Some Morphological Aspects of the Synaptonemal Complex in Higher Plants

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Some morphological aspects of the synaptonemal complex in higher plants

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[Plates 1–3]

The synaptonemal complex is illustrated in electron micrographs from pollen mother cells (p.m.cs) of the following plants: *Fritillaria lanceolata, Allium fistulosum, Tulbaghia violacea, Luzula purpurea, Phaedranassa viridiflora* and the tulip cultivar Keiserkroon. The possibility that the lateral elements in synaptonemal complexes of plants are tubiform structures is discussed in relation to their fine structure and in the light of a deformity seen in them. An assessment of the evidence suggesting that both lateral and central elements in the complex are ribonucleoprotein structures is made. The effect of brief water treatment on the chromatin and synaptonemal complex at zygotene in p.m.cs of the *Phaedranassa* is discussed, particularly with reference to two precisely orientated axial strands then seen running between the lateral elements.

Examination of stages of premeiotic interphase and early leptotene in p.m.cs of the *Fritillaria*, revealed that the axial cores laid down at leptotene are formed first in heterochromatic regions, which in this species are locked in chromocentres that persist until pachytene. Further, at leptotene the chromatin in these parts was singularly more decondensed (diffuse) than at any other period, including the premeiotic interphase, subsequent stages of meiosis and mitotic cycle in meristems. It is suggested that the diffuse state of the chromatin in chromocentres at the onset of leptotene, allows the necessary freedom of movement required to promote homologous pairing of the heterochromatic segments. Evidence of such a movement was indicated by a change in position of the nucleoli, which moved from a more central position at early premeiotic interphase to a peripheral one at the onset of leptotene, when they are seen adpressed to the nuclear envelope.

Introduction

The mechanism by which two homologous chromosomes pair during prophase of meiosis poses one of the most intriguing problems in cytogenetics. As shown in a sequence of stages with the light microscope, the homologous chromosomes are unpaired at leptotene, begin to become paired along their length at zygotene and are tightly paired at pachytene.

Almost 20 years have elapsed since Moses (1956) published the first electron micrographs of the synaptonemal complex, a tripartite structure which is in some obscure way involved in the close pairing of the homologous pachytene chromosomes. It is composed of two usually distinctly defined electron-dense lateral elements, intimately associated with the axes of the paired chromosomes and separated by a transparent region containing a central element of medium electron density. The bulk of the chromatin of each homologue representing the chromomeres lies at the outer side of the lateral elements and thus outside the synaptonemal complex.

The universal occurrence of the synaptonemal complex at prophase of meiosis in eukaryotic organisms and the uniformity of its structure have recently been illustrated by Westergaard & von Wettstein (1972), following the review by Moses (1968). The slight deviations from a

common configuration so far reported involve only small details of ultrastructure such as presence or absence of periodicity in the arrangement of the transverse components of the central element and banded pattern in lateral elements. Any particular structural pattern has been found constant within groups.

The outer disposition of the chromomeral chromatin, as well as the actual location of the chromosome axes in relation to the lateral elements and the apparent separation of the axes by a distance of about 100 nm or more, provide interesting problems concerning chromosome structure and the perplexing phenomenon of recombination. In terms of actual structure, the exact relationship of the chromatin fibres to the lateral elements perhaps provide the area of widest contention.

Our observations come from a series of studies of the synaptonemal complex in pollen mother cells (p.m.cs) of various plants, mostly made when the senior author was at the John Innes Institute.

Observations and discussion

General fine structure

Synaptonemal complexes can only be visualized in electron micrographs, as is illustrated in micrographs taken in sequence with light and electron microscopes of the same section of a p.m.c. (figure 1). Electron micrographs of synaptonemal complexes at higher magnification taken from p.m.cs of five other plants are shown in figures 2–5 and 8. The fine structure visible in these examples is typical of that illustrated from many plants (see Westergaard & von Wettstein 1972).

The dimensions of the components in synaptonemal complexes in p.m.cs of some monocotyledonous plants we have studied are given in table 1. They are closely similar to those found in dicotyledonous plants and the wide range of eukaryotic organisms listed by Westergaard

Table 1. Dimensions (in nm) of synaptonemal complexes in some plant p.m.cs

|	distance between l.e.	width of l.e.	width of c.e.
Fritillaria lanceolata	100	50	45
F. ruthenica	100	50	40
Lilium aureliensis × *L. henryi*	100	45	45
Phaedranassa viridiflora	100	45	35
Tulbaghia violacea	100	40	40
Triticum durum	110	50	50
Luzula purpurea	110	30	30
Tulip var. Keiserkroon	100	50	50

Description of plate 1

Figure 1. Light (inset) and electron micrographs of the same section of a p.m.c. at zygotene from *Fritillaria lanceolata* (cf. Wells & La Cour 1971). H, Heterochromatin in chromocentres; EU, euchromatin; SC, synaptonemal complex; N, nucleolus; NO, nucleolar organizer; FB, fat bodies. (Magn. × 2000 and 6000, respectively.)

Figure 2. Electron micrograph of a synaptonemal complex at pachytene in a p.m.c. of *Luzula purpurea*. LE, Lateral element; CE, central element; CH, chromatin. (Magn. × 40000.)

Figure 3. Electron micrograph of a synaptonemal complex at pachytene in a p.m.c. of *Tulbaghia violacea*. (Magn. × 200000.)

