some bearing on these problems. They were made when the senior author was at the John Innes Institute.

Materials and methods

The following plants were used: *Fritillaria lanceolata*, *Phaedranassa viridiflora*, the triploid hybrid lily 'Formobel', *Tulbaghia violacea* and the hybrid *Allium fistulosum* × *Allium cepa*.

The p.m.c. of the first three were fixed as naked strings of cells, expelled from anthers cut at one end, the others as whole anthers. The method of fixation and preparation of thin sections of the p.m.c. for study with the electron microscope are given in an earlier paper (La Cour & Wells 1972).

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Observations

Distribution

The somewhat tortuous shape of the nuclei in p.m.c. during leptotene and zygotene presents a favourable situation for the study of nuclear pores, inasmuch as that in thin sections the envelope is then cut in planes both perpendicular and nearly parallel to the nuclear surface, as illustrated in figure 1. In all the plants presently studied, the pores were irregularly spread over the envelope surface, often in clusters encircled by areas of variable size in which they were widely spaced or did not occur. There was a strong impression that, fostered by the regularity of pore formation seen in some sections of p.m.c. in all plants, wide differences existed between nuclei in the size of areas devoid of pores. Some areas of envelopes where pores were absent are shown in figures 2 to 4.

In lilies and many *Fritillaria* species, the nucleolus is tightly pressed against the nuclear envelope throughout leptotene and pores are apparently always absent in the region where it is adpressed (La Cour & Wells 1972; Scheer & Franke 1972). Partly because of unusual invagination of areas of the envelope in vacuoles within the nucleolus, the p.m.c. of the triploid lily 'Formobel' has provided the clearest examples of this so far (figure 4). This lily has three pairs of nucleolar organizing chromosomes, so that six nucleoli will be formed at telophase of the last pre-meiotic mitosis. Thus, even allowing for some fusion of nucleoli, pores must be excluded from a large area of the envelope at leptotene in p.m.c. of this plant.

With the *Allium* and *Tulbaghia* material the p.m.c. were studied in sections of whole anthers. It was clear from these preparations that the clustering of pores in the envelope was not influenced in any way by proximity of the tapetum. Again, as in our earlier study (La Cour & Wells 1972) there was no obvious indication that the frequency of pores changed from leptotene to pachytene.

Structure of the pore complex

Recent observations (Franke 1970*a*; Roberts & Northcote 1970; La Cour & Wells 1972) have shown that the pore complex has a more intricate structure than once supposed. From these studies it is now clear that annuli with eightfold symmetry in their structure encompass the orifice of the pore at both of its ends (figures 5 and 6). A circlet of eight granules more spherical in shape and constituting the remaining part of the annulus is included within the pore close to the wall (Roberts & Northcote 1970, 1971; La Cour & Wells 1972). These encircle a central granule or plug, which in p.m.c. at early prophase, at least, was present in most pores.

In the p.m.c. of all the plants we have so far studied, the annular subunits as well as the plug were invariably composed of loosely coiled filaments about 3 nm in diameter. Those present in the plug were also seemingly continuous with those comprising the subunits encircling the ends of the pore (figure 5). It was impossible to determine whether those of the inner subunits were so joined. An essential distinction between the plug and repeating elements was that the part of filaments situated in the former were embedded in an amorphous background substance.

The plug was also found to be the most variable structure within the pore complex. Its diameter ranged from about 25 to 30 nm and occasionally it became so compacted as to cast doubt as to whether it was always the same structural entity under observation (figure 7).

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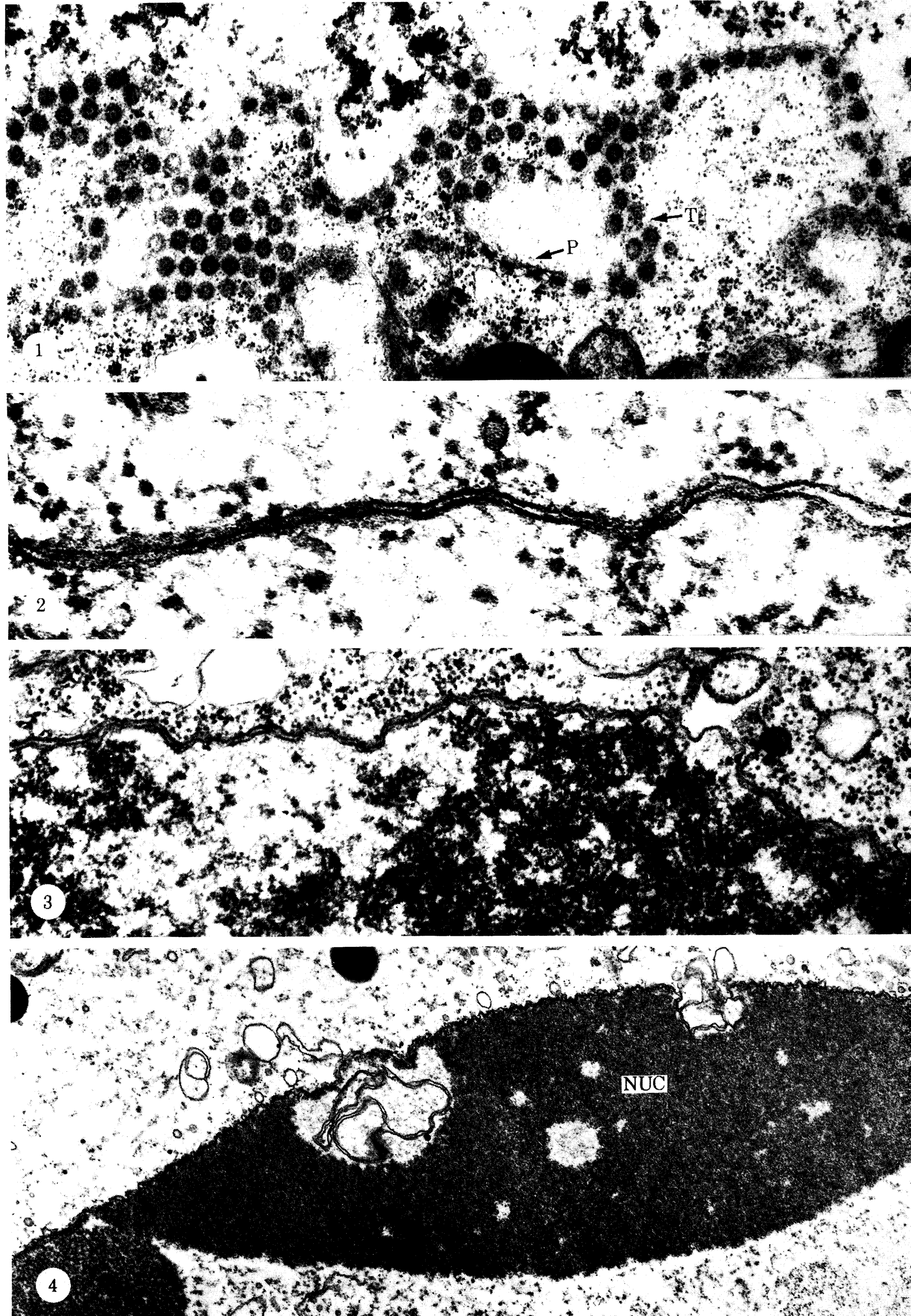

FIGURE 1. Electron micrograph from a p.m.c. at late zygotene of *Fritillaria lanceolata*, showing arrays of annuli face-on and pore complexes in perpendicular (P) and tangential (T) section. All the annuli seen face-on contain a central granule. (Magn. × 30000.)

