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Meiosis in Bombyx mori Females [and Discussion]

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Meiosis in *Bombyx mori* females

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[Plates 1–4]

Crossing over is absent in oocytes of the silkworm, *Bombyx mori*. Synaptonemal complexes are present during pachytene between the paired chromosomes. At leptotene, lateral components of the synaptonemal complex are attached in a bouquet to a limited region of the nuclear envelope. Before completion of lateral components, synaptonemal complex formation begins at the nuclear envelope. With synaptonemal complex formation proceeding from both ends bivalents occasionally become interlocked. After pairing is completed, the bouquet arrangement is dissolved possibly as a result of a flow of the inner membrane of the nuclear envelope thereby separating the telomeres. After the telomeres are released from the nuclear envelope, material is deposited onto the lateral components of the synaptonemal complex. The modified synaptonemal complexes are retained by the bivalents until metaphase I. It is suggested that these modified synaptonemal complexes substitute for chiasmata in order to ensure regular disjunction of homologous chromosomes in the absence of crossing over.

Introduction

In all organisms investigated so far, meiotic crossing over is accompanied by the presence of a tripartite structure termed the synaptonemal complex. This structure which consists of two lateral components separated by a central region is located between homologously paired chromosomes during part of the meiotic prophase. A possible exception are males of *Drosophila ananassae* (Grell, Bank & Gassner 1972). Reviews of this structure have been presented by Moses (1968), Westergaard & von Wettstein (1972), and Gillies (1975*b*). In several cases of achiasmatic meiosis, the biogenesis and possibly also the function of the complex differ from that observed for chiasmatic meiosis (Gassner 1969; Welsch 1973).

In typical chiasmatic meiosis, the synaptonemal complex is eliminated after crossing over has occurred during pachytene. At diplotene short stretches of the complex are retained at the positions of chiasmata (Gillies 1975*a*; Solari 1970; Sotelo, Garcia & Wettstein 1973; Westergaard & von Wettstein 1968, 1970). The association of the homologous chromosomes from diplotene until metaphase I is ensured by the presence of chiasmata. In the absence of crossing over and chiasmata, substitute mechanisms are required to hold the homologues together and to effect co-orientation of the bivalents. Instead of being eliminated, the synaptonemal complex in the achiasmatic meiosis of *Bolbe nigra* (Gassner 1969) and *Panorpa communis* (Welsch 1973) is further elaborated and persists until metaphase I. As data on crossing over frequencies in these two species are lacking, it is uncertain whether the absence of chiasmata in these organisms is due to the prolonged presence of the synaptonemal complex or alternatively, due to absence of crossing over.

In *Bombyx mori*, crossing over and chiasmata are limited to the male sex (for references to the literature on meiosis in *Bombyx*, see Rasmussen 1976). Since both sexes possess synaptonemal

complexes, *Bombyx* seems to be a favourable organism for studying the relation between crossing over, chiasmata, and the synaptonemal complex. The present paper will describe the development and differentiation of the synaptonemal complex in *Bombyx* females from the time of its formation until, in a modified form, at metaphase I it is converted into an amorphous mass of material known historically as 'elimination chromatin'.

Materials and methods

The material for this work was kindly provided by the late Professor B. U. Astaurov, Institute of Developmental Biology, Academy of Sciences, U.S.S.R., Moscow. Wild type, bisexual ($2n = 56$ and $3n = 87$) females were used. The material for the first part of the investigation was prepared, fixed, and embedded as previously described (Rasmussen 1976). The later stages were treated as follows. The preparation of ovaries and eggs was performed in cold phosphate 4 % buffered glutaraldehyde with a purification index of less than 1.0. The material was immediately placed in fresh glutaraldehyde solution and fixed for several days at 4 °C. Mature or almost mature eggs were punctured in order to facilitate the fixation. After washing in buffer for one day, ovaries were post fixed in 2 % phosphate buffered OsO_4 for 48 h, washed in buffer followed by careful wash in distilled water for 24 h. Osmium staining was followed by staining in 2 % aqueous uranyl acetate at 60 °C for 3 h. Ovaries and eggs were then dehydrated in a graded alcohol series and embedded in Spurr low viscosity resin. All steps in the embedding procedure were prolonged to ensure a uniform infiltration. Individual eggs were cut into halves and the corion removed from the half containing the micropyle. This portion of the egg was then embedded and 4–5 μm sections beginning from the micropylar region were inspected in the light microscope in order to localize the nucleus. The thick sections containing the nucleus were then re-embedded for ultramicrotoming. The thin sections were double stained in uranyl acetate and lead citrate as previously described.

Results and conclusions

The first part of oocyte development covering the stages from leptotene to modified pachytene has been described in detail previously (Rasmussen 1976) and will be reviewed briefly. The analysis concerning the stages of oocyte development up to metaphase I as well as those on pairing in triploid females is still in progress and the data presented are to some extent preliminary being based on relatively little material.

The earliest stage at which stretches of unpaired lateral components of the synaptonemal complex can be identified is characterized by the relatively condensed chromatin and by the almost spherical nucleolus usually located asymmetrically in the nucleus, opposite the region of the cell in which the majority of cellular organelles has accumulated. Shortly thereafter, a number of dense plates can be observed on the inner membrane of the nuclear envelope at sites where chromatin touches the membrane. These dense plates are later incorporated into the attachment sites of the lateral components of the synaptonemal complex on the nuclear envelope. The attachment of lateral components is restricted to a region of the nuclear envelope opposite the nucleolus leading to the formation of a chromosome bouquet. At the time when most of the telomeres (2 per each of 56 chromosomes) are attached by their lateral component, homologous telomeres have approached by movements on the nuclear envelope and synaptonemal

complexes begin to appear. The organization of the synaptonemal complex always start close to the attachment site on the nuclear envelope and usually from one end only. In a few cases (1–3 per nucleus) a bivalent with a completed synaptonemal complex was found to be trapped between the unpaired lateral components of another bivalent (figure 1). The latter must have had two starting and growing points for synaptonemal complex formation one close to each telomere, resulting in the interlocking of the bivalents.

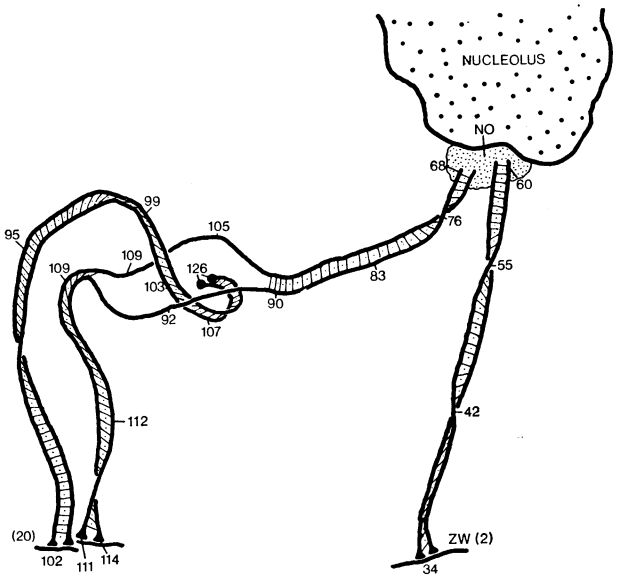
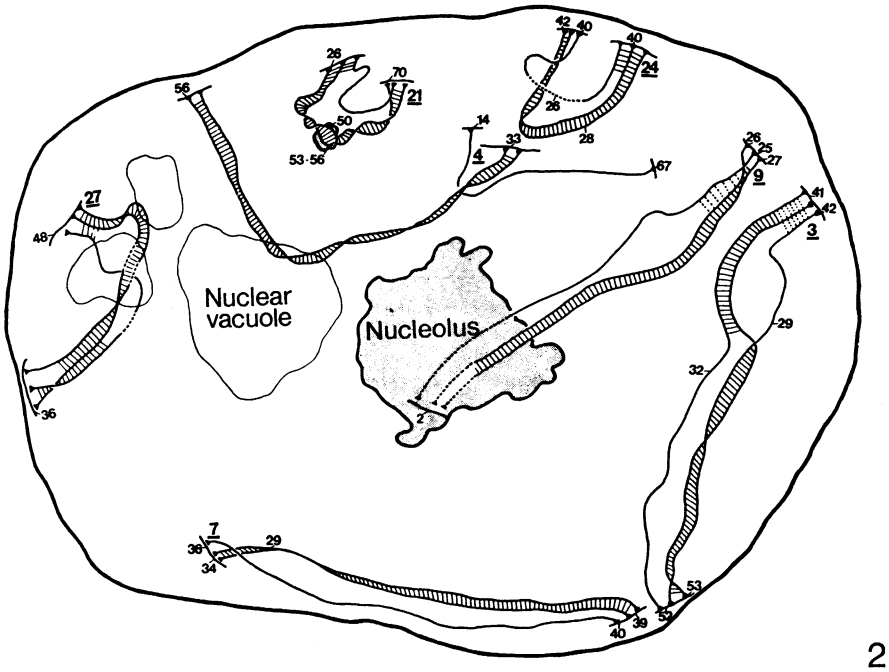


FIGURE 1. An example of bivalent interlocking at late zygotene, involving chromosomes 2 and 20.