Figure 4. Electron micrograph of a synaptonemal complex at zygotene in a p.m.c. of the tulip Keiserkroon. (Magn. × 100000.)
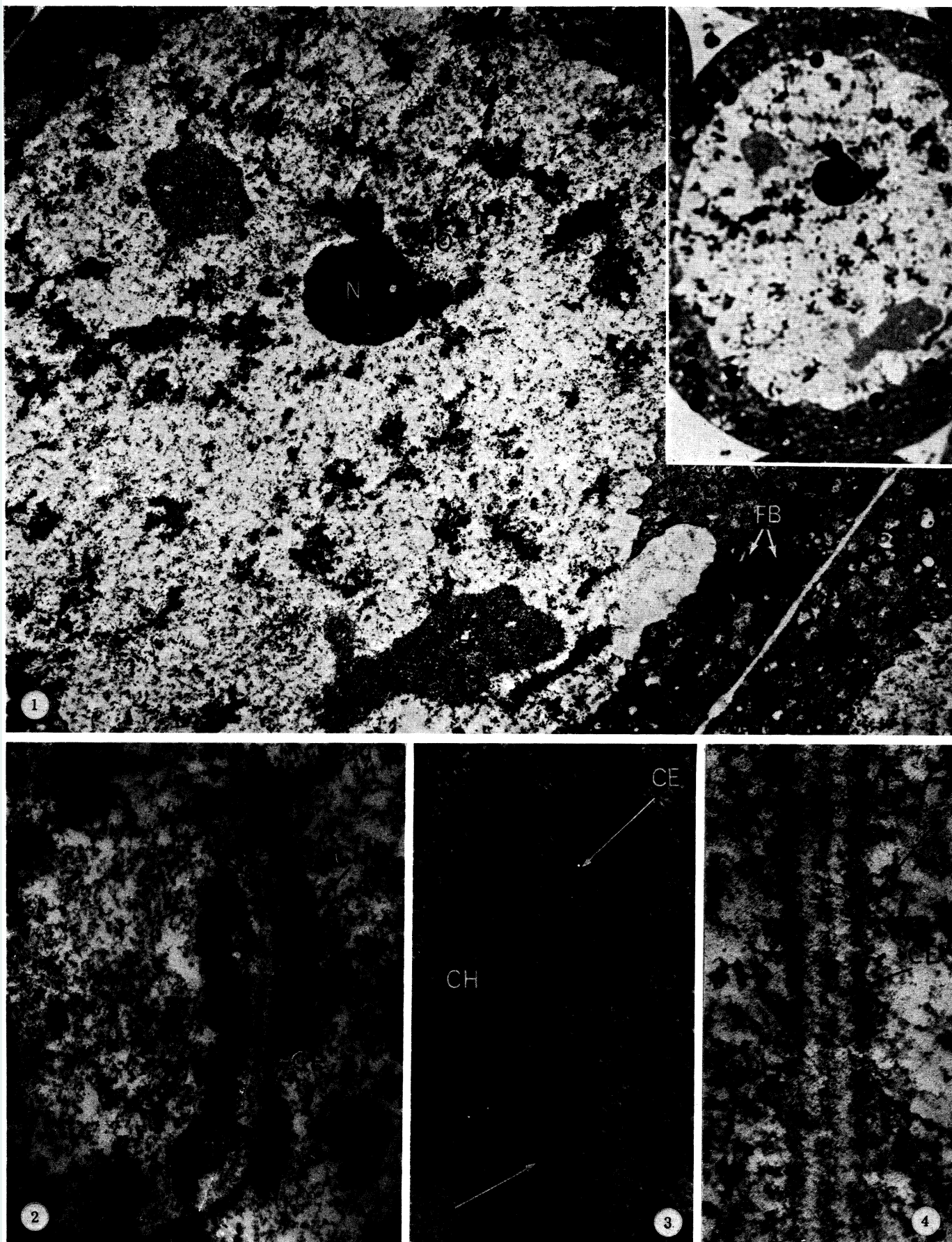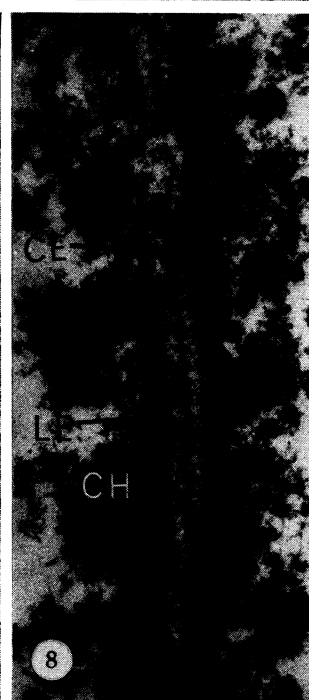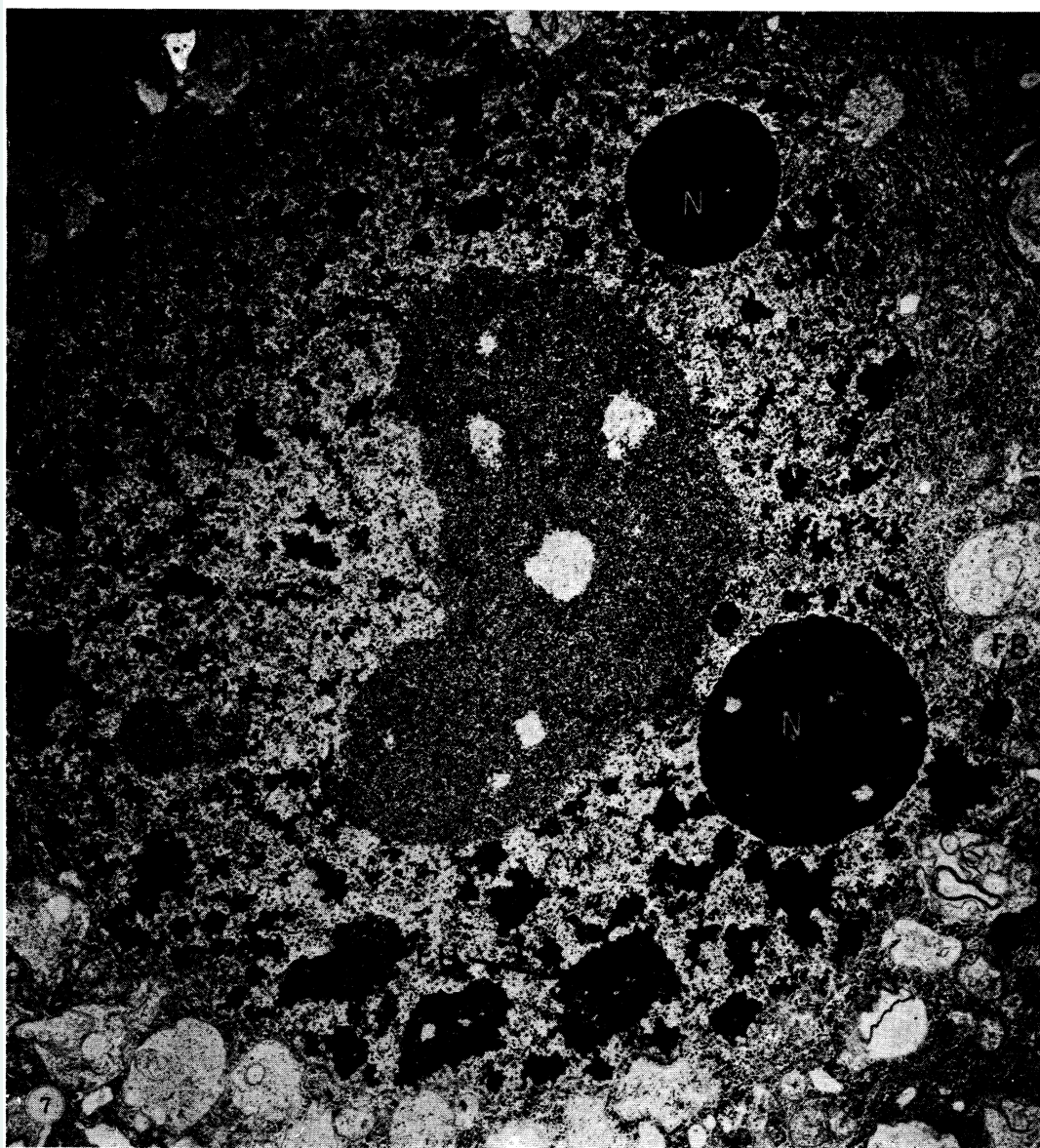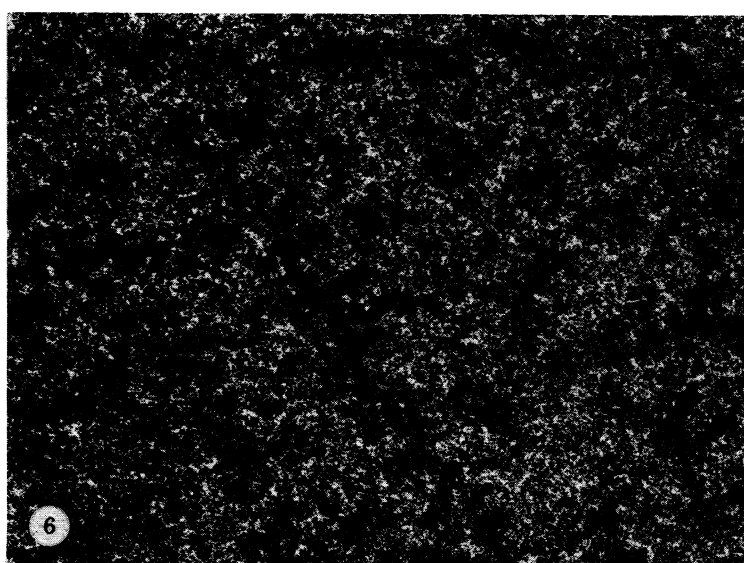
FIGURES 1-4. For description see opposite.

FIGURES 5–9. For description see opposite.

& von Wettstein (1972). The dimensions can vary somewhat with the fixative and staining procedure employed (McQuade & Wells 1975). The central component is more prominent at late zygotene and pachytene than at early zygotene.

For the purpose of classification Westergaard & von Wettstein (1972) have used the designation amorphous for the structure of the lateral and central elements of plants and some other organisms, as distinct from classes where a regular repeating structure is found. As for example the banded lateral elements of Ascomycetes, e.g. *Neottiella* (Westergaard & von Wettstein 1968, 1970a) and some Orthoptera, e.g. *Lapatacris* (Wettstein, Rodolfo & Sotelo 1971), and latticed central elements observed in synaptonemal complexes of some insects e.g. *Bombyx* (King & Akai 1971) and *Locusta* (Moens 1969).

It is obvious that the lateral elements are flexible structures which bend and twist as one with the chromosome axes. In cross section they have the appearance of rods, with a slightly flattened inner face. Their fine structure in plants, as seen at high magnification in p.m.cs of some monocotyledonous ones, is indicative of a tubular structure composed of fibres about 10 nm wide that are helically disposed (figure 3). This premise is further supported by the form of an occasional deformity in their structure which has been illustrated in p.m.cs of three plants, namely, *Lilium tigrinum* (Moens 1968b), *Phaedranassa viridiflora* (La Cour & Wells 1973) and *Zea mays* (Gillies 1973). A consideration of various models has indicated that this particular kind of deformity (figures 10 and 11) could only arise in a tubiform structure (La Cour & Wells 1973).

Because of the apparent uniformity of structure in systematic groups, it seems possible that the lateral elements in synaptonemal complexes of all plants, or at least all monocotyledonous ones, have this tube-like structure.

It is of interest to note that the deformity illustrated appears to occur also in the length of the lateral element of the X chromosome aligned with its unpaired portion in spermatocytes of both mouse (Solari 1970) and man (Solari & Tres 1970).

The fine structure of the central element in p.m.cs is rather more difficult to define. It appears to arise as the result of interdigitation, as suggested by Moens (1968a), of filaments (about 10 nm wide) extending laterally from the inner face of the lateral elements. We have found no evidence for the possibility that it is synthesized, or assembled, in the nucleolus prior to synapsis and then transported and laid down between the homologous chromosomes so as to join the

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DESCRIPTION OF PLATE 2

FIGURE 5. Electron micrograph of a synaptonemal complex at pachytene in a p.m.c. of *Allium fistulosum*. The fine filaments traversing the central space to form the central element (CE) are particularly clear in this example. The chromomeral chromatin is noticeably diffuse. (Magn. ×120000.)

FIGURE 6. Electron micrograph illustrating axial cores (marked by arrow heads) at leptotene in a p.m.c. of *Tulbaghia violacea*. (Magn. ×16000.)

FIGURE 7. Electron micrograph of a premeiotic interphase nucleus (condensed phase) in a p.m.c. of *Fritillaria lanceolata*. The vacuolated appearance of the chromocentral chromatin (H) is probably a reflection of spaces between heterochromatic segments. The fat bodies (FB), which are confined to the p.m.cs, increase markedly in number with the onset of meiosis, cf. figures 1 and 12. (Magn. ×7000.)

FIGURE 8. Electron micrograph of a synaptonemal complex at pachytene in a p.m.c. of *Phaedranassa viridiflora*. (Magn. ×50000.)

FIGURE 9. Electron micrograph of a synaptonemal complex at pachytene in a p.m.c. of *Fritillaria lanceolata*. Section stained by the preferential RNA-staining method of Bernhard. Note high contrast of the lateral elements. (Magn. ×80000.)

lateral elements, as is thought to occur in the ascomycete *Neottiella* (Westergaard & von Wettstein 1970*b*).

Moens (1968*a*) has suggested that the materials required for the synthesis of the laterally extending filaments participating in the formation of the central element are already present in the lateral elements (axial cores) at leptotene. Some support for this premise comes from our observations at prophase of meiosis in anthers of asynaptic wheat (La Cour & Wells 1970*a*), where fine extended filaments arise laterally on the axial cores of persistently unpaired chromosomes.