FIGURE 2. Electron micrograph of an area of the nuclear envelope devoid of nuclear pores from a p.m.c. at pachytene of *Tulbaghia violacea*. (Magn. × 120000).

FIGURE 3. Electron micrograph showing absence of pores in part of the envelope of a pachytene nucleus from a p.m.c. of the hybrid *Allium fistulosum* × *A. cepa*. (Magn. × 40000.)

FIGURE 4. Electron micrograph from a p.m.c. of the lily 'Formobel' showing absence of pores in the region of an envelope at which the nucleolus (NUC) is adpressed during leptotene. The envelope runs tight against the nucleolus and at two places invaginates vacuoles. (Magn. × 15000.)

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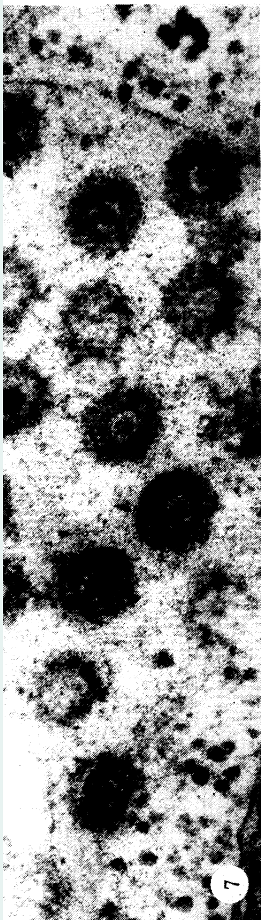