Results from serial reconstructions of pachytene nuclei of triploid females support the notion (cf. Moens 1973) that the pairing of homologous chromosomes occurs in two steps. First, a gross alignment takes place which brings the homologues together to a distance of about 300–400 nm. This step is possibly dependent upon and initiated by telomeric recognition and movement on the nuclear envelope. The second step is a more precise alignment of homologues by the formation of a synaptonemal complex. In triploid *Bombyx* females, the most common situation at pachytene is that two of the three homologous chromosomes are paired with a normal looking synaptonemal complex from one telomere to the other while the third chromosome is aligned with the bivalent, the distance between the unpaired component and the completed synaptonemal complex being about 500 nm. Frequently, all three homologous lateral components are combined for a short stretch in parallel into a 'polycomplex' at the region near the nuclear envelope, similar to those observed in triploid chickens (Comings & Okada 1971). Formation of trivalents, i.e. shift of pairing partner in synaptonemal complex formation, seems to be a relatively rare event. In the two nuclei reconstructed, ten partner shifts could be identified unequivocally. In one instance in each of the two nuclei, an unpaired lateral component was not associated with the homologous bivalent. In six cases, one telomere and arm of the third chromosome was aligned with the bivalents while the other telomere was attached at a site on the nuclear envelope very distant from that of the corresponding telomeres of the completed synaptonemal complex of the bivalent (figures 2 and 3).

The pachytene stage in normal diploid females is characterized by the presence of a synaptonemal complex spanning the distance between the attachment points of the telomeres on the



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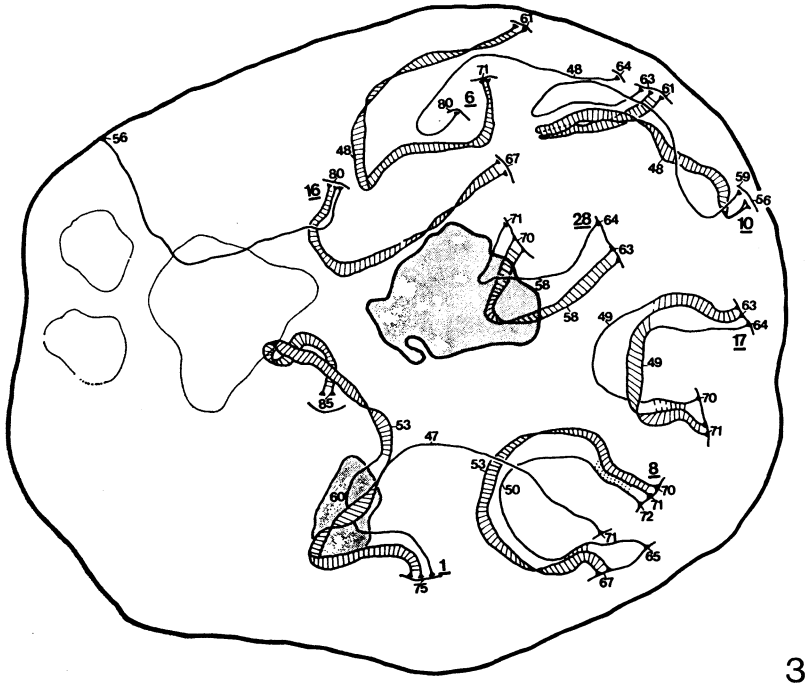

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FIGURES 2 AND 3. Serial reconstruction of a portion of a triploid nucleus. Note the trivalent (number 3 on figure 2) and the unpaired lateral component of bivalent 6 on figure 3.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

nuclear envelope. The bouquet arrangement of the chromosomes is no longer present, the bivalents being distributed evenly in the nucleus. Pachytene bivalents in *Bombyx* lack identifiable centromeres and can with present techniques thus only be characterized by length. The majority of bivalents have approximately the same length. Chromosome 1 carries consistently a knob and the sex chromosomes, no. 2 contain the nucleolus organizer region. The data given in tables 1 and 2 show that in a diploid nucleus, the length of the synaptonemal complexes in all bivalents is fairly constant during the zygotene/pachytene interval. The length of the lateral components and thereby the length of the synaptonemal complexes of the chromosomes in the triploid nuclei was found to be much shorter than those of a diploid nucleus. As the present measurements of synaptonemal complex lengths in triploid pachytene nuclei have been performed on only two nuclei of one ovariole, these data need further verification before definite conclusions can be made concerning the significance of this drastic shortening of complex lengths in the presence of an extra set of chromosomes.

TABLE 1. COMPARISON OF SYNAPTONEMAL COMPLEX LENGTHS IN OOCYTES OF *BOMBYX MORI* (IN μm)

chromosome number	zygotene diploid 1‡	pachytene diploid 6‡	pachytene triploid† 2‡	early modified pachytene diploid 1‡	mid modified pachytene diploid 1‡
1	11.9	10.9	6.3	12.1	15.8
2	11.7	10.3	5.7	11.6	14.5
3	10.4	9.7	5.6	11.6	—
4	9.9	9.4	5.5	10.8	—
5	9.3	9.1	5.3	10.7	12.6
6	9.3	8.7	5.1	10.5	12.6
7	8.8	8.5	4.8	10.2	—
8	8.6	8.4	4.8	9.9	—
9	8.4	8.2	4.7	9.2	11.7
10	8.0	8.0	4.5	9.0	11.4
11	8.0	8.0	4.4	9.0	11.4
12	8.0	7.8	4.4	8.9	—
13	7.8	7.7	4.3	8.9	—
14	7.8	7.5	4.3	8.8	—
15	7.6	7.5	4.2	8.6	—
16	7.5	7.4	4.1	8.5	9.9
17	7.5	7.1	4.1	8.4	9.7
18	7.4	7.0	4.0	8.4	9.6
19	7.4	6.9	4.0	8.4	9.6
20	7.0	6.8	3.9	8.0	9.6
21	7.0	6.6	3.8	7.2	8.7
22	6.9	6.5	3.6	6.5	8.7
23	6.6	6.4	3.5	6.3	8.6
24	6.2	6.1	3.5	6.2	7.9
25	6.0	5.9	3.4	6.2	7.8
26	5.5	5.7	3.2	5.6	7.3
27	5.4	5.4	3.2	5.5	6.4
28	4.9	5.0	2.8	4.5	6.2
sum	221.0	212.5	121.0	239.0	296.0§

† All three lateral components were measured and their combined length divided by three.
‡ Number of nuclei analysed.
§ The whole nucleus was not reconstructed due to missing sections. The total complement length is estimated from the length of bivalent no. 2 (14.5 μm) and the information given in table 2 that this bivalent represents 4.9% of the total pachytene length.