Molecular nature of the complex

Recent studies employing DNase digestion confirm that the structure of the components of the synaptonemal complex is unaltered by the treatment (Comings & Okado 1970; Westergaard & von Wettstein 1970*a*). This does not remove the possibility that DNA may be present within the complex in trace amounts, as for example either in the central region (Moses 1969) or in a DNase-sensitive strand (6.5 nm wide) axially associated with the lateral elements (Solari 1972).

Claims differ as to the digestibility of the components of the complex with RNase. Early studies (see Moses 1968) as well as some recent investigations on complexes from five species of animals have failed to demonstrate any effect of the enzyme (Comings & Okado 1970). On the other hand, Westergaard & von Wettstein (1970*a*) found that, in the Ascomycete *Neottiella*, the central component as well as much of the lateral elements were digestible with RNase. They concluded that the synaptonemal complex consists of ribonucleoproteins.

Recently, use has been made of a staining procedure developed by Bernhard (1969) for selective contrasting of RNA-containing organelles (figure 9). Using this method, Esponda & Sockert (1971) obtained preferential contrast in the lateral elements of complexes in spermatocytes of *Helix aspera* and p.m.cs of *Allium jesdianum*. The contrast was not obtained after RNase digestion.

Although not discussed by them, slight contrast was also obtained by these authors in the less densely structured central elements of non-digested preparations and this was likewise absent in digested tissues. These observations, therefore, appear to corroborate the findings of Westergaard & von Wettstein (1970*a*) in *Neottiella* mentioned above.


DESCRIPTION OF PLATE 3

FIGURE 10. Electron micrograph of a synaptonemal complex at zygotene in a p.m.c. of *Phaedranassa viridiflora*. One of the lateral elements (DLE) is deformed. (Magn. × 60 000.)

FIGURE 11. Electron micrograph illustrating the same kind of deformity shown in figure 10, but in cross section and in both lateral elements at identical loci in a p.m.c. of the same plant. (Magn. × 80 000.)

FIGURE 12. Electron micrograph of a p.m.c. of *Fritillaria lanceolata* at the onset of leptotene. The axial cores (AC) are first formed in the heterochromatin (H) which is still contained in chromocentres, but is now diffuse (highly decondensed). The nucleoli (N) are now adpressed to the nuclear envelope. (Magn. × 6000.)

FIGURE 13. Electron micrograph of a synaptonemal complex at zygotene in a p.m.c. of *Phaedranassa viridiflora*, after 5 min water treatment at 3–4 °C before fixation. The chromomeral chromatin is mostly splayed out from the lateral elements and an axial strand is visible in the central region between them. At some points (marked with arrow heads) the chromatin fibres appear to join with the strand. The hollow nature of the lateral elements is apparent. (Magn. × 60 000.)

FIGURE 14. Electron micrograph of a synaptonemal complex at zygotene in a p.m.c. of *Phaedranassa viridiflora*, after water treatment as in figure 13. Two axial strands are now visible when the complex is cut tangentially in the longitudinal plane. (Magn. × 60 000.)
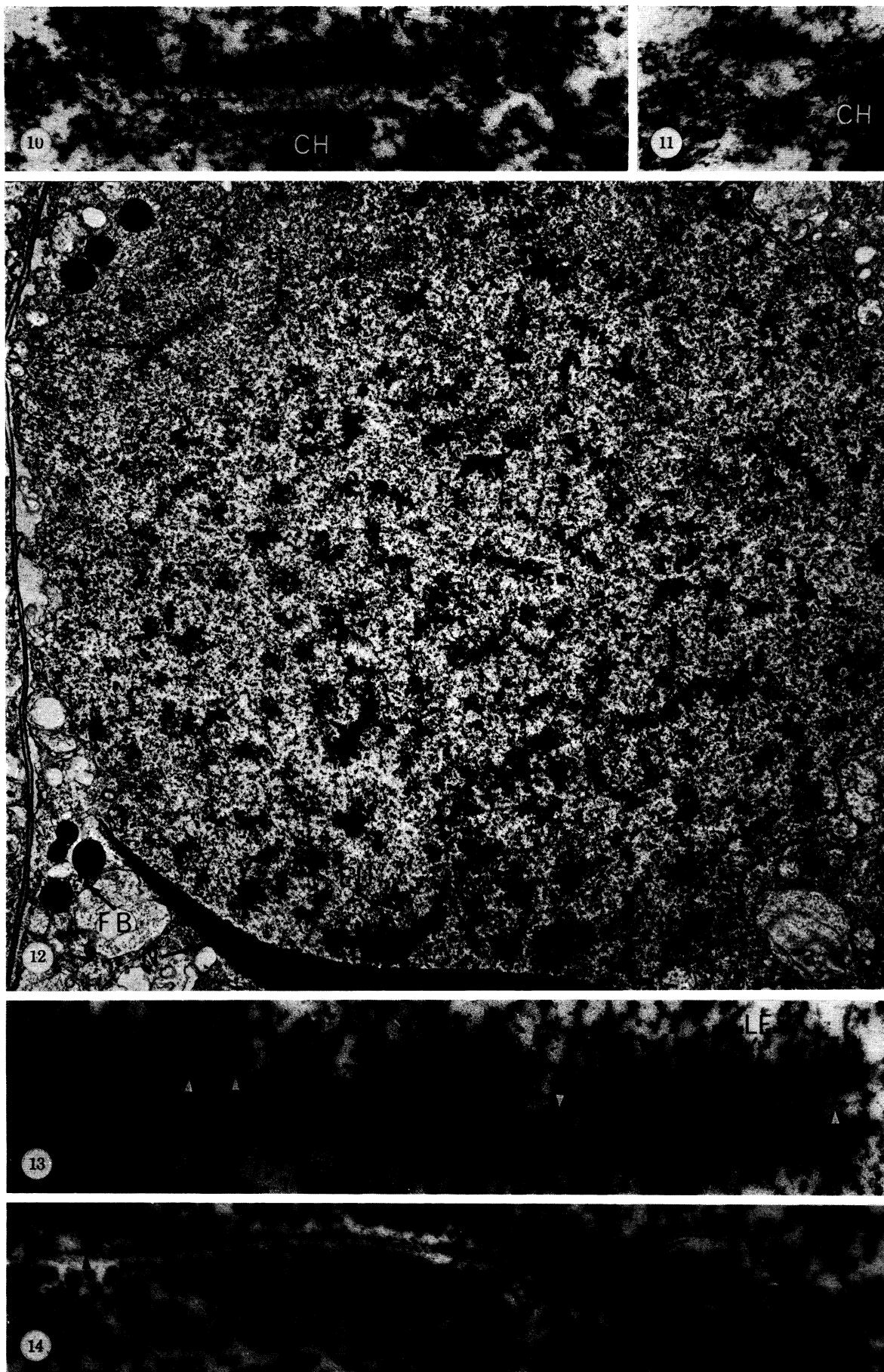
FIGURES 10–14. For description see opposite.

The Bernhard technique incidentally provides a useful method of enhancing the contrast of lateral elements, in genera where a poorly contrasted image obtained by conventional staining appears to be correlated with a diffuse light microscope-image of zygotene/pachytene, as for example in p.m.cs of *Rhoeo spathacea* (McQuade & Wells 1975).

The proteinaceous nature of the synaptonemal complex is evidenced by studies showing that its components are effectively digested by trypsin (Comings & Okado 1970; Westergaard & von Wettstein 1970*a*).

At pachytene in *Lilium* (Sheridan & Barrnett 1969) and at leptotene in *Tulbaghia* (La Cour & Wells 1971), the lateral component has been shown to react rather more strongly to ethanolic phosphotungstic acid (PTA) than the chromatin. The selectivity of PTA is attributed largely to staining of basic proteins (Bloom & Aghajanian 1966), probably by binding with lysine and arginine residues (Sheridan & Barrnett 1969).

The deposition at pH 8–9 of metallic silver in the lateral elements of synaptonemal complexes in asci of *Neottiella* after formalin fixation, is interpreted by Westergaard & von Wettstein (1970*a*) as a reaction between silver ions and the guanidino groups of arginine residues in basic proteins. No reaction to silver ions was obtained in the central region and central component of these complexes.

Although there is no knowledge of its exact location, it is of interest to note that a unique histone is synthesized during premeiotic interphase in cells of lily anthers and persists into the mature pollen (Sheridan & Stern 1967).

Genesis of the lateral elements

A part of a leptotene nucleus in which these elements are first seen as so-called axial cores is shown in figure 6.

It has been demonstrated with the light microscope that a period of chromosome condensation followed by decondensation occurs between premeiotic interphase and leptotene in p.m.cs of certain lilies (Walters 1970, 1972; Bennett & Stern 1975). A similar sequence of changes in condensation is also seen with the electron microscope in p.m.cs of *Fritillaria lanceolata*, in which it is obvious that the axial cores are first laid down in the heterochromatic regions (figure 12). There is reason to suspect that, from other observations concerning changes in condensation in these regions (see next section), a decondensation threshold may be required before the cores can be laid down.

Opinions differ concerning both the spatial and structural relationship of the axial cores/ lateral elements with the chromosome axes (see references in Moses 1968; Westergaard & von Wettstein 1972). In our view, it seems best to believe that, at leptotene as a general rule, the then axial core lies between the two sister chromatids as a distinct structural entity. This has recently been illustrated by Westergaard & von Wettstein (1970*a*) in asci of *Neottiella*, in which uniquely at this time the sister chromatids can already be identified. The all important question of whether in the completed complex, the chromosome axes are situated at the inner or outer face of these cores has yet to be resolved?