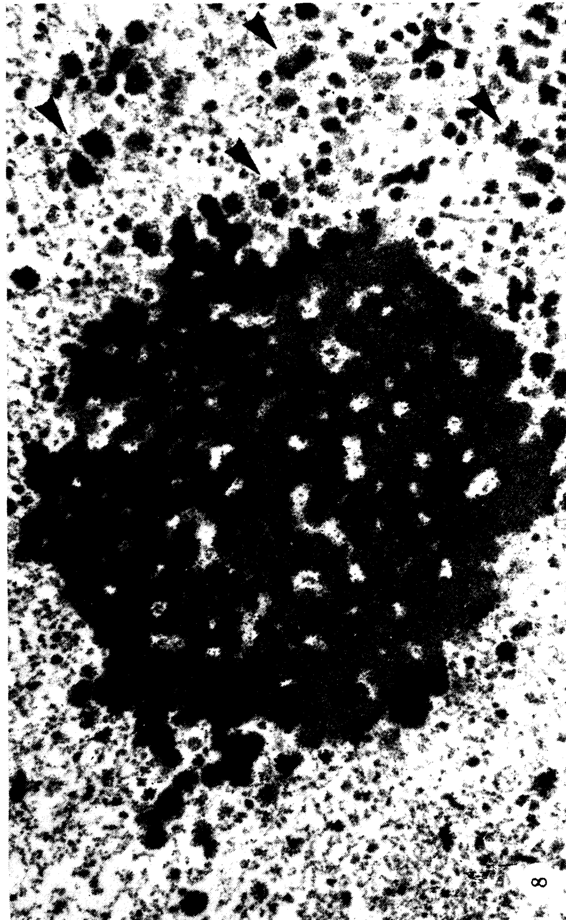

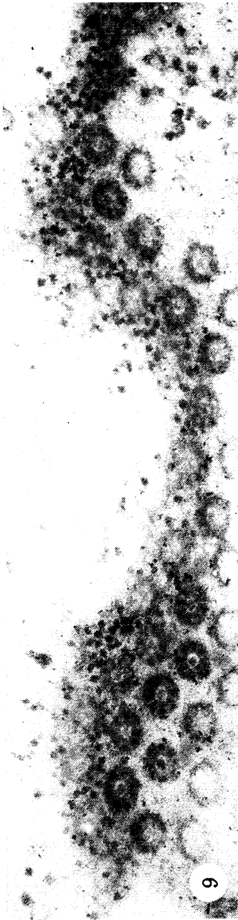

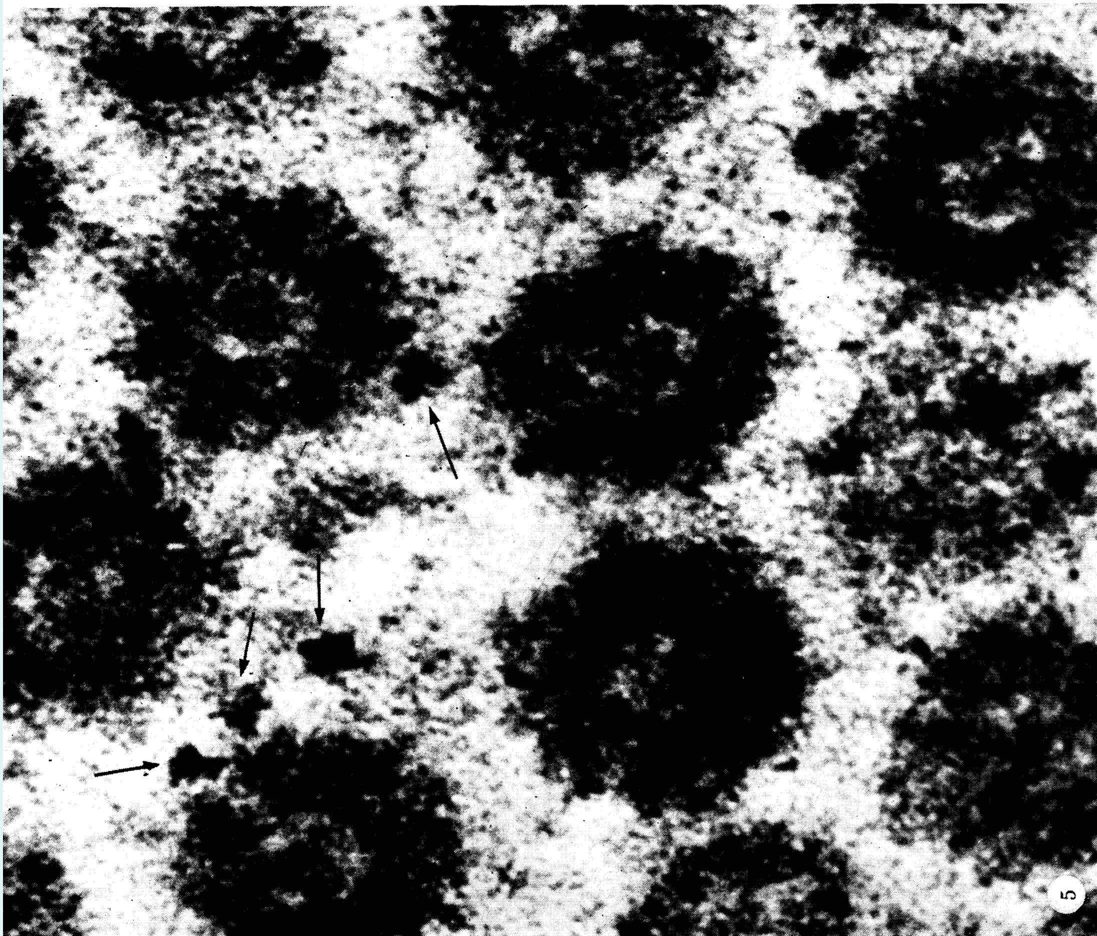

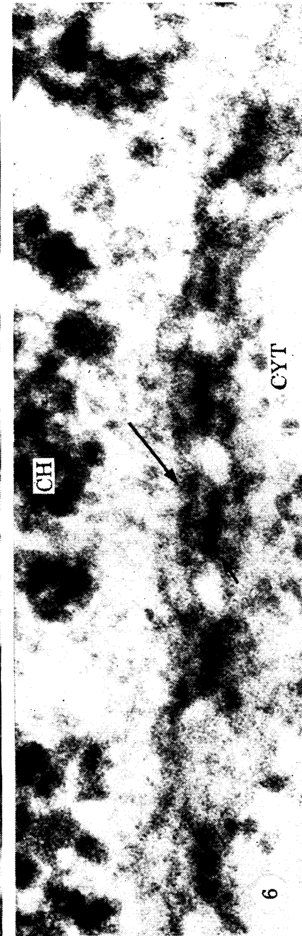

FIGURES 5–10. For description see opposi

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The relative stability of nucleoli and annuli to osmotic shock

Some of our observations on nuclear pores have been made in p.m.c. that were also used for the study of synaptonemal complexes. In some such studies, naked strings of p.m.c. of *Phaedranassa viridiflora* were kept in distilled water at 5 °C before fixation for periods ranging from 5 to 30 min, in order to unravel the compacted chromomeral chromatin at zygotene. The difference in the relative stability of nucleoli and annuli was markedly noticeable in these experiments.

Invariably, even with the shortest treatment (5 min), the 15 nm diameter ribosomes located at the periphery of the nucleus as part of its structure became disassociated and were scattered throughout the nucleus (figure 8). The pore complex and central granule, on the other hand, always remained intact and apparently undisturbed with up to at least four times the length of treatment (figures 9 and 10). With longer treatment there was an increasing tendency for the nuclear envelope to break up.

Discussion

The present observations and our earlier ones (La Cour & Wells 1972) suggest that, as a general rule, pores in prophase nuclei of p.m.c. are randomly distributed over the envelope in clusters of variable size from leptotene to pachytene. It also seems probable that continuous variation exists in the frequency of nuclear pores per p.m.c. within an anther. In p.m.c. of lilies and some *Fritillarias*, where the nucleolus is adpressed to the nuclear envelope at leptotene, there are most likely, particularly in triploid forms of these plants, fewer pores formed than in other species where the nucleolus has a more central position at this time.

There is no bouquet stage or evidence of milder polarization of the chromosomes of *Fritillaria* and *Lillium* at the prophase of meiosis, as in some animals and insects. The absence of pores, therefore, in these plants in regions of the envelope where the nucleolus is adpressed at leptotene,

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Description of plate 35

Figure 5. Electron micrograph of an array of annuli face-on from a p.m.c. at zygotene of *Fritillaria lanceolata*. Continuity is apparent between filaments in the repeating members of the annulus and central plug, which also contains an amorphous background substance. Arrows indicate ribosomes on the surface of the nucleus. (Magn. ×400000.)

Figure 6. Electron micrograph of pore complexes in profile from a p.m.c. at pachytene of *Fritillaria lanceolata* showing subunits of the annulus (long arrow) encircling the orifice at the nuclear end of the pore and internal subunits (short arrow) encompassing the central plug. CH, chromatin, CYT, cytoplasm. (Magn. ×160000.)

Figure 7. Electron micrograph of nuclear pores from a p.m.c. at zygotene of *Fritillaria lanceolata*, illustrating variability in appearance of the central plug. (Magn. ×120000.)

Figure 8. Electron micrograph from a p.m.c. at zygotene of *Phaedranassa viridiflora*, showing a nucleolus depleted of ribosomes after 5 min treatment of cell in water at 5 °C. The disassociated ribosomal aggregates (arrow heads) lie scattered mostly on the right of the nucleolus. (Magn. ×20000.)

Figure 9. Electron micrograph of pore complexes face-on and in tangential section from a p.m.c. at zygotene of *Phaedranassa viridiflora* treated in water for 20 min at 5 °C, illustrating ability of pore complex and central plug to withstand osmotic shock. (Magn. ×60000.)

Figure 10. Electron micrograph of an array of annuli from a p.m.c. at zygotene from *Phaedranassa viridiflora* after treatment of cells in water for 20 min at 5 °C. Some ribosomal aggregates (arrow heads) from the dismembered nucleolus lie close at hand. (Magn. ×40000.)

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scarcely favours the notion that the pore complex is a 'press-stud' method of attaching chromosomes to the nuclear envelope (Engelhardt & Pusa 1972). Furthermore, there is no conclusive evidence that the pore complex contains DNA (Scheer 1972). Roberts & Northcote (1971) have also shown that, in somatic tissues of plants, a clear area encompasses the pore like a halo in which chromatin does not impinge.

In p.m.c. of *F. lanceolata* large blocks of heterochromatin, unlike the nucleolus, did not appear to influence the frequency of pores in its immediate vicinity one way or the other, even though these chromosome parts lay near the nuclear surface and appeared more active than others in the passage of material toward the envelope (La Cour & Wells 1972).

We are inclined to the belief that a large number of pores are not required by the nucleus at mid-prophase in the p.m.c. This view is in part prompted by our observation of the extreme paucity of pores that occurs at meiotic prophase in p.m.c. of synaptic and asynaptic forms of *Triticum durum* var Aziziah (La Cour & Wells 1972). Further support for this premise comes from observations which indicate that there is most likely a low incidence in movement of material from the nucleus to the cytoplasm at this time. For example in p.m.c. of two plant species Mackenzie, Heslop-Harrison & Dickinson (1967) have shown that there is a decline in RNA during mid-prophase concomitant with a pronounced reduction in the number of ribosomes. The latter was also noticeable in our pachytene preparations. A decline in RNA synthesis has also been noted in the nucleolus at meiotic prophase in *Zea Mays* (Das 1965) and similarly in germ cells of the Chinese hamster (Utakoji 1966).