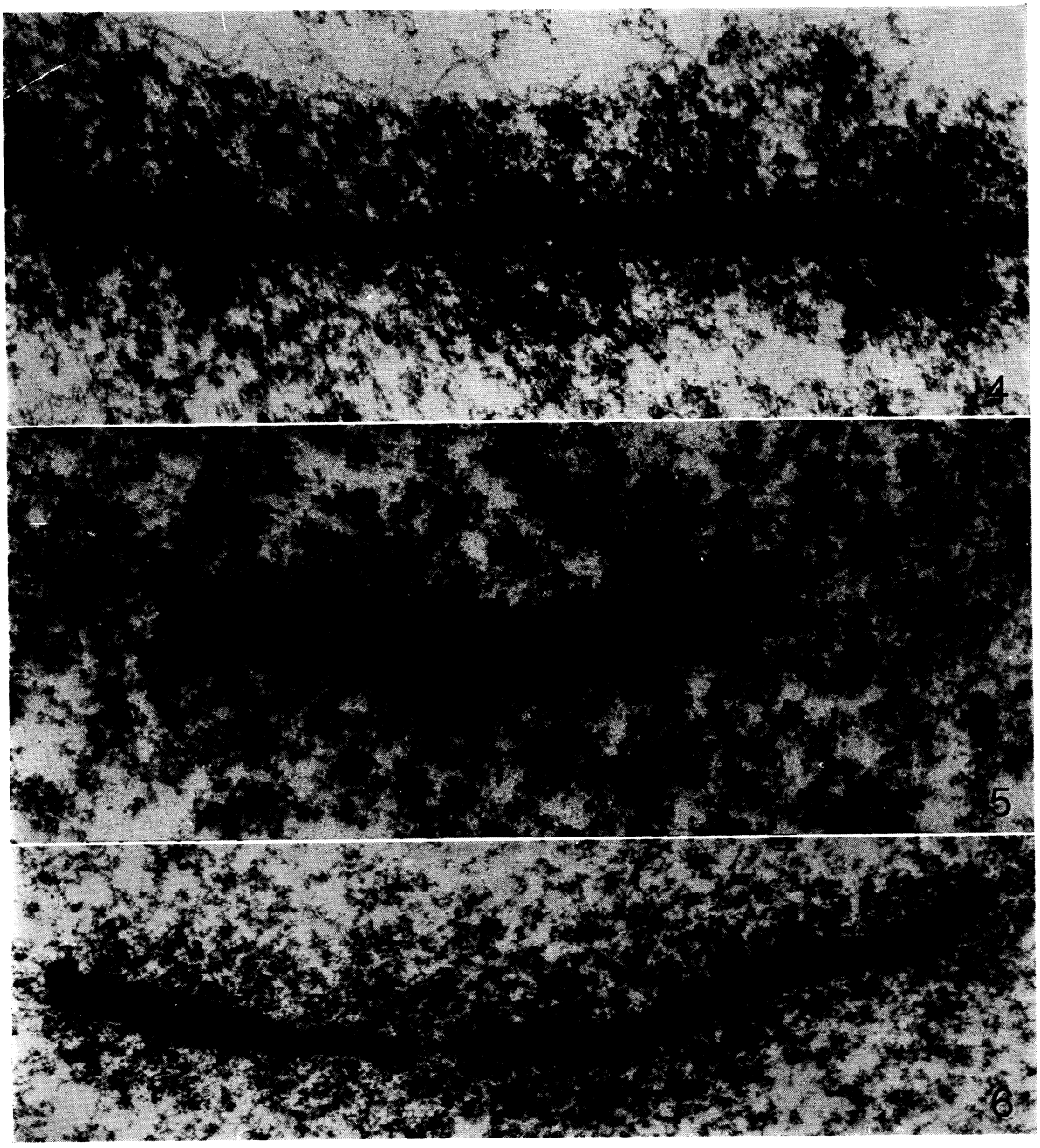
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Until the end of pachytene, the oocyte and the seven nurse cells are following the same pattern of development. After pachytene is completed, the nurse cells start on an independent course. The chromosomes begin to condense and the synaptonemal complexes detach from the bivalents forming various aggregates of reorganized synaptonemal complex subunits (figure 8). Ultimately, after nuclear degeneration the nurse cells empty their content into the oocyte.

TABLE 2. COMPARISON OF SYNAPTONEMAL COMPLEX LENGTHS IN OOCYTES OF *BOMBYX MORI* AS A PERCENTAGE OF THE TOTAL COMPLEMENT LENGTH IN EACH NUCLEUS

chromosome number	zygotene	pachytene $2n$	pachytene $3n$	early modified pachytene	mid modified pachytene
1	5.4	5.2	5.2	5.0	5.4
2	5.3	4.9	4.7	4.9	4.9
3	4.7	4.6	4.6	4.8	—
4	4.5	4.4	4.5	4.5	—
5	4.2	4.2	4.4	4.5	4.3
6	4.2	4.1	4.2	4.4	4.2
7	4.0	4.0	4.0	4.3	—
8	3.9	4.0	4.0	4.2	—
9	3.8	3.9	3.9	3.8	4.0
10	3.6	3.8	3.7	3.8	3.9
11	3.6	3.8	3.6	3.8	3.9
12	3.6	3.7	3.6	3.7	—
13	3.6	3.6	3.6	3.7	—
14	3.6	3.6	3.6	3.7	—
15	3.4	3.5	3.5	3.6	—
16	3.4	3.5	3.4	3.6	3.4
17	3.4	3.3	3.4	3.5	3.3
18	3.4	3.3	3.3	3.5	3.3
19	3.3	3.3	3.3	3.5	3.3
20	3.2	3.2	3.2	3.3	3.2
21	3.2	3.1	3.1	3.2	3.0
22	3.1	3.1	3.0	2.7	2.9
23	3.0	3.0	2.9	2.6	2.9
24	2.8	2.9	2.9	2.6	2.7
25	2.7	2.8	2.8	2.6	2.6
26	2.5	2.7	2.6	2.3	2.5
27	2.4	2.6	2.6	2.3	2.2
28	2.2	2.4	2.3	1.9	2.1

In the nuclei of the oocyte, the synaptonemal complex undergoes a unique differentiation. After telomeres of the bivalents are released from their attachment sites on the nuclear envelope, a growth of the lateral components is initiated. As shown in table 1, the length of the total synaptonemal complex complement increases about 50 %. This increase is followed by a gradual shortening towards the end of the meiotic prophase. The width of the complex increases after pachytene during the lengthening as well as shortening phase reaching about 1 μm at metaphase I as compared to a pachytene width of approximately 130 nm. Figures 4–11, plates 1–3, show the elaboration of the synaptonemal complex. The normal pachytene complex in figure 4 has a distinct central region consisting of numerous, fine filaments attached to the lateral components at regular intervals. These filaments do not traverse the entire space between the lateral components. Alternating filaments overlap and form the scalariform central component of the complex. In figure 5 the growth of the lateral component has begun. New material is added evenly onto the lateral components resulting in a decrease in width of the central region. The scalariform appearance of the central region is no longer recognizable at



FIGURES 4–6. Stages in the modification of the synaptonemal complex of *Bombyx mori* females. (Magns: figure 4, × 62000; figure 5, × 84000; figure 6, × 23500.)