Chromocentres and the synaptonemal complex

The large heterochromatic segments which occur in all but 2 of the 24 chromosomes of *F. lanceolata*, fuse at telophase of mitosis to form 1–4 chromocentres (La Cour 1951). It has been shown that, although these chromocentres persist from premeiotic interphase until pachytene in p.m.cs, they do not impede formation of the synaptonemal complex throughout the entire length of the paired homologous chromosomes (La Cour & Wells 1970). This led us to believe that the homologues were already paired at the heterochromatic parts at the onset of meiosis.

Our recent observations on the chromosome condensation–decondensation sequence in p.m.cs of this plant while confirming that, as in some lilies (Walters 1970, 1972; Bennett & Stern 1975), the chromosomes pass directly into leptotene from a decondensed interphase state, seem also to point at the period at which initially the heterochromatic regions become paired.

To demonstrate this we must first refer to some other observations made with the electron microscope. In root tips of *F. lanceolata*, we found that the level of condensation in hetero-chromatic regions remains at a constant but nevertheless incomplete level throughout the whole mitotic cycle (La Cour & Wells 1974). This level is also closely comparable to that found in chromocentres of p.m.cs during zygotene (figure 1, and La Cour & Wells 1970*b*). The present observations, we shall now see, not only show that a similar degree of condensation occurs in these parts throughout most if not all of premeiotic interphase in the p.m.cs, but also that it decreases in a most striking way at the onset of leptotene. The chromatin fibrils in the chromo-centres are then more loosely packed (decondensed than at any other time (figure 12)). Ob-viously it would be of great interest to know what is responsible for triggering such an abrupt change in the state of condensation in this otherwise tightly packed conglomerate of hetero-chromatic regions. One can imagine that it may well be inseparable from the mechanism that triggers the onset of meiosis itself.

Although we have yet to see a later stage of leptotene showing chromocentres with 'paired' axial cores, it seems highly probable that the lifting of the restriction on changes in condensation of the chromatin fibrils in chromocentres at the onset of leptotene, is an event provided to ensure freedom of movement of the packed segments. Without such movement, it is difficult to imagine how the heterochromatic regions of homologous chromosomes could ever become homologously paired.

That a movement of chromosomes does indeed occur is reflected by a change in position of the 4 nucleoli, from a more central location at the condensed phase in premeiotic interphase (figure 7) to a peripheral one just before the onset of leptotene. With the start of leptotene, as in the p.m.cs of some other *Fritillaria* species, they are already closely adpressed to the nuclear envelope (figure 12). It should be noted that all four nucleolar chromosomes have hetero-chromatic regions in the arm containing the organizer, but chromosomes other than nucleolar ones must be involved.

Paradoxically, although the axial cores in the heterochromatic segments in p.m.cs of *F. lanceolata* are the first to be formed, our earlier observations in p.m.cs of this plant suggest that the synaptonemal complex in these parts is last to be fully completed (La Cour & Wells 1970*b*). The reason for this is obscure.

Water treatment of the synaptonemal complex

When naked p.m.cs are exposed to cold distilled water briefly before fixation, they swell and the normally compacted chromomeral chromatin is mostly extended outwards in the form of loosely coiled fibrous loops. The fine structure of the synaptonemal complex has been studied at zygotene in p.m.cs of *Phaedranassa viridiflora* after such treatment (La Cour & Wells 1974). Treated and untreated stretches of the complex are illustrated in figures 8, 13 and 14.

In water-treated preparations the ribonucleoprotein filaments comprising the central elements were usually dispersed and surprisingly in their absence one and sometimes two fine strands were then seen running linearly between the lateral elements (figures 13 and 14). Observations in complexes cut in frontal and tangential planes, showed that the two strands were actually situated one above the other, so that only one was visible in the frontal plane. The contrast of the strands was markedly increased when hot aqueous PTA was used as a secondary stain to uranyl acetate in place of lead. This suggests that the strands contained a basic protein.

In many instances, in complexes cut in the longitudinal plane, the chromatin fibres appeared to terminate on the strands (figures 13 and 14). Both the fibres and strands were composed of fibrils about 3–3.5 nm in diameter and these were coiled so as to give the former a width approximately double that of the strands, about 20 nm and 10–12 nm, respectively. A further order of far looser coiling was also present in the fibres.

The strong probability that the lateral elements in the complexes of *Phaedranassa* are tubiform structures seems to preclude the possibility that the axial strands revealed after water treatment are derived from these elements. A choice thus remains as to whether the strands are part of the central organization between lateral elements or the actual chromosome axes displaced by the treatment. This has yet to be resolved. Whatever the strands may turn out to be, their precise orientation within the central space seems to signify that they may have a specific pairing face. They may therefore still have an important role to play, if not as part of the chromosomes, in the mechanism of precise pairing.