There are also a number of observations indicating a variation in number of nuclear pores according to the metabolic activity of the cell. Oocytes of amphibia (Afzelius 1955; Franke & Scheer 1970*b*), the macronucleus of *Tetrahymena pyriformis* (Franke 1967) and salivary gland nuclei of diptera (Wiener, Spiro & Loewenstein 1965) are notable for a high number of pores and intense metabolic activity. Old years cells (Moor & Mühlethaler 1963), acidophil cells in mammalian tissue (Barnes & Davis 1959) and late erythroblasts of mammalian foetal tissue (Grasso, Swift & Ackerman 1962), all have a lower number of pores and low metabolic activity.

Although it can be assumed that pores are mostly formed during reconstruction of the envelope at telophase, seemingly with the envelope essentially in contact with the surface of the chromosomes (Moses 1964; Robbins & Gonatus 1964; Murray *et al.* 1965), there is an indication that the number can increase in some types of cell as metabolic activity of the nucleus increases, as in oocytes of amphibia (Franke & Scheer 1970*b*). We do not know whether pores are sometimes short-lived.

Although it seems highly probable that the frequency of pores is to some extent correlated with the metabolic activity of the nucleus, in respect of the p.m.c. this must be pre-determined at the pre-meiotic telophase. The reason, however, for the extreme paucity of pores at prophase of meiosis in p.m.c. of *T. durum* is obscure, inasmuch as more than one plant of the synaptic and asynaptic forms showed the same behaviour. A possibility, not easily dismissed, is that all the plants in this particular race were defective for a gene controlling the synthesis of a protein involved in pore formation at the pre-meiotic telophase.

The apparent universality of the intricate structure of the pore complex has already been stressed (Franke 1970*a*). Although it is obvious that the pores must provide the pathway for nucleocytoplasmic transfer of macromulecules, the means by which this is controlled are obscure. Several observations show that movement of material through the pore centre is

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limited to a pathway about 15 nm wide (see, for example, Anderson & Beams 1956; Feldherr 1962, 1965, 1969; Feldherr & Harding 1964; Beermann 1964; Stevens & Swift 1966; Franke & Scheer 1970*b*). There is no clearly defined channel and amorphous material within the pore probably constitutes a barrier to diffusion. The 8 units of the free annulus lining the wall inside the pore will themselves impose some limit on the size of the exit.

Because of its position and complex architecture some consideration must be given to the possibility that the annulus is in some way involved in opening and closing the pore. Kessel (1969) has assigned such a role to the central granule. Our observations indicate that its comprising filaments are continuous with those in the encompassing repeating units of the annulus, and elsewhere we have suggested that these may have contractile properties (La Cour & Wells 1972). The more recent finding that the pore complex is rich in RNA makes this suggestion most unlikely. Stevens & André (1969) have proposed that the annulus is probably endowed with enzymic activities which determine when pores are penetrable and impenetrable.

Many observations like the present ones indicate that the central granule is a dynamic structure, but it remains an open question as to whether its structure is so transitory as to represent ribonucleoprotein (RNP) regularly in transit through the pores. By reason of its very regular inclusion in the pore complex of the p.m.c. at zygotene – that is, before recombination and when as the evidence suggests transcriptional activity is low – it is difficult to avoid the conclusion that it is an integral part of the pore complex architecture.

Mepham & Lane (1969) have suggested that nuclear pores are sites at which polyribosomes are assembled from units of the annulus before leaving the nucleus. Although the annular components undoubtedly consist of RNP, the central granule and annular units are the wrong size to be either ribosomes or their subunits. It also appears improbable in view of the greater ability of the pore complex to withstand osmotic shock as compared with the ribosomal aggregates of the nucleolus, as shown by our experiments. This does not preclude the possibility that the pore complex architecture is, in some at present obscure way, involved both in assemblage of ribosomes and regulation of their egress to the cytoplasm.

Both Franke (1970*b*) and Scheer (1972) have put forward a strong argument for the supposition that pore complex structures pass through dynamic and static states, depending on the transcriptional activity of the nucleus. In terms of their observations in amphibian oocytes, the pore complex would be in a dynamic phase during the lampbrush stage when transcription is intense and a static one in the mature oocyte when it has lapsed. Thus, on this view the fine components of the pore complex would be RNP in transit through a regulated pathway and integrated structural constituents in turn. If this is indeed so, it might be expected that, after recombination at pachytene and renewed transcription, the orderly architecture of the pore complex in the p.m.c. would, like the nucleolus in our water experiments at zygotene, collapse under similar conditions of osmotic shock.

References (La Cour & Wells)

Afzelius, B. A. 1955 The ultrastructure of the nuclear membrane of the sea urchin oocyte as studied with the electron microscope. *Expl Cell Res.* **8**, 147–158.
Anderson, E. & Beams, H. W. 1956 Evidence from electron micrographs for the passage of material through pores of the nuclear membrane. *J. biophys. biochem. Cytol.* **2**, Suppl.
Barnes, B. G. & Davis, J. M. 1959 The structure of nuclear pores in mammalian tissue. *J. ultrastruct. Res.* **3**, 131–146.
Beermann, W. 1964 Control of differentiation at the chromosome level. *J. exp. Zool.* **157**, 49–61.

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Das, N. K. 1965 The inactivation of the nucleolar apparatus during meiotic prophase in corn anthers. *Expl Cell Res.* **40**, 360–364.

Engelhardt, P. & Pusa, K. 1972 Nuclear pore complexes: 'Press-stud' elements of chromosomes in pairing and control. *Nature New Biol.* **240**, 163–166.

Feldherr, C. M. 1965 The effect of the electron-opaque pore material on exchanges through the nuclear annuli. *J. Cell Biol.* **25**, 43–54.

Feldherr, C. M. 1969 A comparative study of nucleocytoplasmic interactions. *J. Cell Biol.* **42**, 841–845.

Feldherr, C. M. & Harding, C. V. 1964 The permeability characteristics of the nuclear envelope at interphase. *Protoplasmatologia* (*Wien*) **5**, 35–50.

Franke, W. W. 1967 Zur Feinstruktur isolierter Kernenmembranen aus tierischen Zellen. *Z. Zellforsch. mikrosk. Anat.* **80**, 585–593.

Franke, W. W. 1970*a* On the universality of nuclear pore complex structure. *Z. Zellforsch. mikrosk. Anat.* **105**, 405–429.

Franke, W. W. 1970*b* Nuclear pore flow rate. *Naturwissenschaften* **57**, 44–45.

Franke, W. W. & Scheer, U. 1970*a* The ultrastructure of the nuclear envelope of the amphibium oocyte: A re-investigation. I. The mature oocyte. *J. ultrastruct. Res.* **30**, 288–316.

Franke, W. W. & Scheer, U. 1970*b* The ultrastructure of the nuclear envelope of the amphibian oocyte: A re-investigation. II. The immature oocyte and dynamic aspects. *J. ultrastruct. Res.* **30**, 317–327.

Grasso, J. A., Swift, H. & Ackerman, G. A. 1962 Observations on the development of erythrocytes in mammalian fetal liver. *J. Cell Biol.* **14**, 235–254.