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

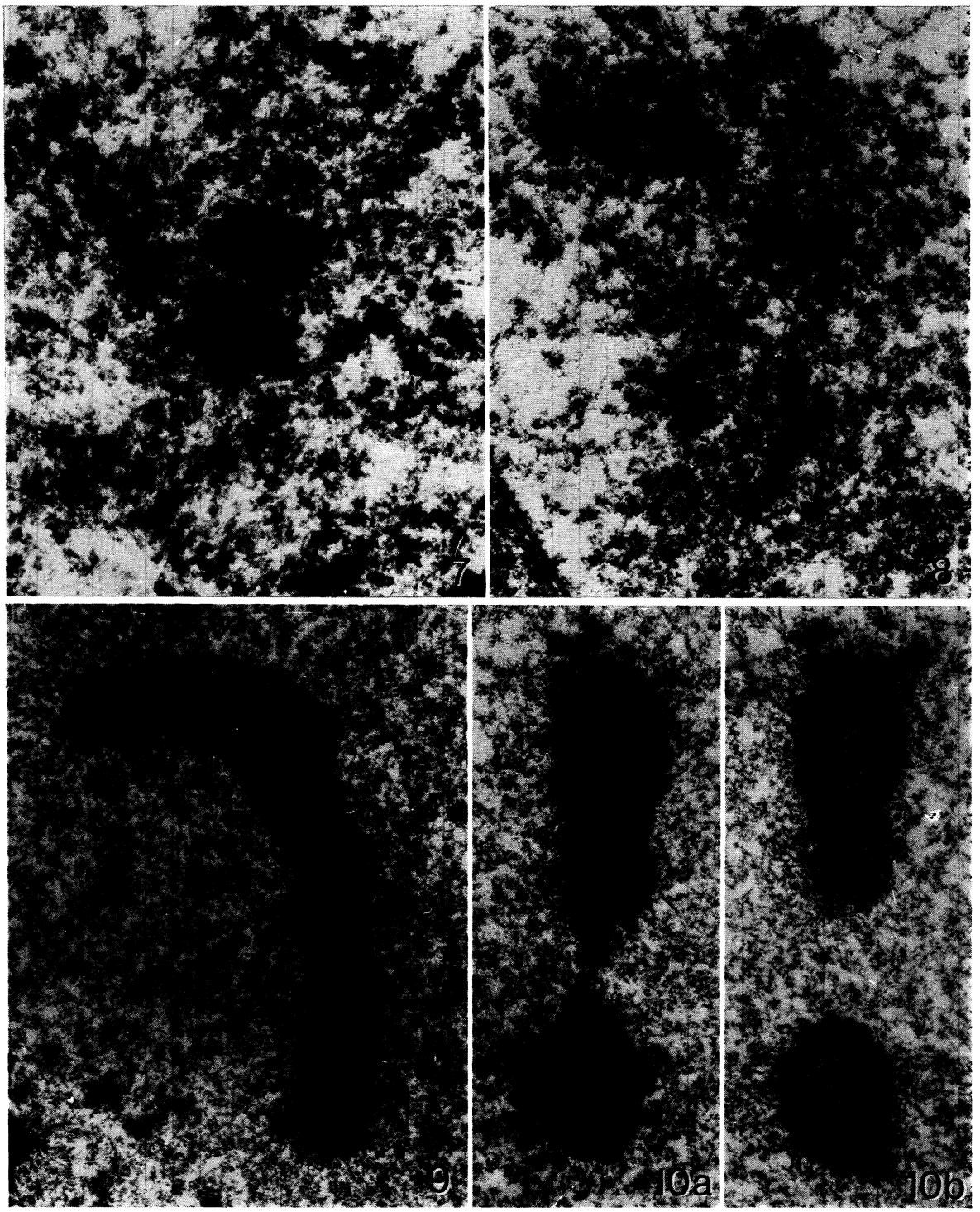

FIGURE 7. Cross section of a modified synaptonemal complex. (Magn. × 84000.)

FIGURE 8. Reorganized synaptonemal complex subunits of a post-pachytene nurse cell nucleus. (Magn. × 46000.)

FIGURE 9. Synaptonemal complex in a progressed state of modification. Note the less electron-dense material inside the dense complex. (Magn. × 22400.)

FIGURES 10*a* AND 10*b*. Two consecutive sections through an advanced modified synaptonemal complex. Note the dense material inside the complex. (Magn. × 28000.)

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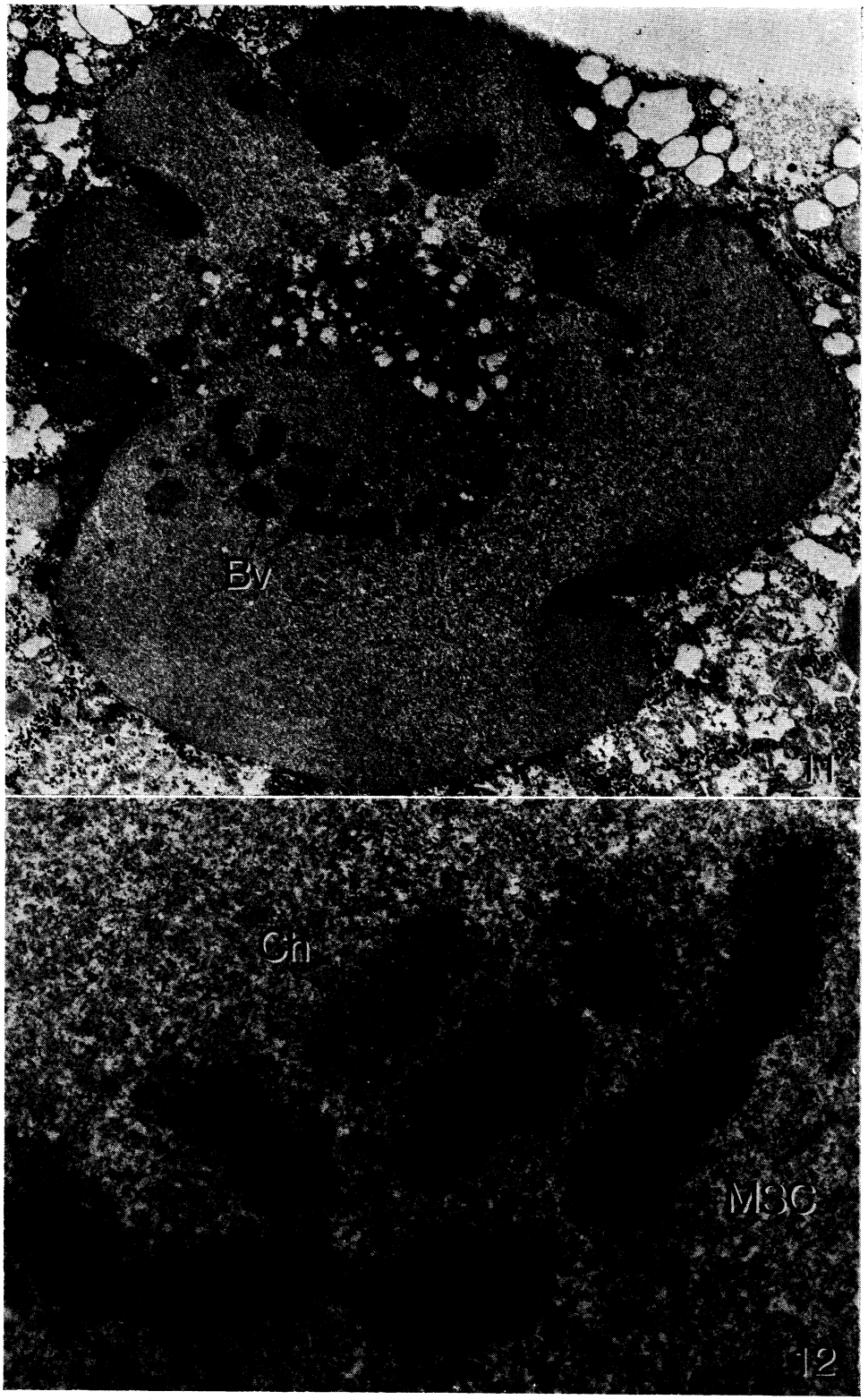

FIGURES 11 AND 12. Section through an almost mature egg. The chromosomes in the meiotic nucleus are still paired with a modified synaptonemal complex. MSC, Modified synaptonemal complex; Ch, chromatin; Bv, bivalent. (Magns: figure 11, × 3000; figure 12, × 13 800.)

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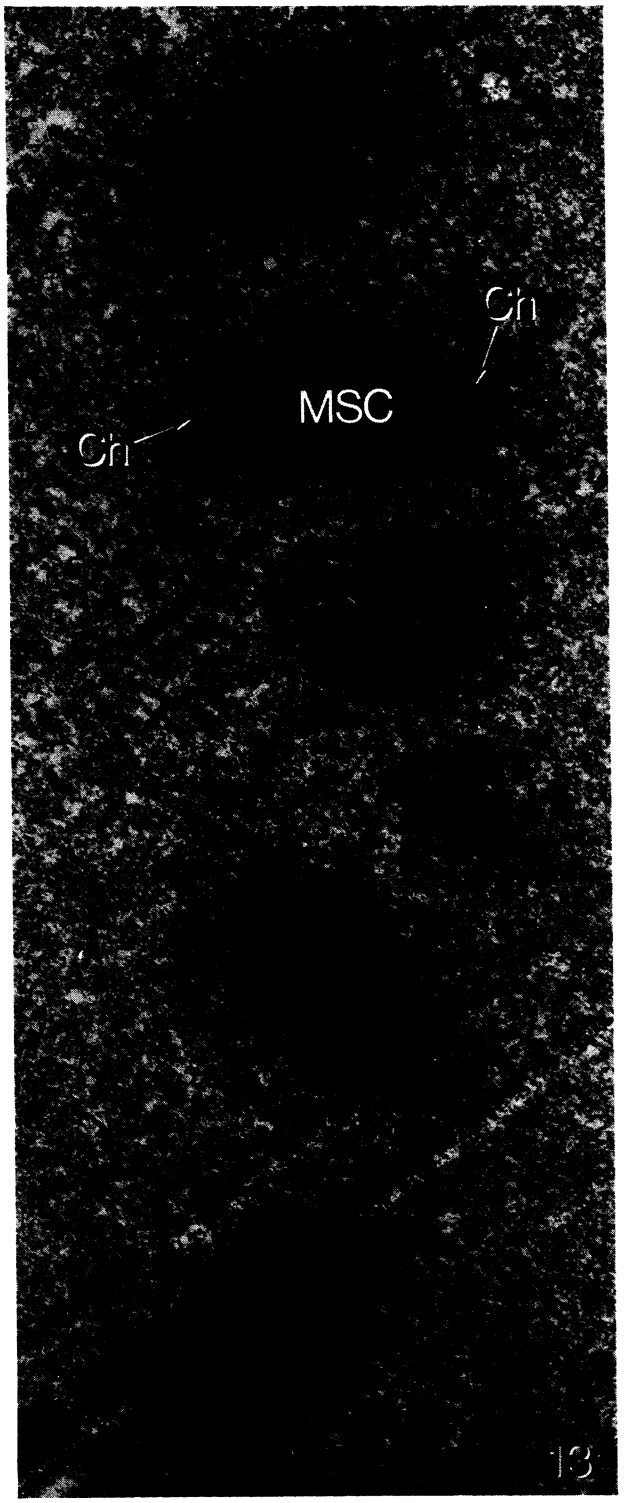