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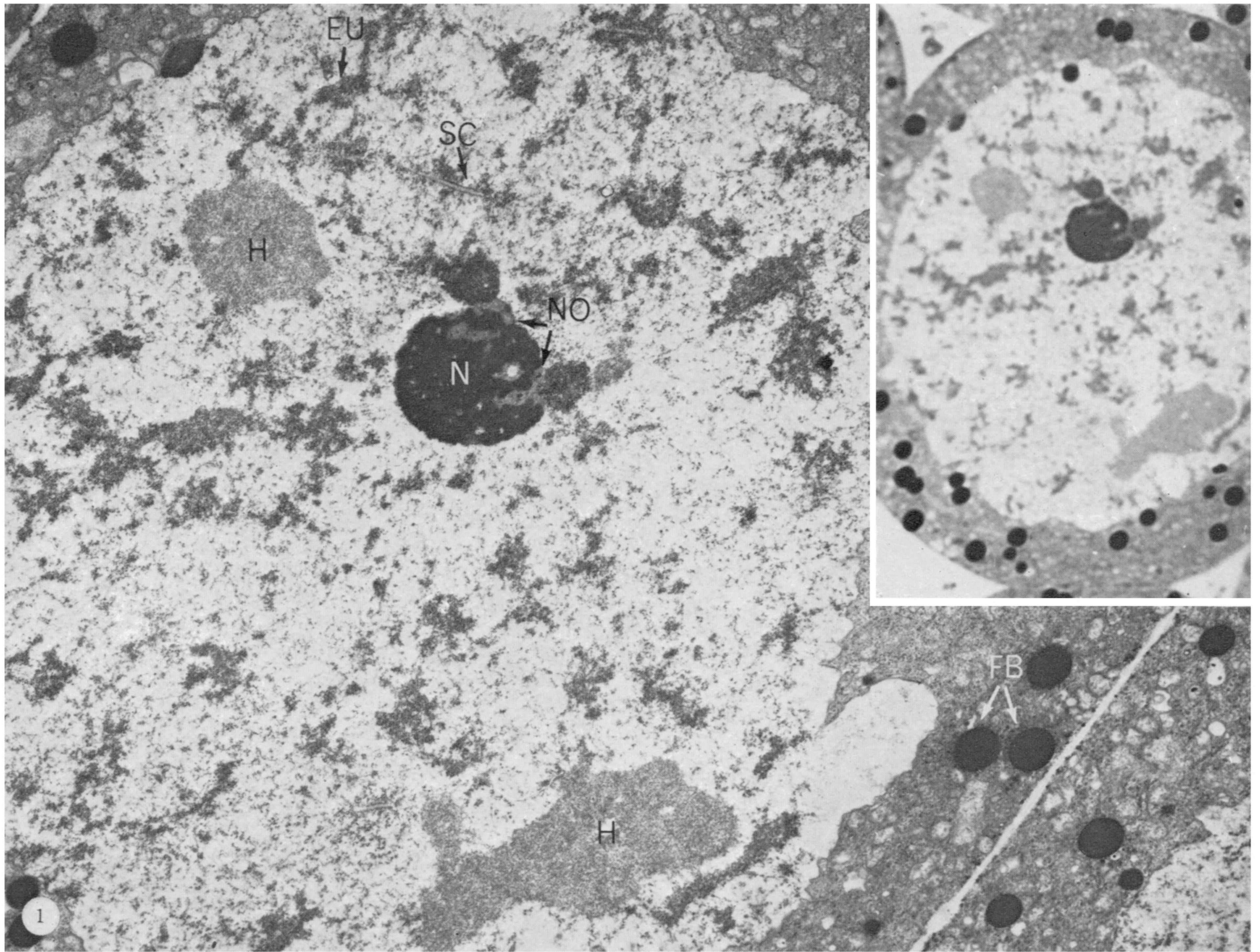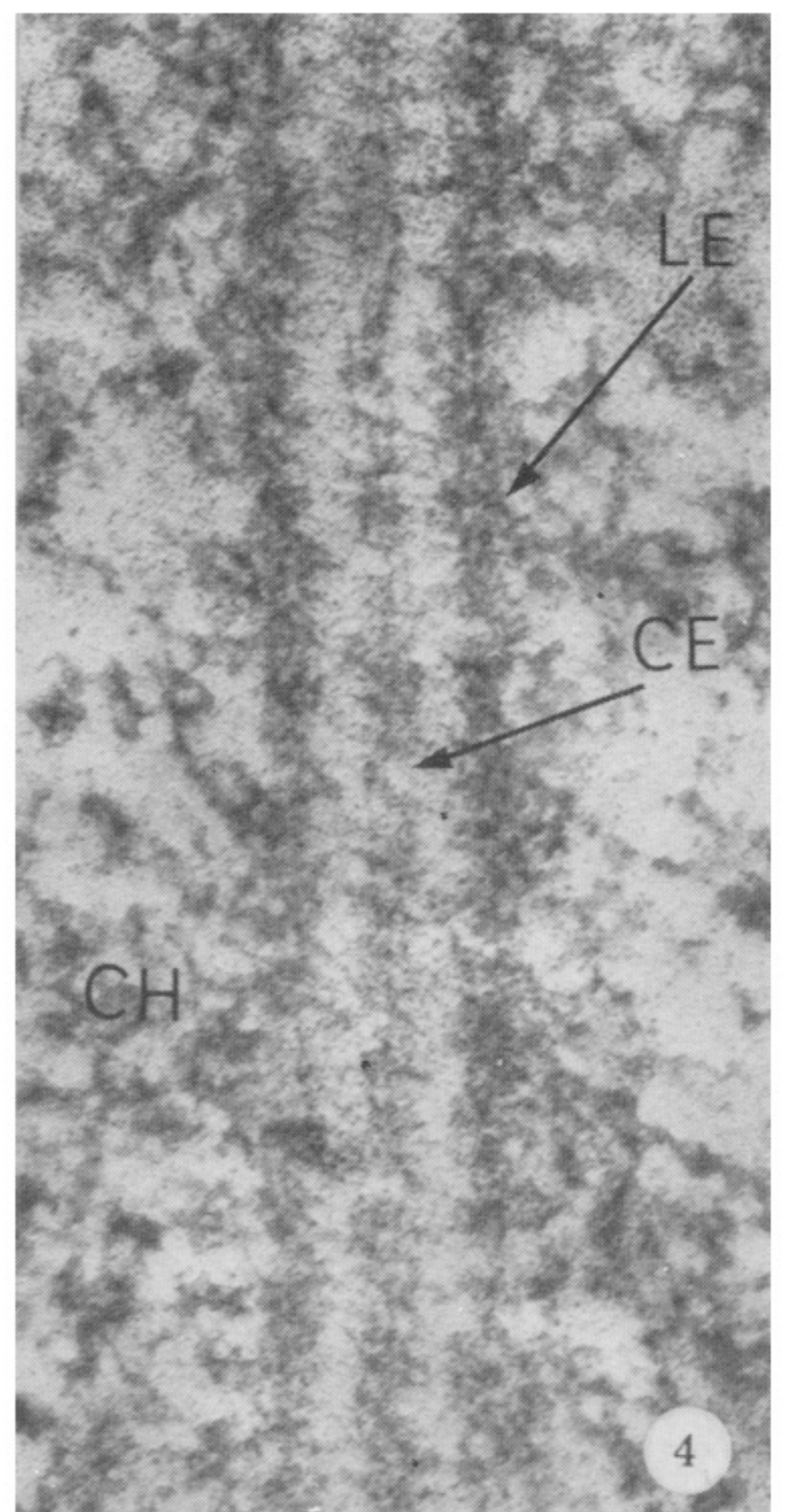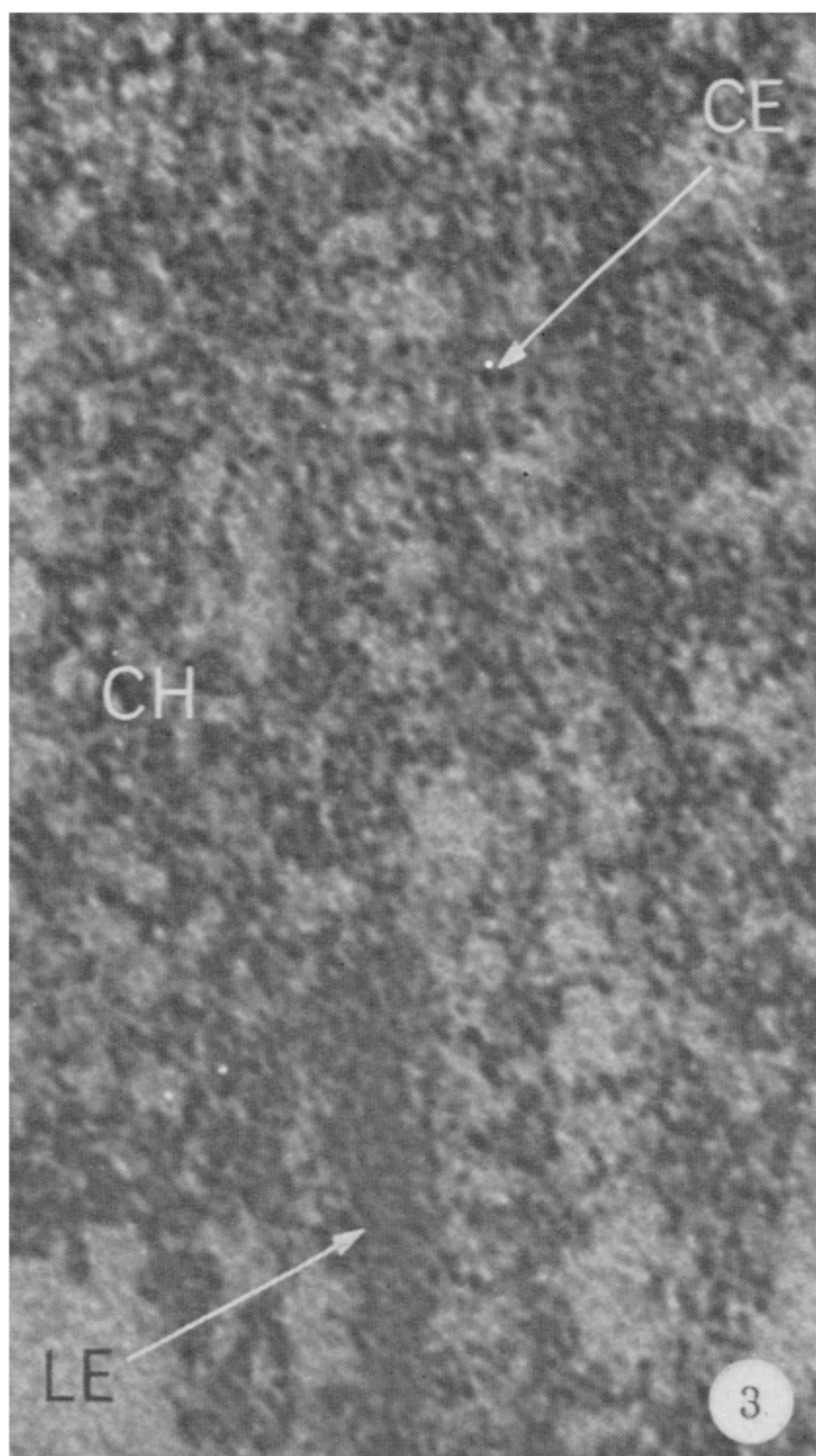