Kessel, R. G. 1969 Fine structure of the pore–annulus complex in the nuclear envelope and annulate lamellae of germ cells. *Z. Zellforsch. mikrosk. Anat.* **94**, 441–453.

La Cour, L. F & Wells, B. 1972 The nuclear pores of early meiotic prophase nuclei of plants. *Z. Zellforsch. mikrosk. Anat.* **123**, 178–194.

Mackenzie, A., Heslop-Harrison, J. & Dickinson, H. G. 1967 Elimination of ribosomes during meiotic prophase. *Nature, Lond.* **215**, 997–999.

Mepham, R. H. & Lane, G. R. 1969 Nucleopores and polyribosome formation. *Nature, Lond.* **221**, 288–289.

Moor, H. & Mühlethaler, K. 1963 Fine structure in frozen-etched yeast cells. *J. Cell Biol.* **17**, 609–628.

Moses, M. J. 1964 *The nucleus and chromosomes: A cytological perspective in cytology and cell physiology*, 3rd ed. (ed. G. H. Bourne). New York: Academic Press.

Murray, R. G., Murray, A. S. & Pizzo, A. 1965 The fine structure of mitosis in rat lymphocytes. *J. Cell Biol.* **26**, 601–619.

Robbins, E. & Gonatus, N. K. 1964 The ultrastructure of a mammalian cell during the mitotic cycle. *J. Cell Biol.* **21**, 429–463.

Roberts, K. & Northcote, D. H. 1970 Structure of the nuclear pore in higher plants. *Nature, Lond.* **228**, 385–386.

Roberts, K. & Northcote, D. H. 1971 Ultrastructure of the nuclear envelope: structural aspects of the interphase nucleus of sycamore suspension culture cells. *Microscopica Acta* **71**, 102–120.

Scheer, U. 1972 The ultrastructure of the nuclear envelope of amphibian oocytes. IV. On the chemical nature of the nuclear pore complex material. *Z. Zellforsch. mikrosk. Anat.* **172**, 127–148.

Scheer, U. & Franke, W. W. 1972 Annulate lamellae in plant cells: formation during microsporogenesis and pollen development. *Planta* **107**, 145–159.

Stevens, B. J. & André, J. 1969 The nuclear envelope. In *Handbook of molecular cytology* (ed. A. Lima-de-Faria), pp. 837–871. Amsterdam: North-Holland.

Stevens, B. J. & Swift, H. 1966 RNA transport from nucleus to cytoplasm in *Chironomus* salivary glands. *J. Cell Biol.* **31**, 55–71.

Utakoji, T. 1966 Chronology of nucleic acid synthesis in meiosis of the male Chinese hamster. *Expl Cell Res.* **42**, 584–596.

Wiener, J., Spiro, D. & Loewenstein, W. R. 1965 Ultrastructure and permeability of nuclear membranes. *J. Cell Biol.* **27**, 107–117.

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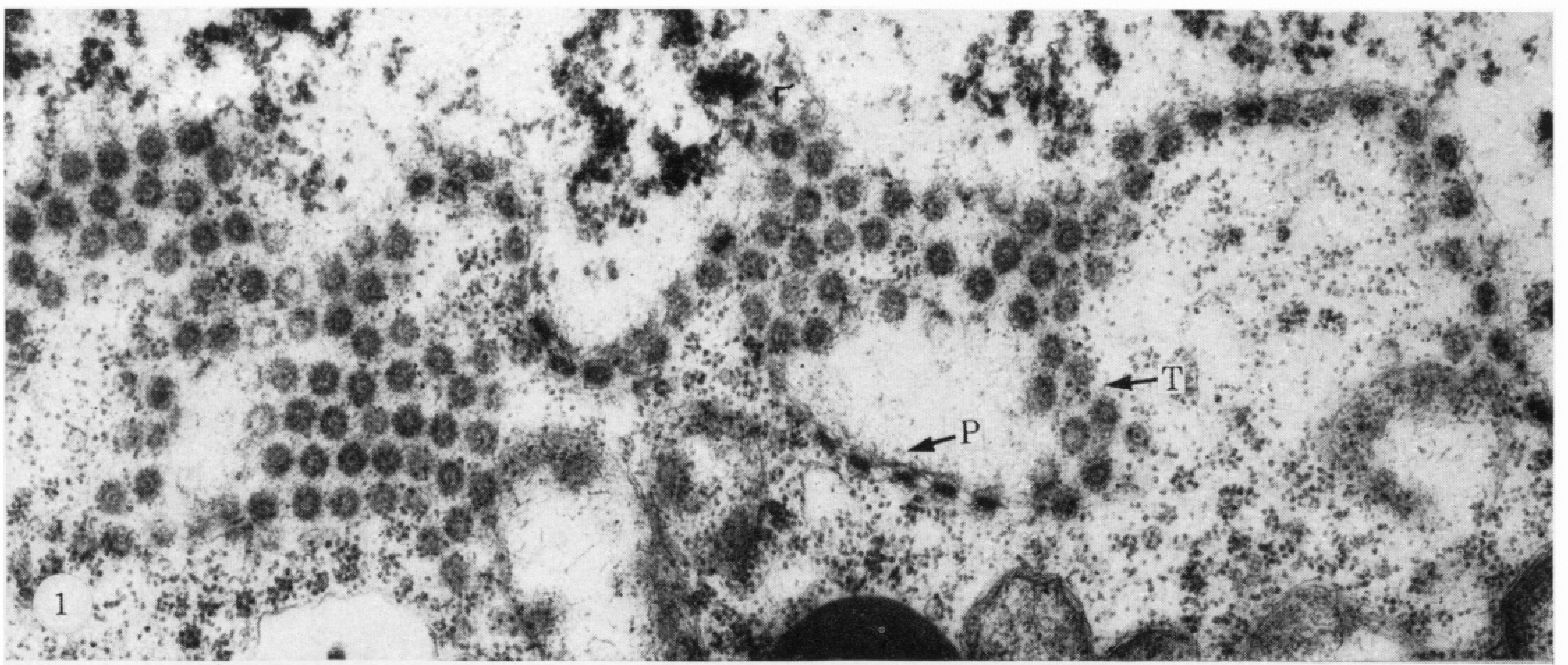