FIGURE 13. Section through a metaphase plate of a mature egg of *Bombyx mori*. MSC, Modified synaptonemal complex; Ch, chromatin. (Magn. × 22800.)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

this stage. Figure 6 shows a synaptonemal complex in a progressed state of reorganization. The lateral components have increased tremendously in width, almost filling out the central region of the complex. A cross section of a complex in a similar state of development is depicted in figure 7. Individual lateral components can still be recognized separated by a narrow central region.

The further fate of the modified complex is illustrated in figures 9–13. In figure 9 a small amount of medium dense material is embedded in the electron scattering lateral components. The lateral components have fused and a central region can no longer be identified. It is possible that the medium-dense material represents remnants of central region subunits. This material becomes further condensed and is possibly expelled from the modified lateral components as indicated in figure 10*b*. At this stage, the bivalents are still dispersed in the nucleus and their chromatin is completely uncondensed.

Meiotic prophase is terminated by the formation of a metaphase plate as illustrated in figures 11 and 12, plate 3. The reorganized synaptonemal complexes have by the end of the prophase lost their substructure and are present as uniformly staining, thick sausage-shaped structures. The two homologous chromosomes are attached on opposite sides of the complex. In figure 13, plate 4, the modified complexes have condensed further and attained their final spherical shape with the homologous chromosomes attached at opposite poles. A rough estimate of the ratio between the volume of the modified complex and the volume of the condensed chromosomes shows that the volume of the modified complex is approximately ten times greater than that of the condensed, stainable chromatin.

Although anaphase has not yet been studied, it is anticipated that the modified synaptonemal complexes which are present between the bivalents at metaphase I constitute the elimination chromatin characteristic of female meiosis in *Lepidoptera*. The term elimination chromatin has been coined because this structure remains behind in the position of the metaphase plate, when the homologous chromosomes move to opposite poles at anaphase, as demonstrated in the beautiful light microscopic investigations of Seiler (1914) in several Lepidopteran species. The cytochemical analysis of Ris & Kleinfeld (1952) demonstrated that the elimination chromatin consists of protein and RNA while reactions for DNA were negative. In an electron microscopical study of *Cidaria*, Sorsa & Suomalainen (1975) have recently reported on the elimination chromatin at metaphase I. The structural characteristics of the material between the homologous chromosomes in these species are comparable to that observed for *Bombyx*. From the results presented in the present paper, the following conclusion can be drawn : In the meiosis of female *Bombyx*, the lack of chiasmata and crossing over is substituted for by retainment of an elaborated and structurally reorganized synaptonemal complex, which insures regular disjunction of the homologous chromosomes at anaphase I.

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References (Rasmussen)

Comings, D. E. & Okada, T. A. 1971 Triple chromosome pairing in triploid chickens. *Nature, Lond.* **231**, 119–121.

Gassner, G. 1969 Synaptinemal complexes in the achiasmatic spermatogenesis of *Bolbe nigra* Giglio-Tos (Mantoidea). *Chromosoma* **26**, 22–34.

Gillies, C. B. 1975*a* An ultrastructural analysis of chromosome pairing in maize. *C. r. Trav. Lab. Carlsberg* **40**, 135–161.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Gillies, C. B. 1975*b* Synaptonemal complex and chromosome structure. *A. Rev. Genet.* **9**, 91–110.
Grell, R. F., Bank, H. & Gassner, G. 1972 Meiotic exchange without the synaptinemal complex. *Nature New Biol.* **240**, 155–157.
Moens, P. B. 1973 Quantitative electron microscopy of chromosome organization at meiotic prophase. *Cold Spring Harbor Symp. Quant. Biol.* **38**, 99–107.
Moses, M. J. 1968 Synaptinemal complex. *A. Rev. Genet.* **2**, 363–412.
Rasmussen, S. W. 1976 The meiotic prophase in *Bombyx mori* females analyzed by three dimensional reconstructions of synaptonemal complexes. *Chromosoma* **54**, 245–293.
Ris, H. & Kleinfeld, R. 1952 Cytochemical studies on the chromatin elimination in *Solenobia* (*Lepidoptera*). *Chromosoma* **5**, 363–371.
Seiler, J. 1914 Das Verhalten der Geschlechtschromosomen bei Lepidopteren. *Arch. Zellforsch.* **13**, 159–269.
Solari, A. J. 1970 The behaviour of chromosomal axes during diplotene in mouse spermatocytes. *Chromosoma* **31**, 217–230.
Sorsa, M. & Suomalainen, E. 1975 Electron microscopy of chromatin elimination in *Cidaria* (*Lepidoptera*). *Hereditas* **80**, 35–40.
Sotelo, J. R., Garcia, R. B. & Wettstein, R. 1973 Serial sectioning study of some meiotic stages in *Scaptericus borrelli* (Grylloidea). *Chromosoma* **42**, 307–333.
Welsch, B. 1973 Synaptonemal Complex und Chromosomenstructur in der achiasmatischen Spermatogenese von *Panorpa communis* (Mecoptera). *Chromosoma* **43**, 19–74.
Westergaard, M. & von Wettstein, D. 1968 The meiotic cycle in an *Ascomycete*. In *Effects of radiation on meiotic systems*, pp. 113–121. International Atomic Energy Agency, Vienna.
Westergaard, M. & von Wettstein, D. 1970 Studies on the mechanism of crossing over. IV. The molecular organization of the synaptinemal complex in *Neottiella* (Cooke) saccardo (ascomycetes). *Compt. r. Trav. Lab. Carlsberg* **37**, 239–268.
Westergaard, M. & von Wettstein, D. 1972 The synaptinemal complex. *A. Rev. Genet.* **6**, 71–110.

Discussion

Dina Raveh (*Department of Zoology, University of Leicester, Leicester LE*1 7*RH*). If we are led to believe from the data of preceding speakers that nodules associated with the synaptonemal complex are associated with chiasma formation, one would not expect to find them in meiocytes in which crossing over does not take place. Indeed, they do not appear in your reconstructions. May we therefore conclude that they are absent from these oocytes?

S. W. Rasmussen. The so-called recombination nodules have not yet been identified unambiguously in *Bombyx* females. Whether the elimination of crossing over is due to a lack of these nodules or if it has a different reason is not known at the present stage.