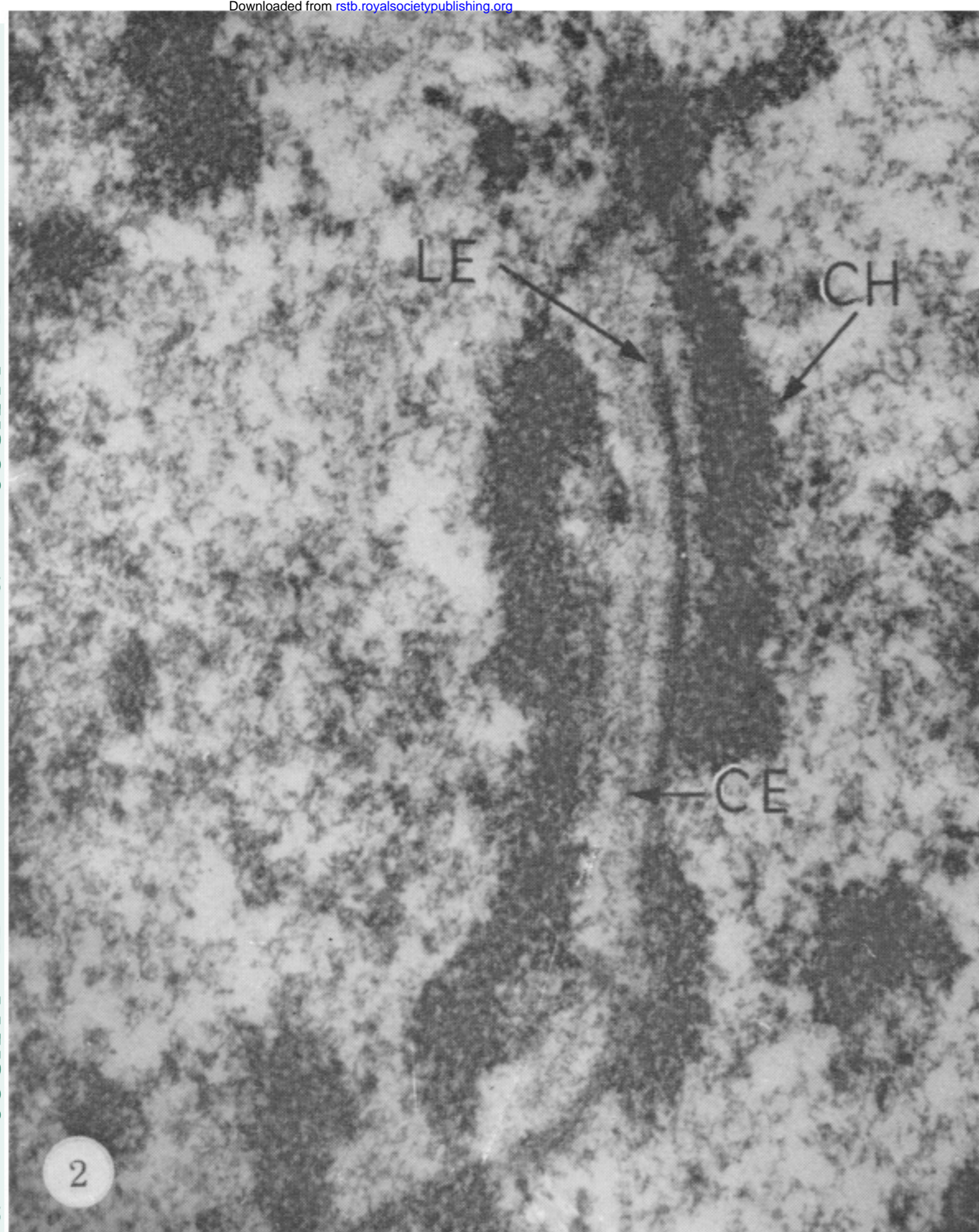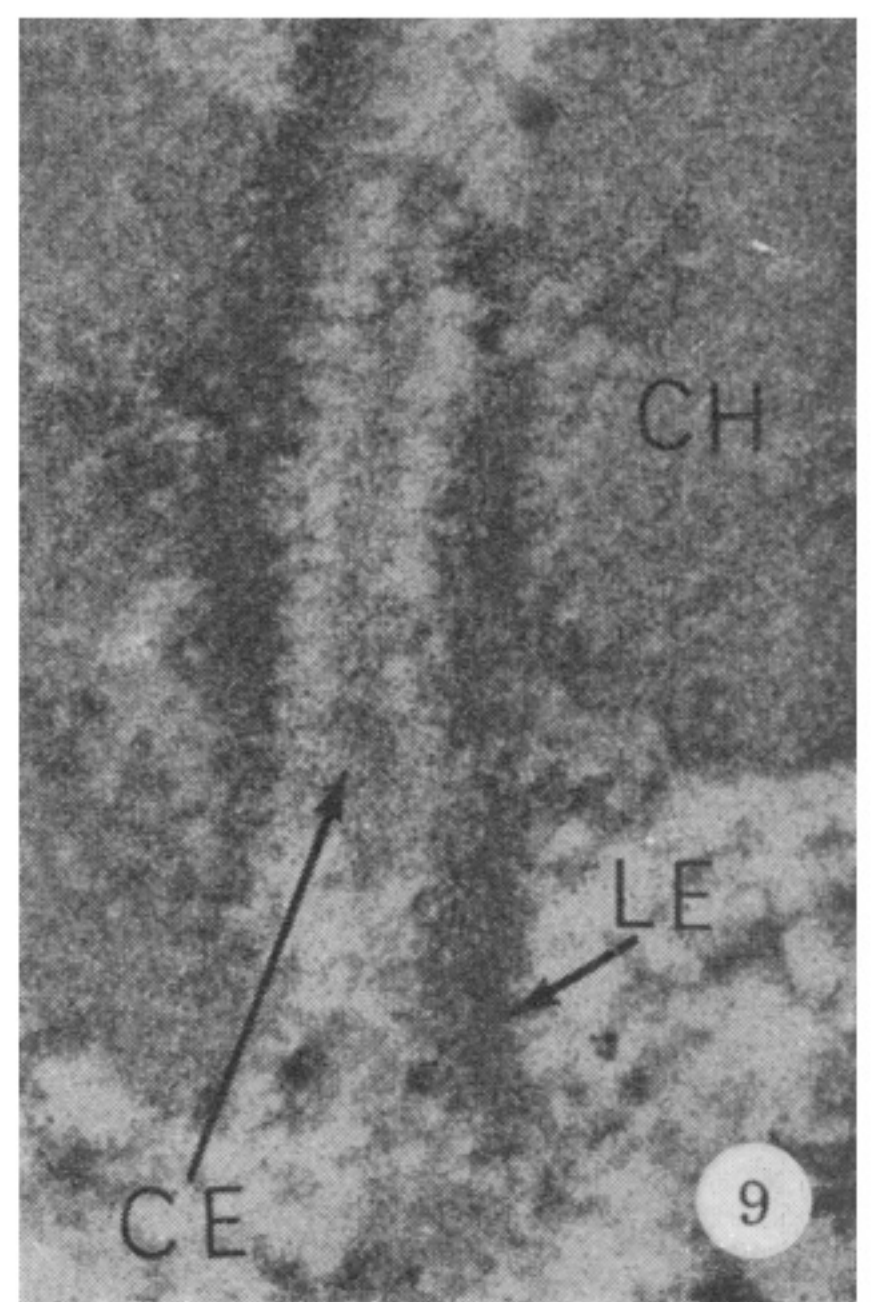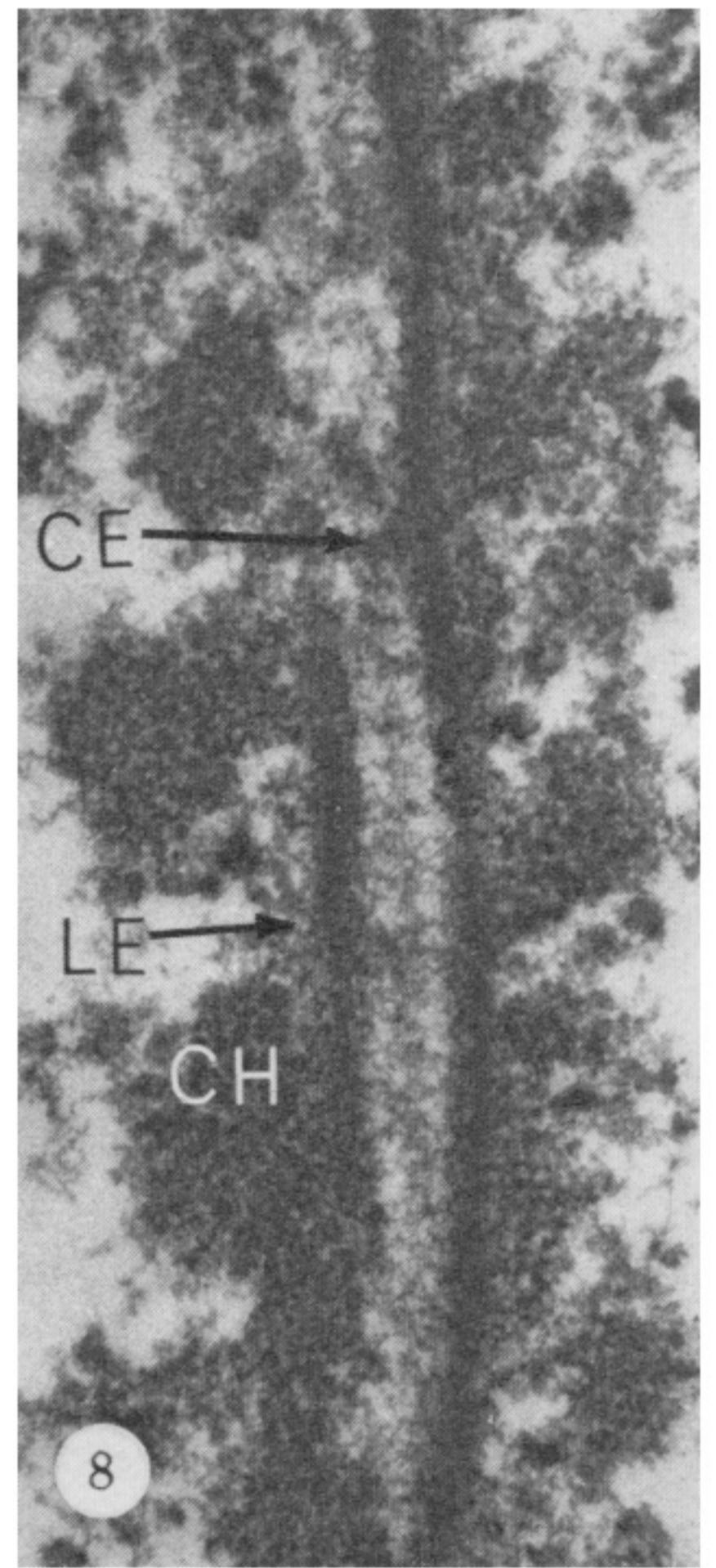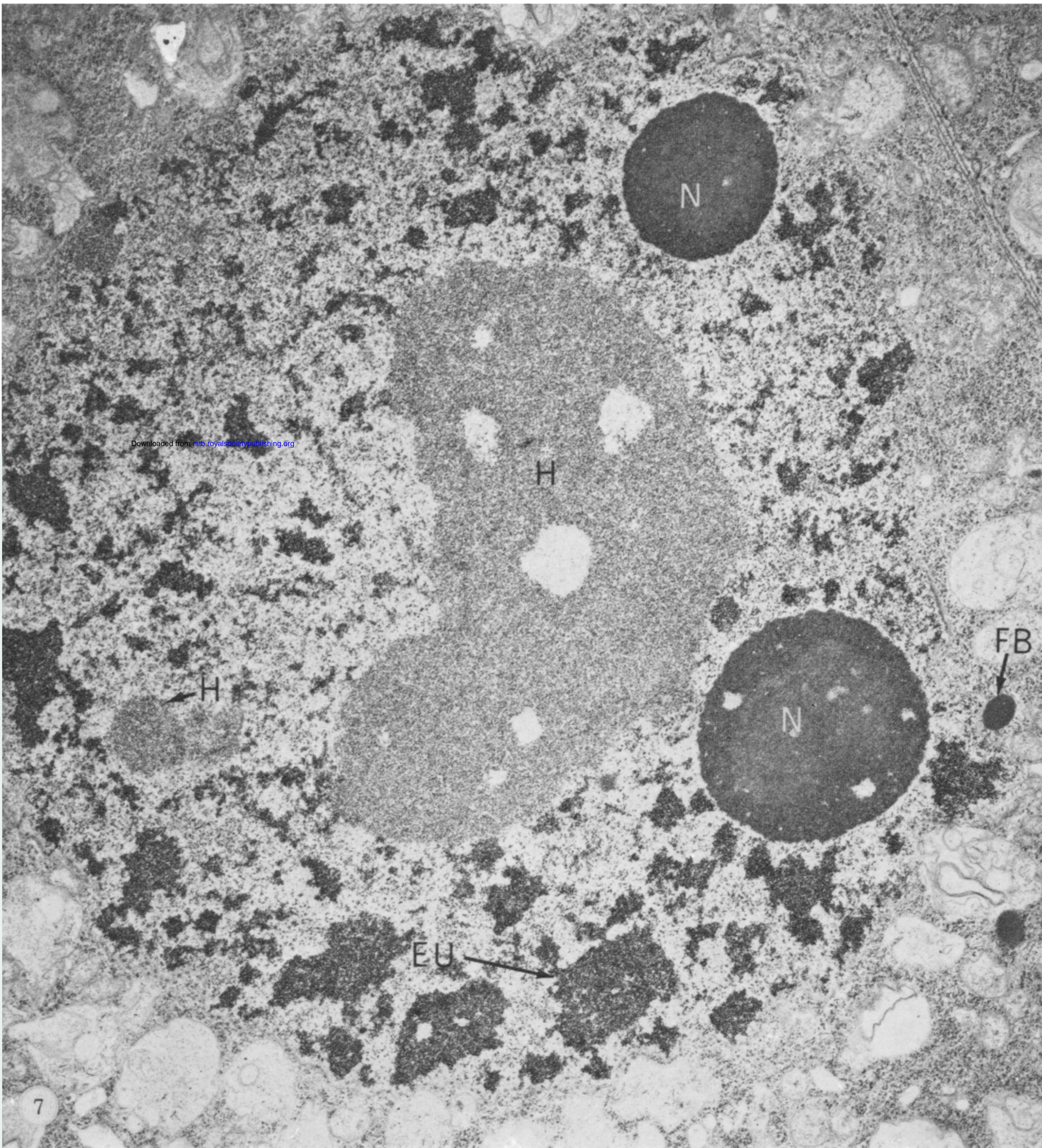