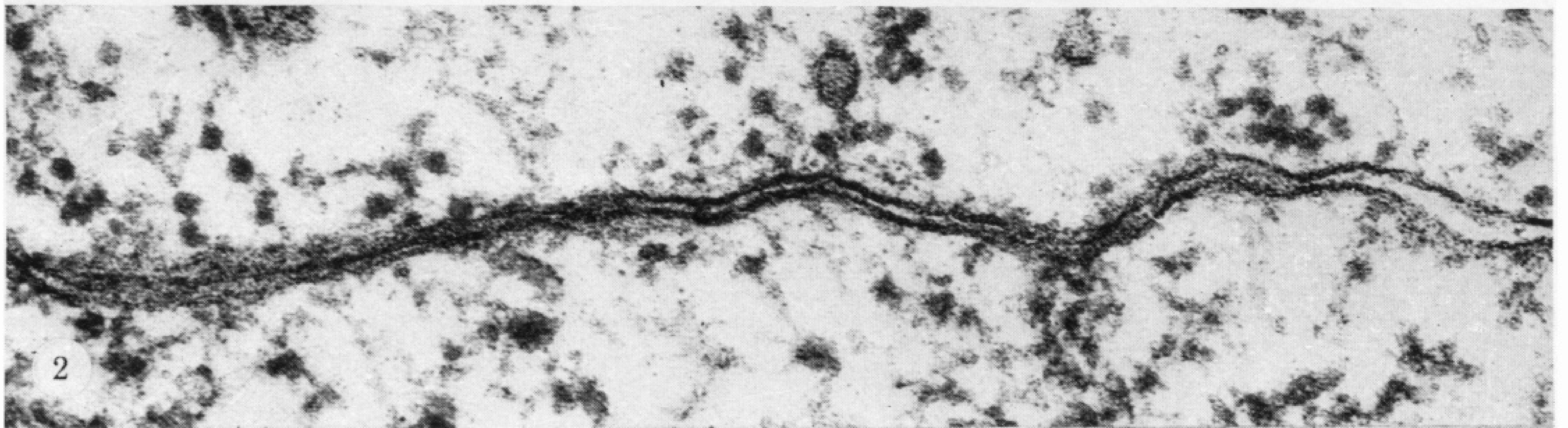

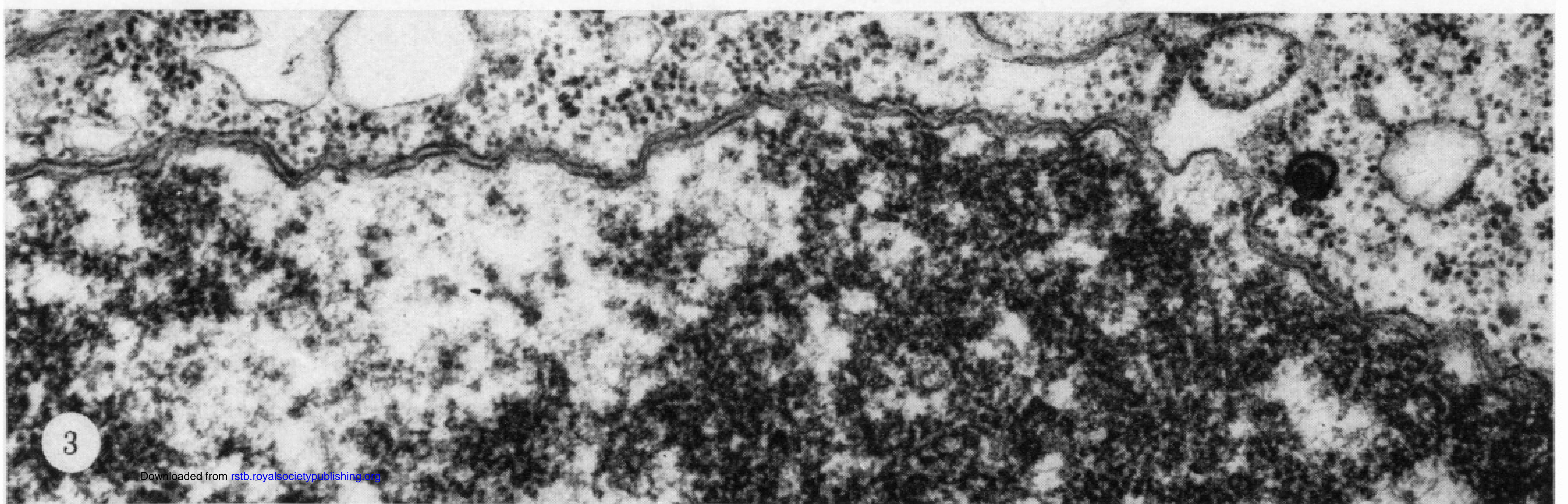

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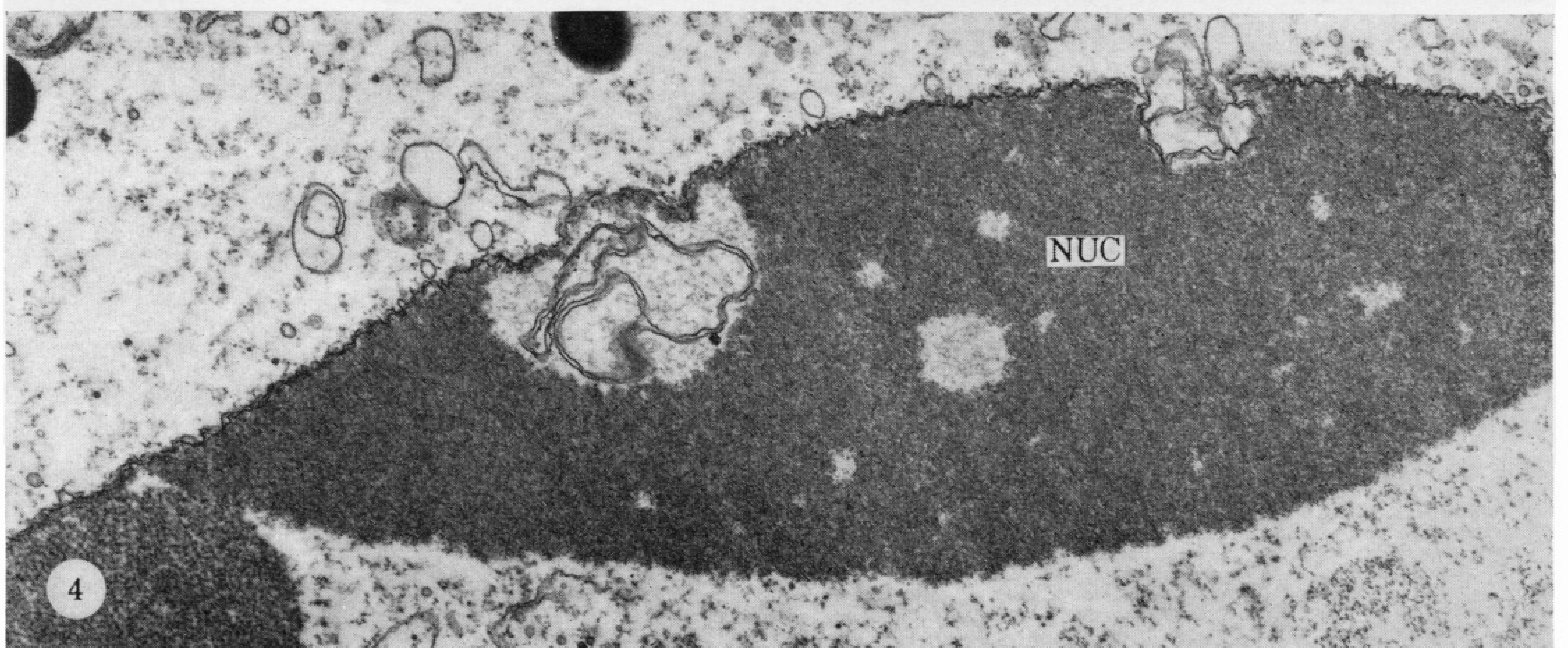