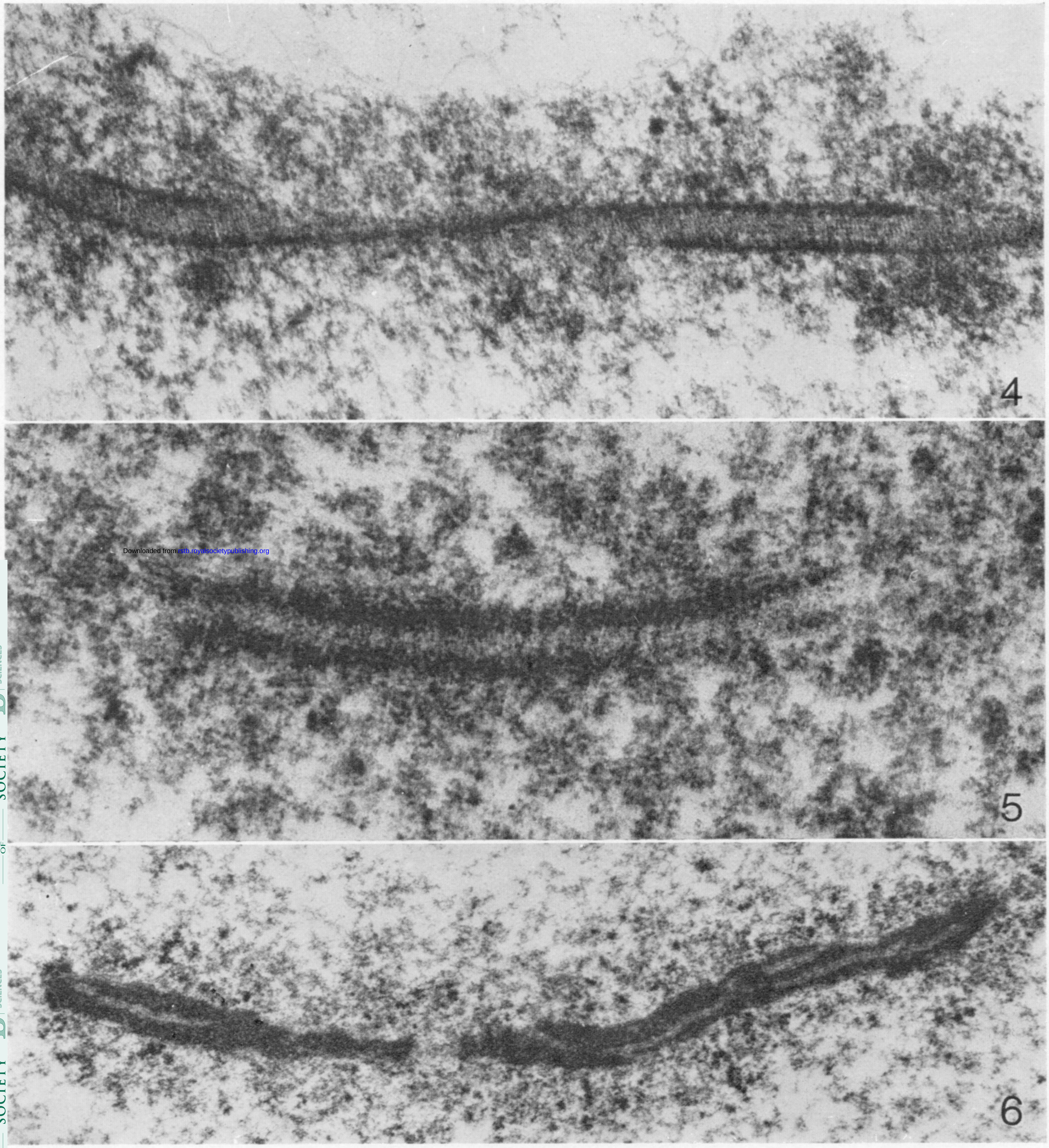
J. Cowen (*Department of Zoology, University of Birmingham*). Have you investigated *Bombyx mori* males? This may be illuminating for many of the pertinent questions.

S. W. Rasmussen. I have just started an examination of the male meiosis in *Bombyx* and hope to have the first nuclei reconstructed in the near future.

K. R. Lewis (*Botany School, University of Oxford*). I was impressed by the extreme asynchrony within and, especially, between bivalents of synaptonemal complex formation in the achiasmate meiosis of *Bombyx mori* females. Is this likely to be general? I am thinking, in particular, of chiasmate systems and a possible connection with chiasma interference within bivalents and possible competition between them.

S. W. Rasmussen. The asynchrony in synaptonemal complex formation within a particular nucleus is presumably a general feature of chromosome pairing.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