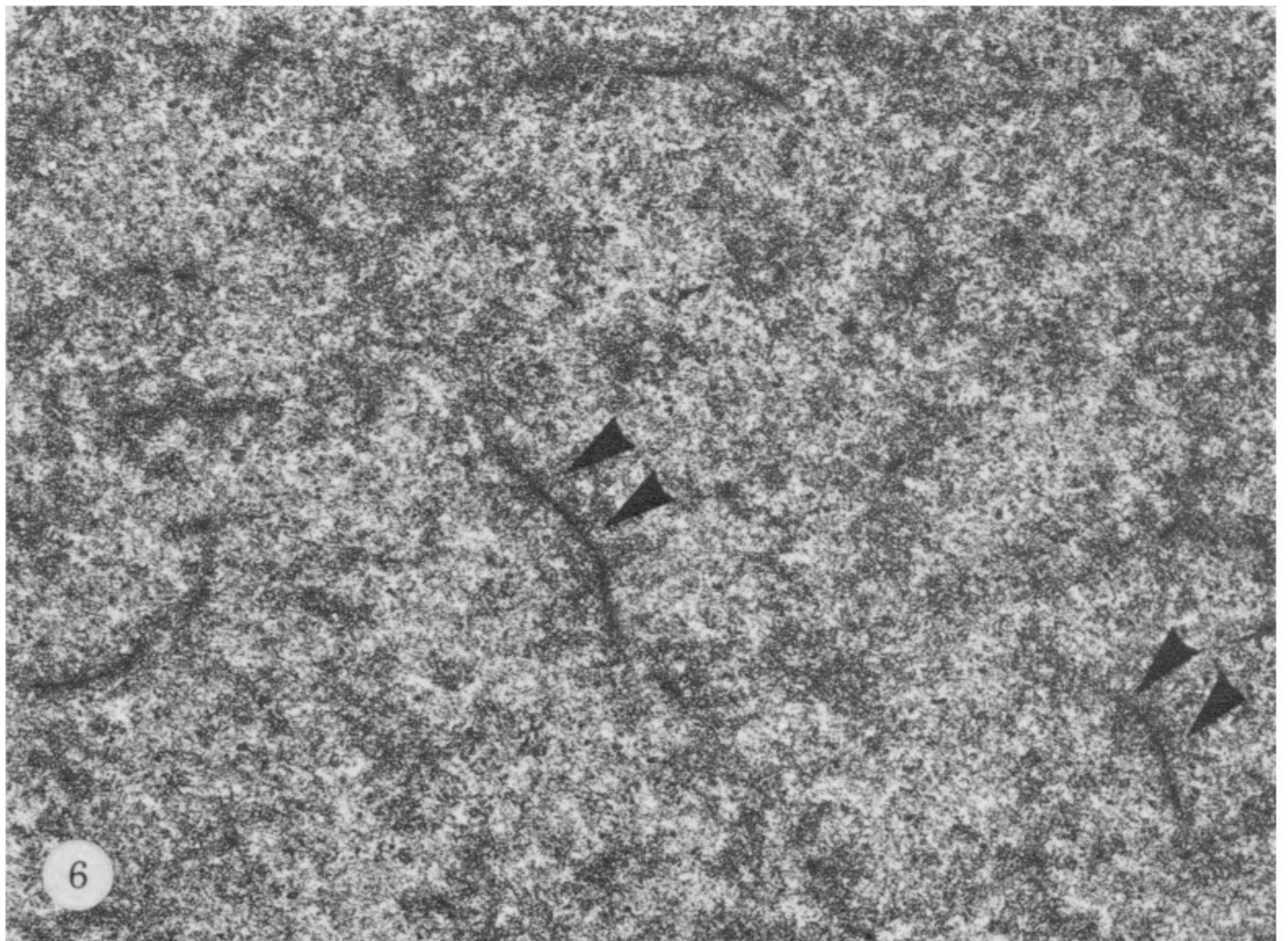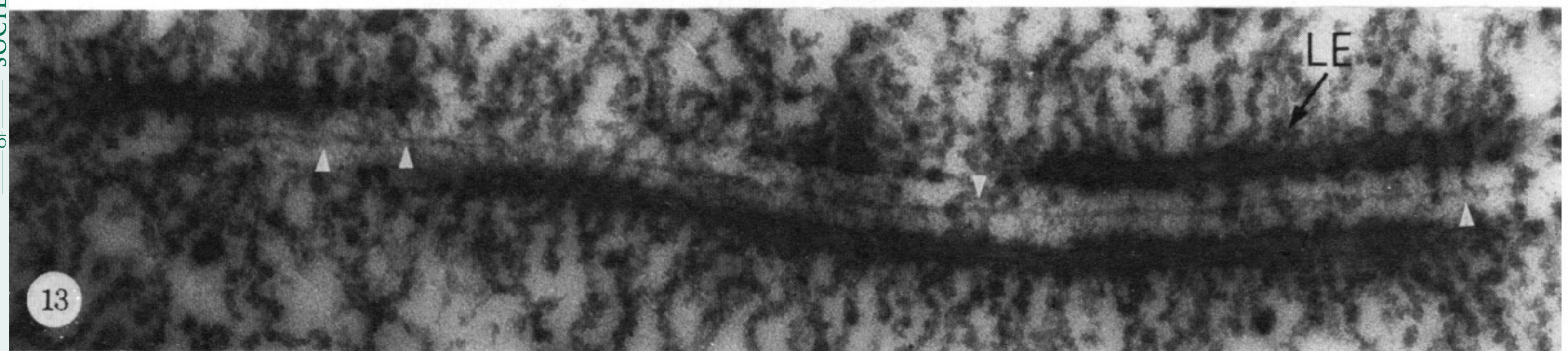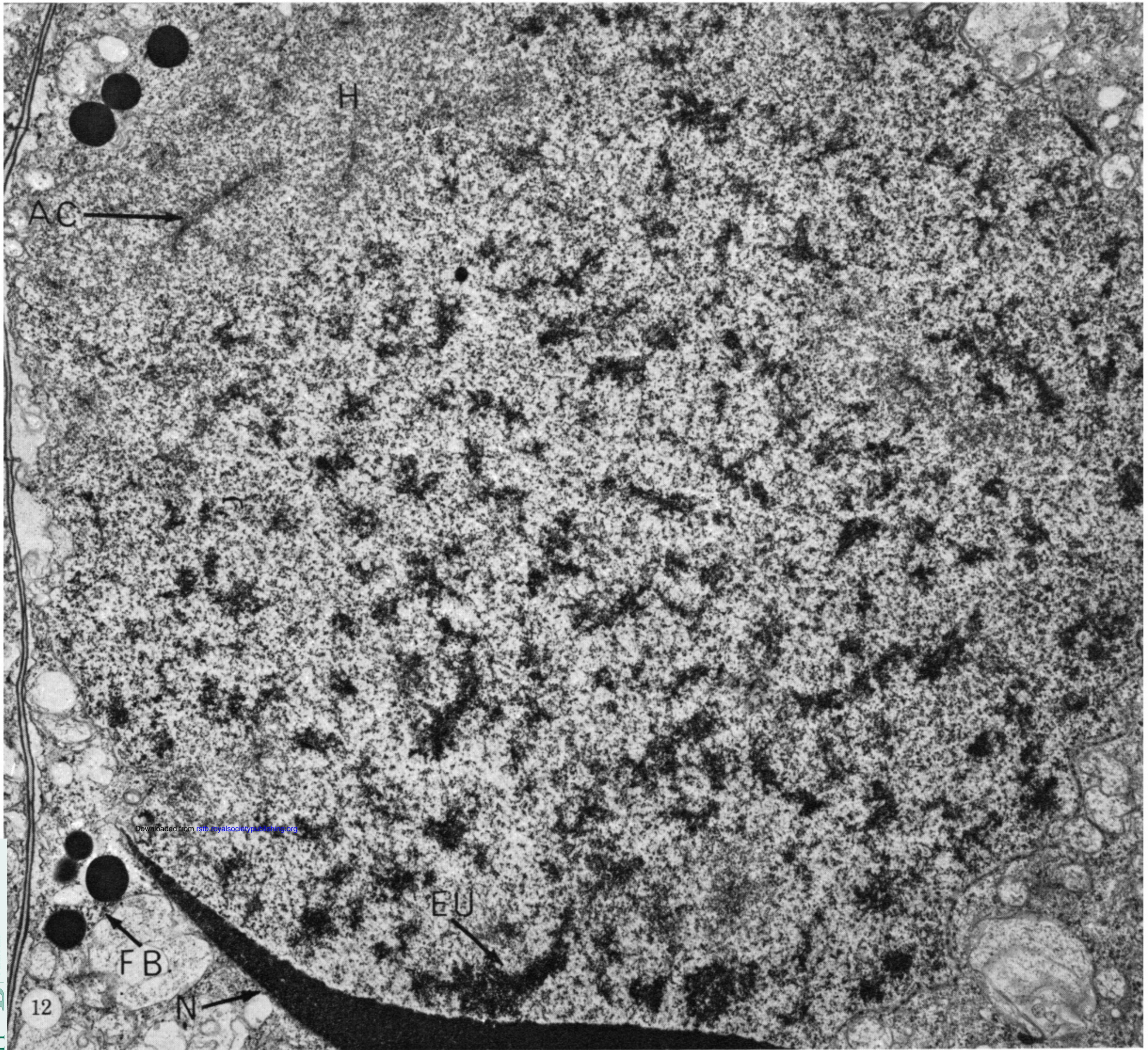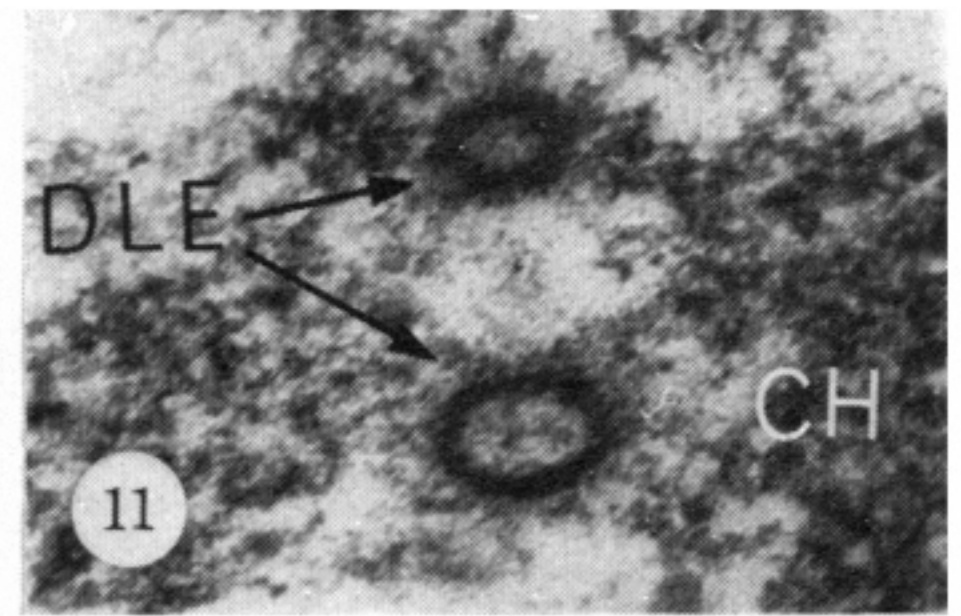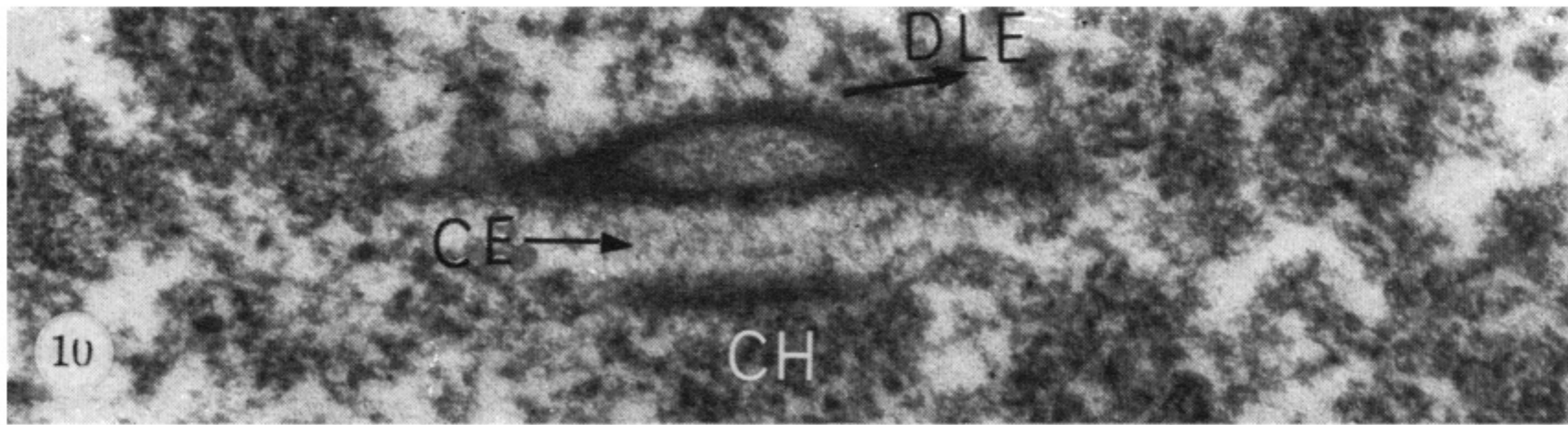