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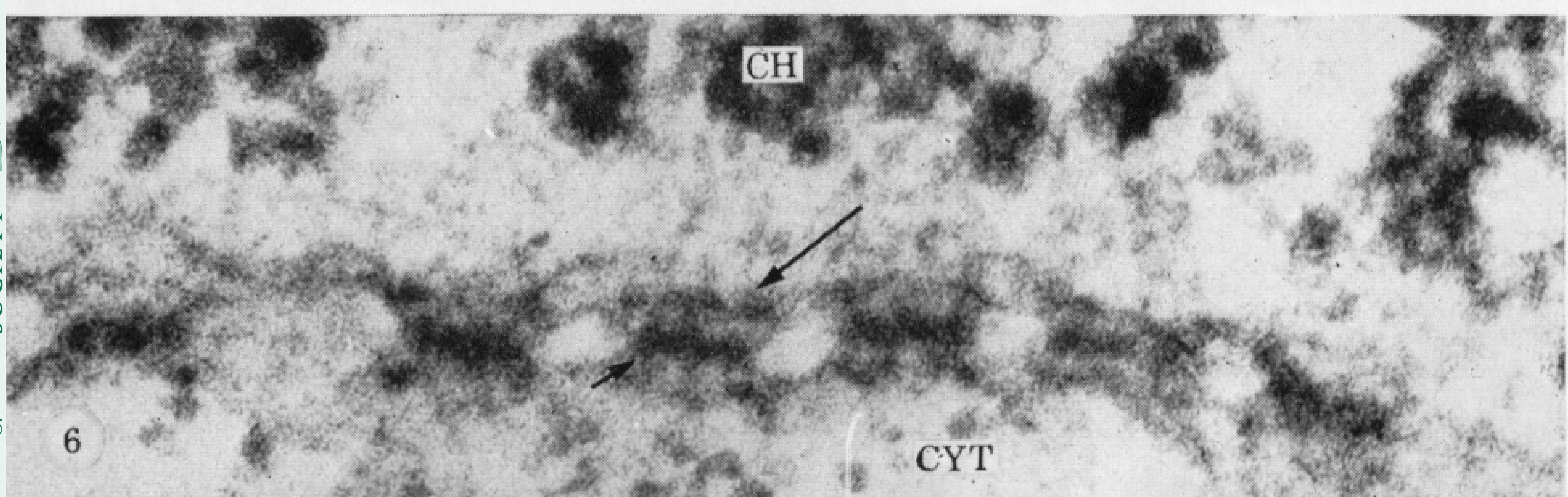