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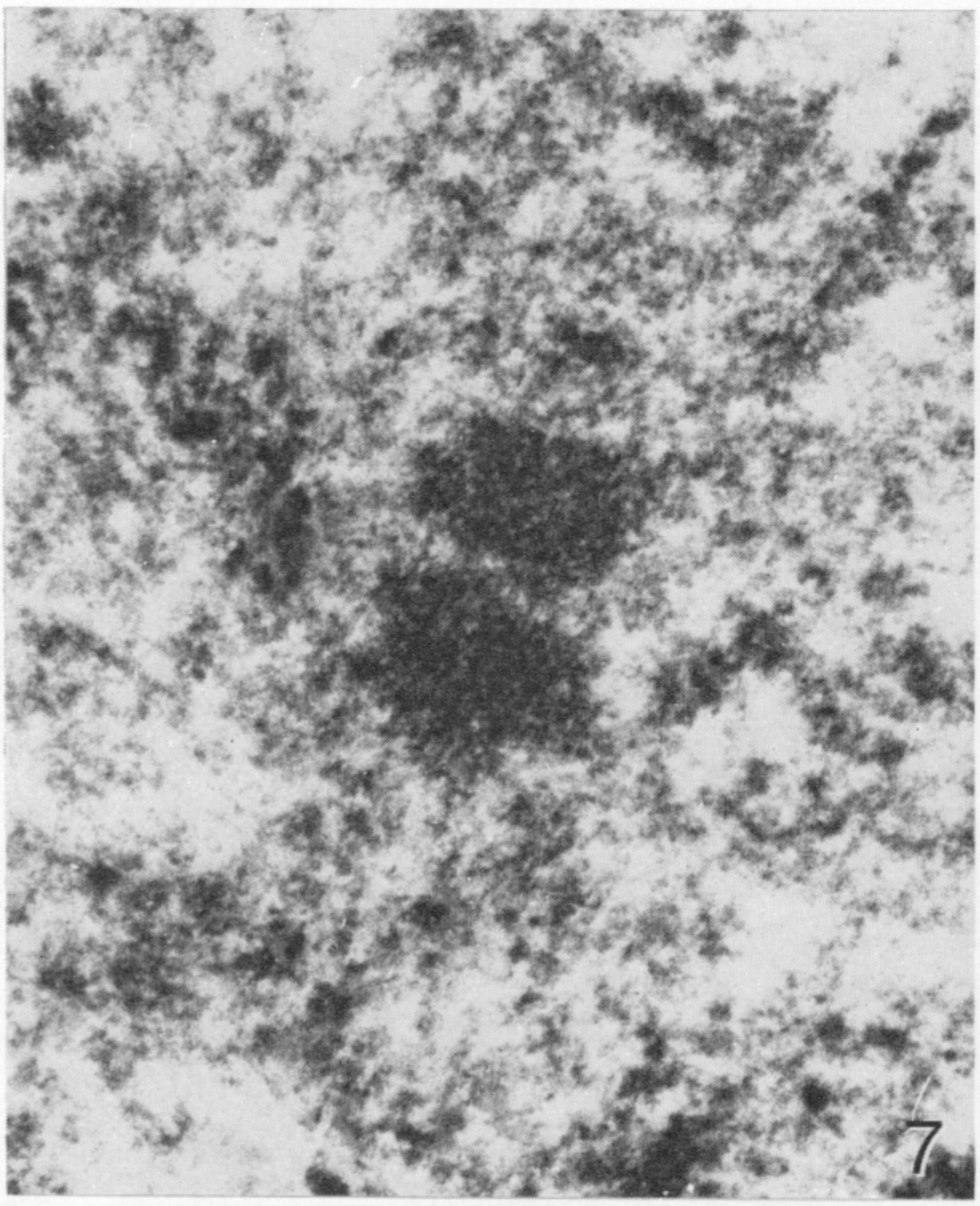
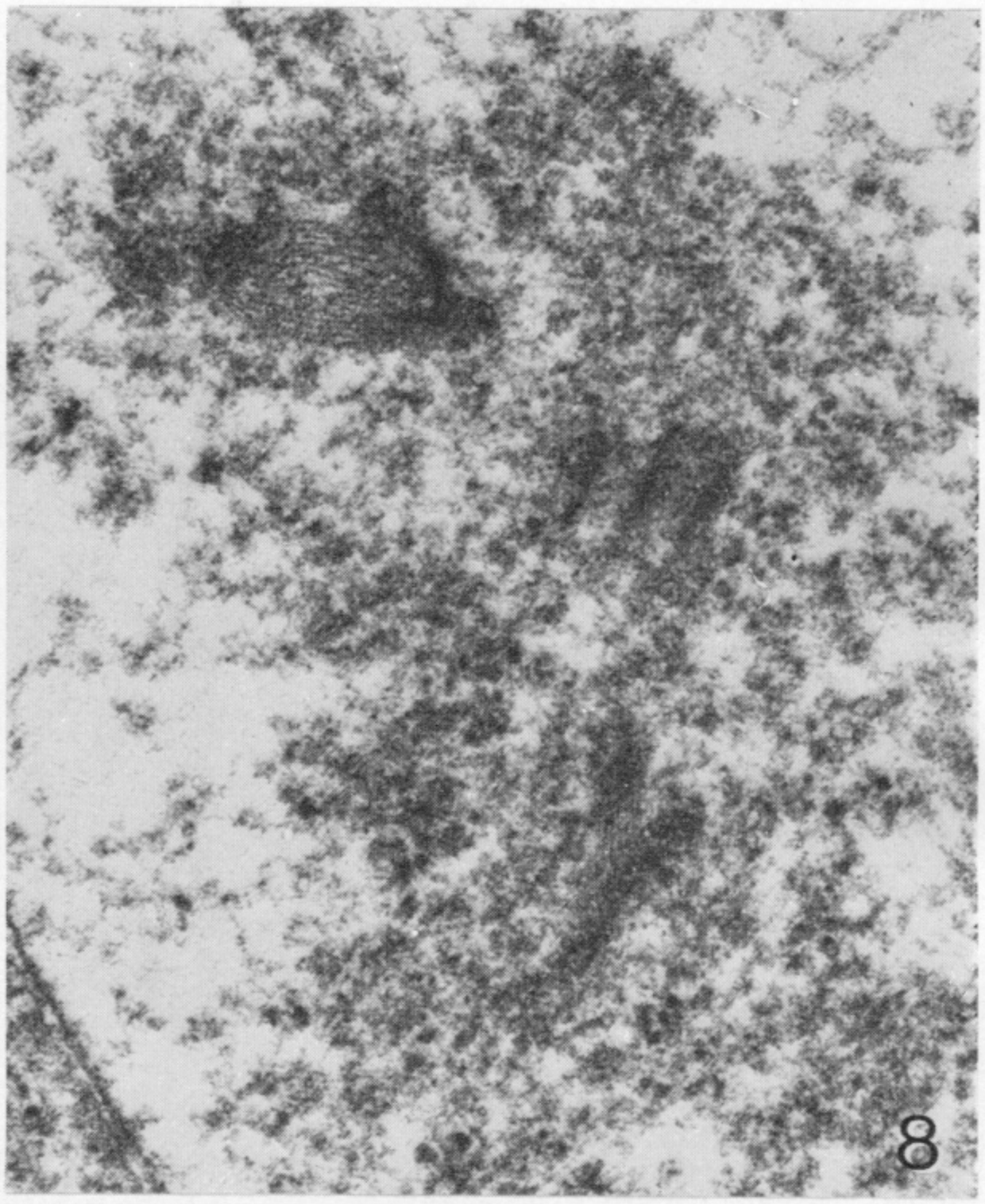
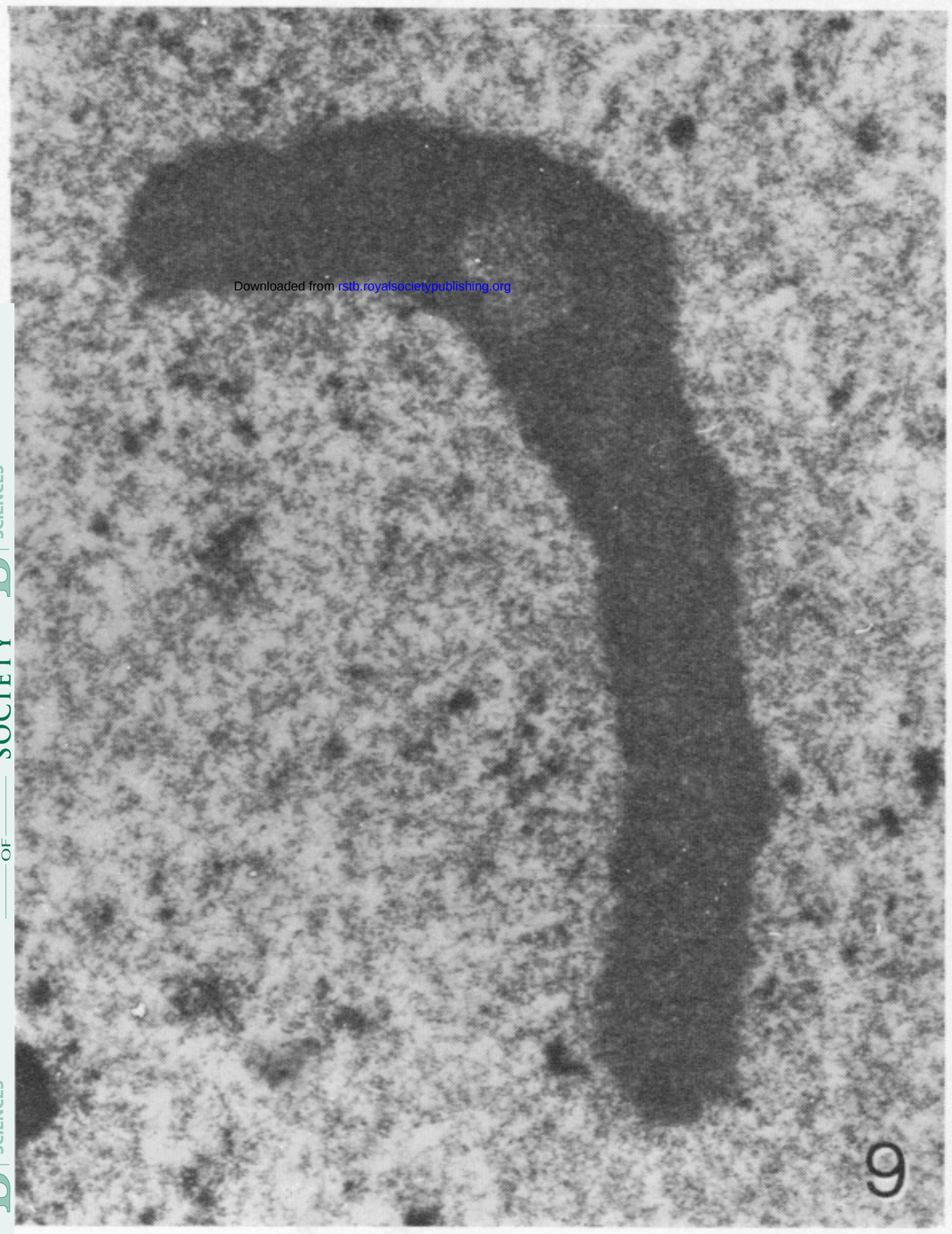
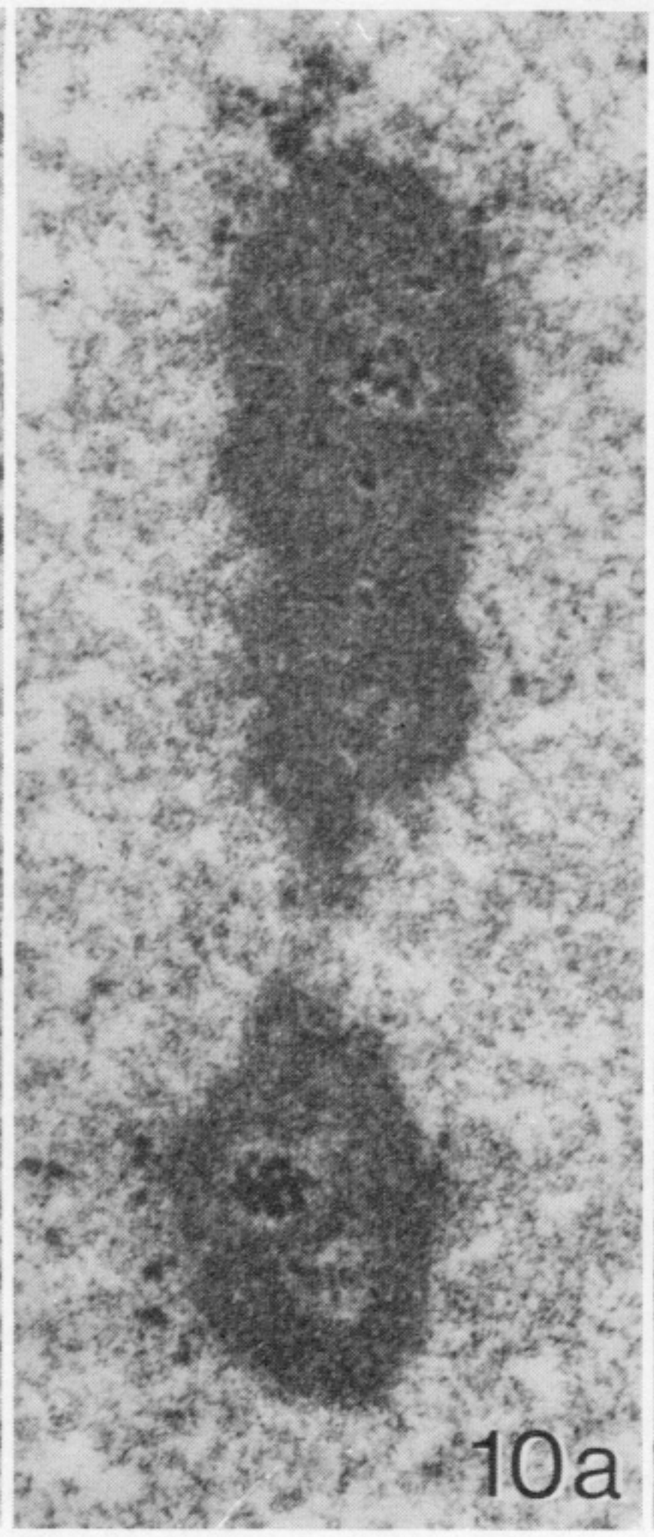