FIGURES 1–4. For description see opposite.
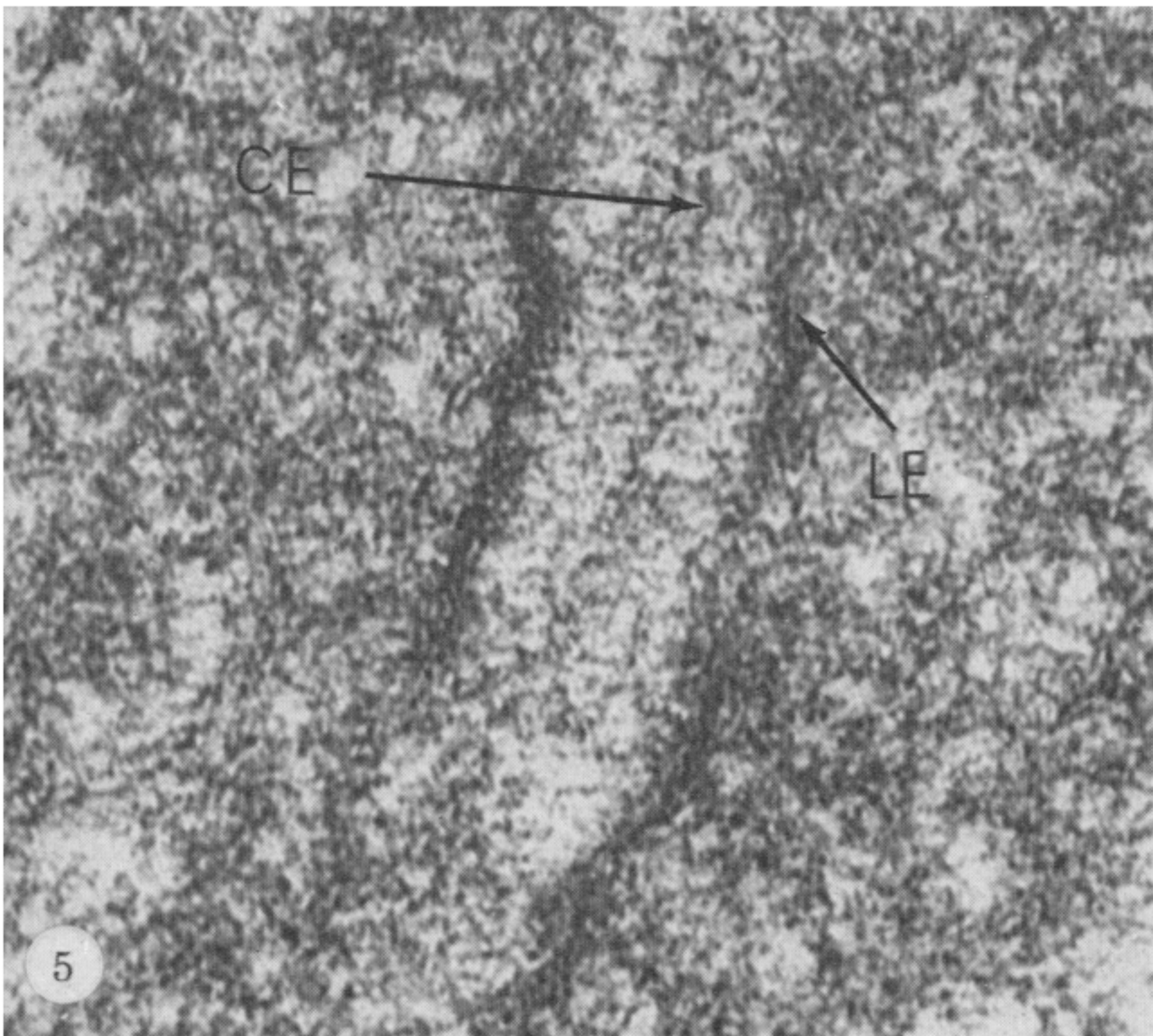
FIGURES 5–9. For description see opposite.

FIGURES 10–14. For description see opposite.