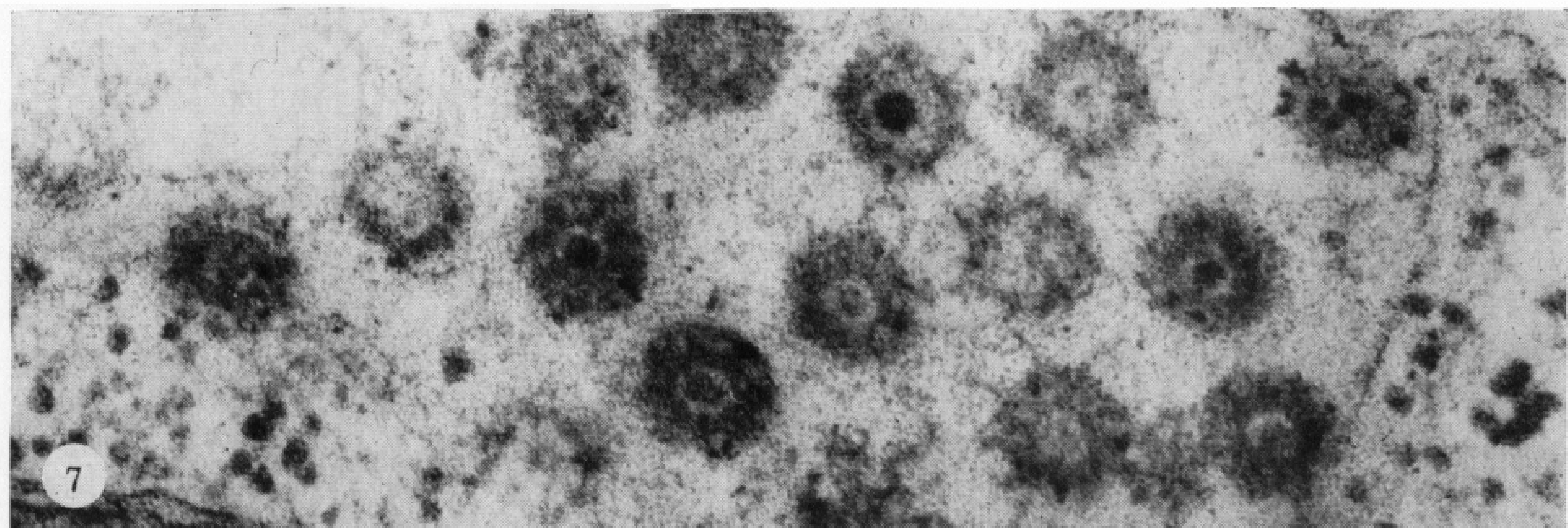

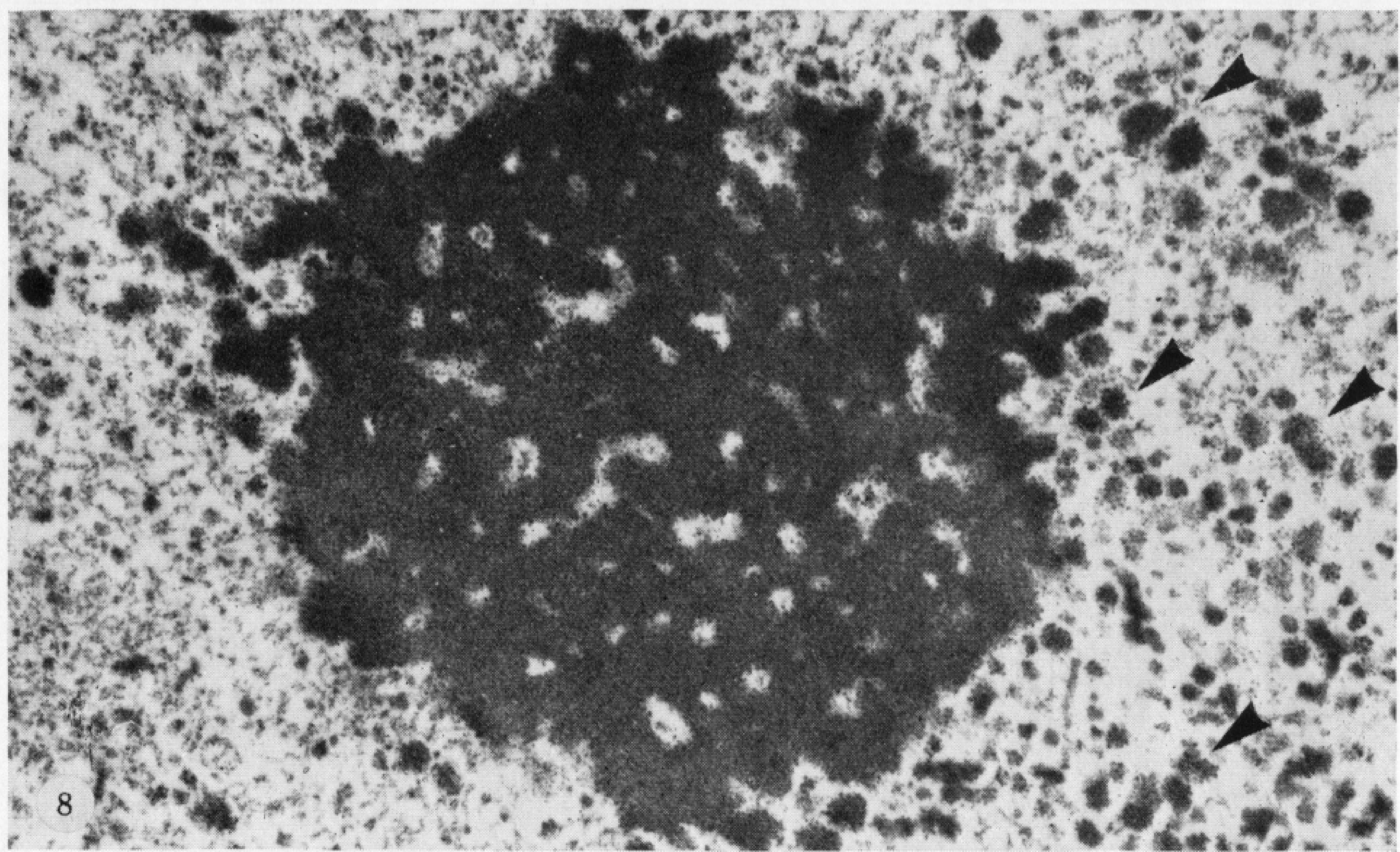

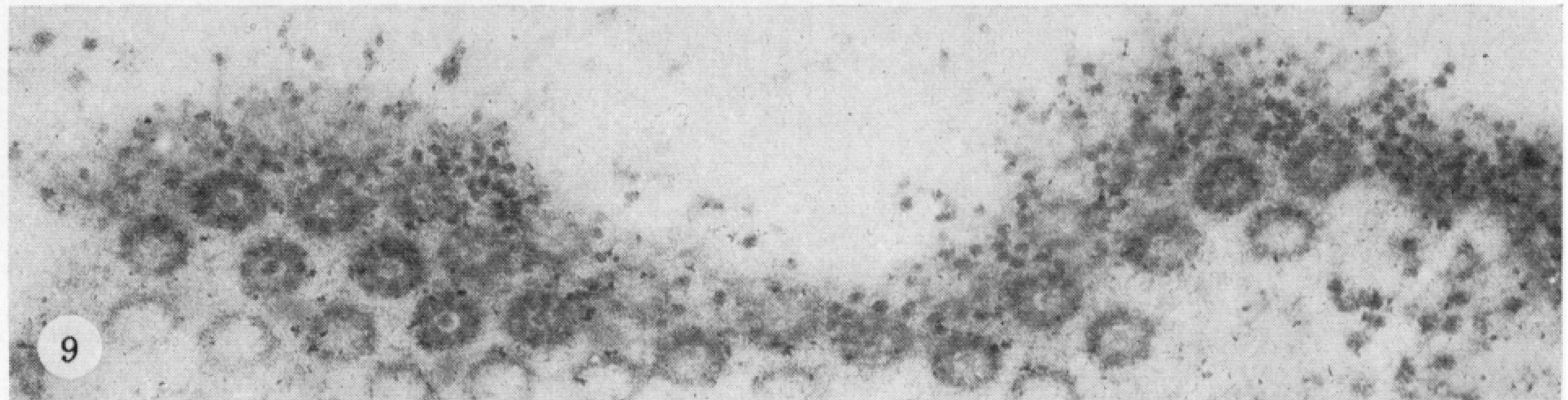

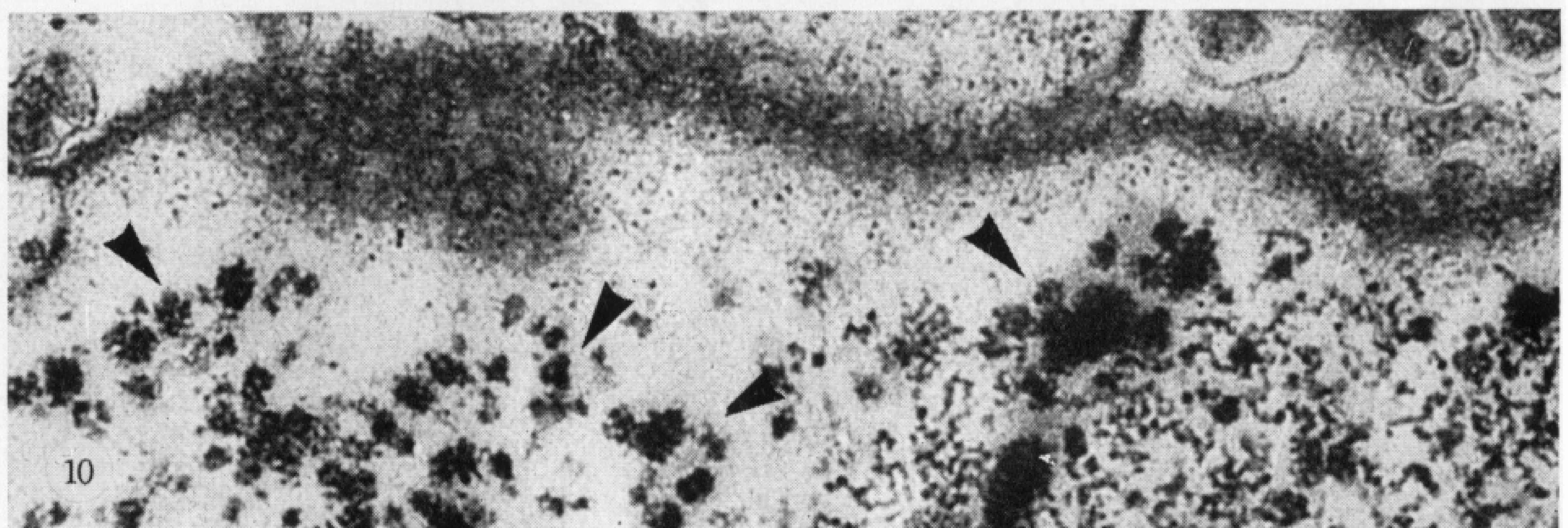

FIGURES 5–10 For description see opposite

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