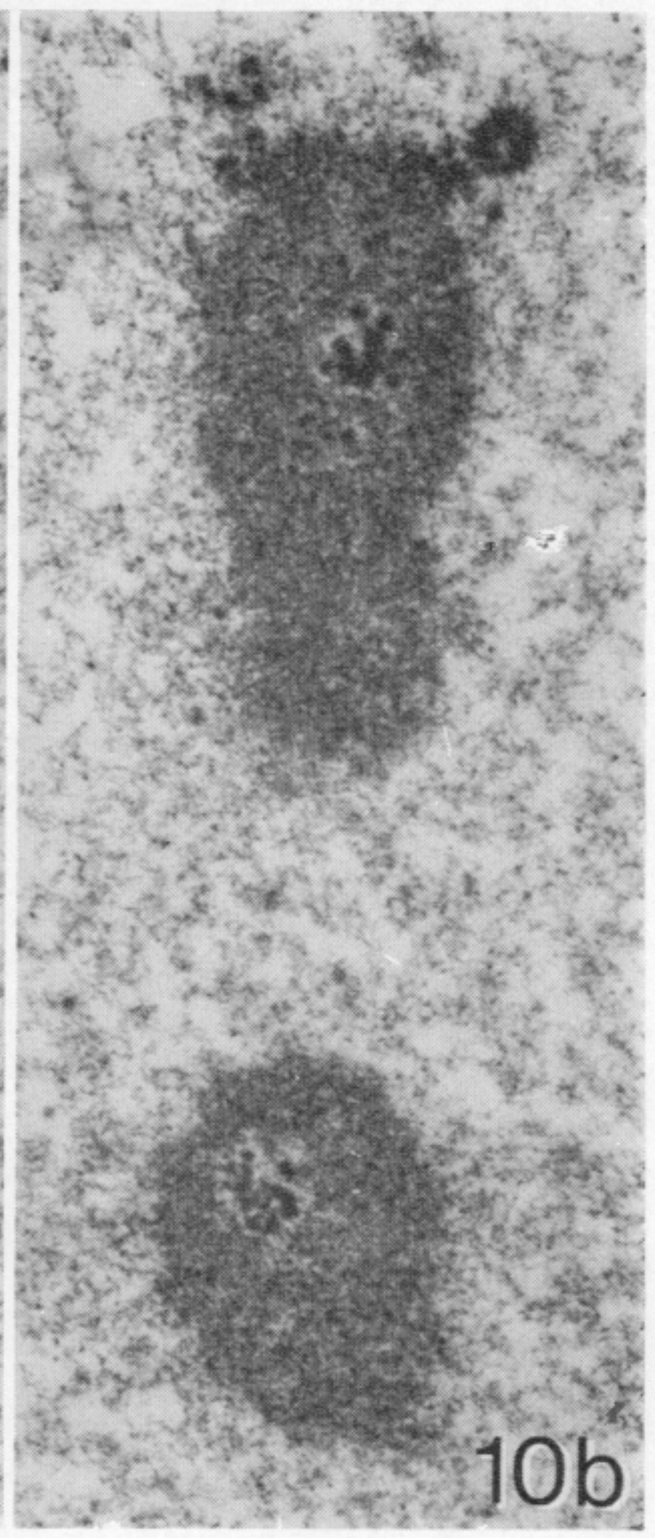
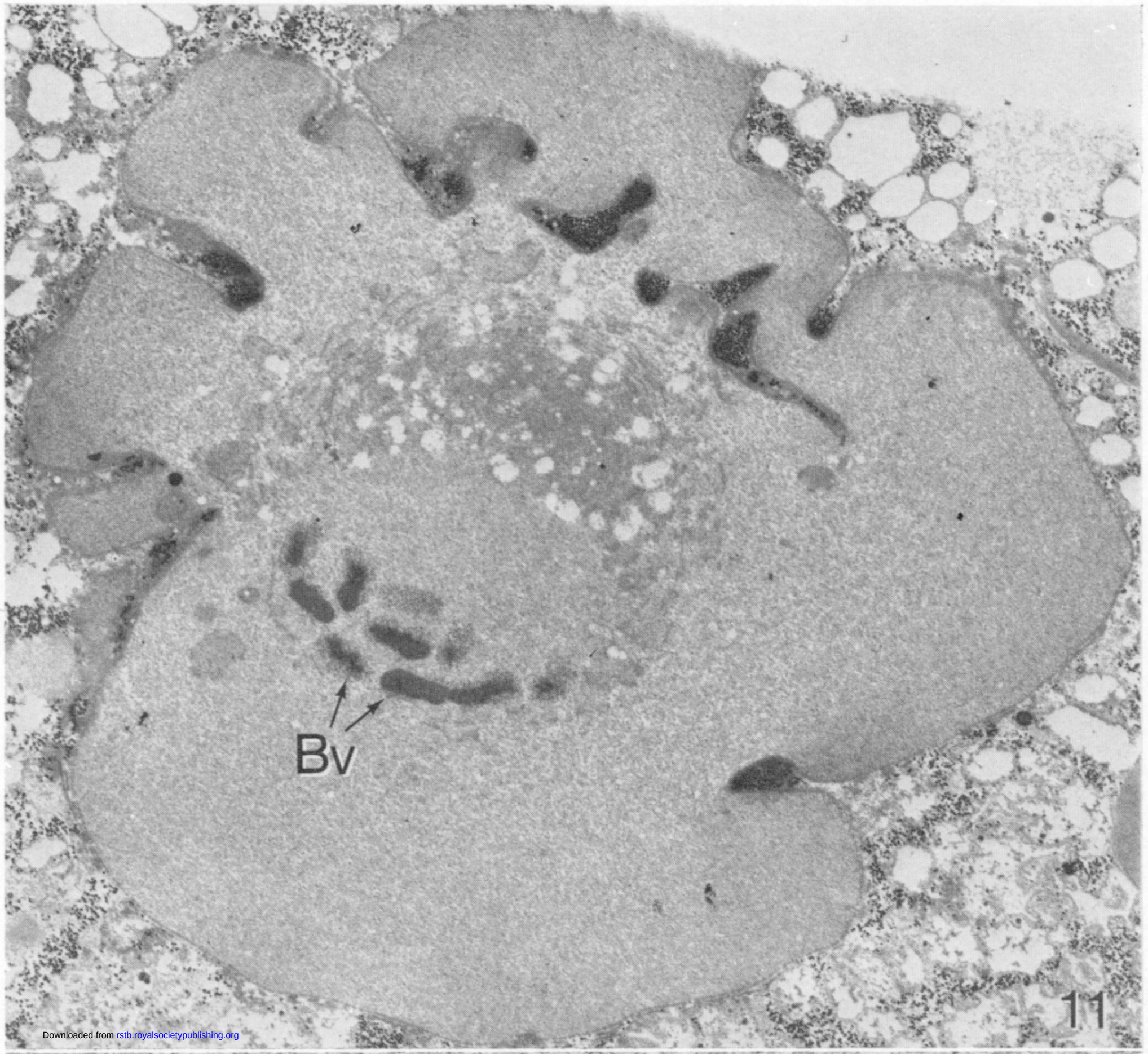


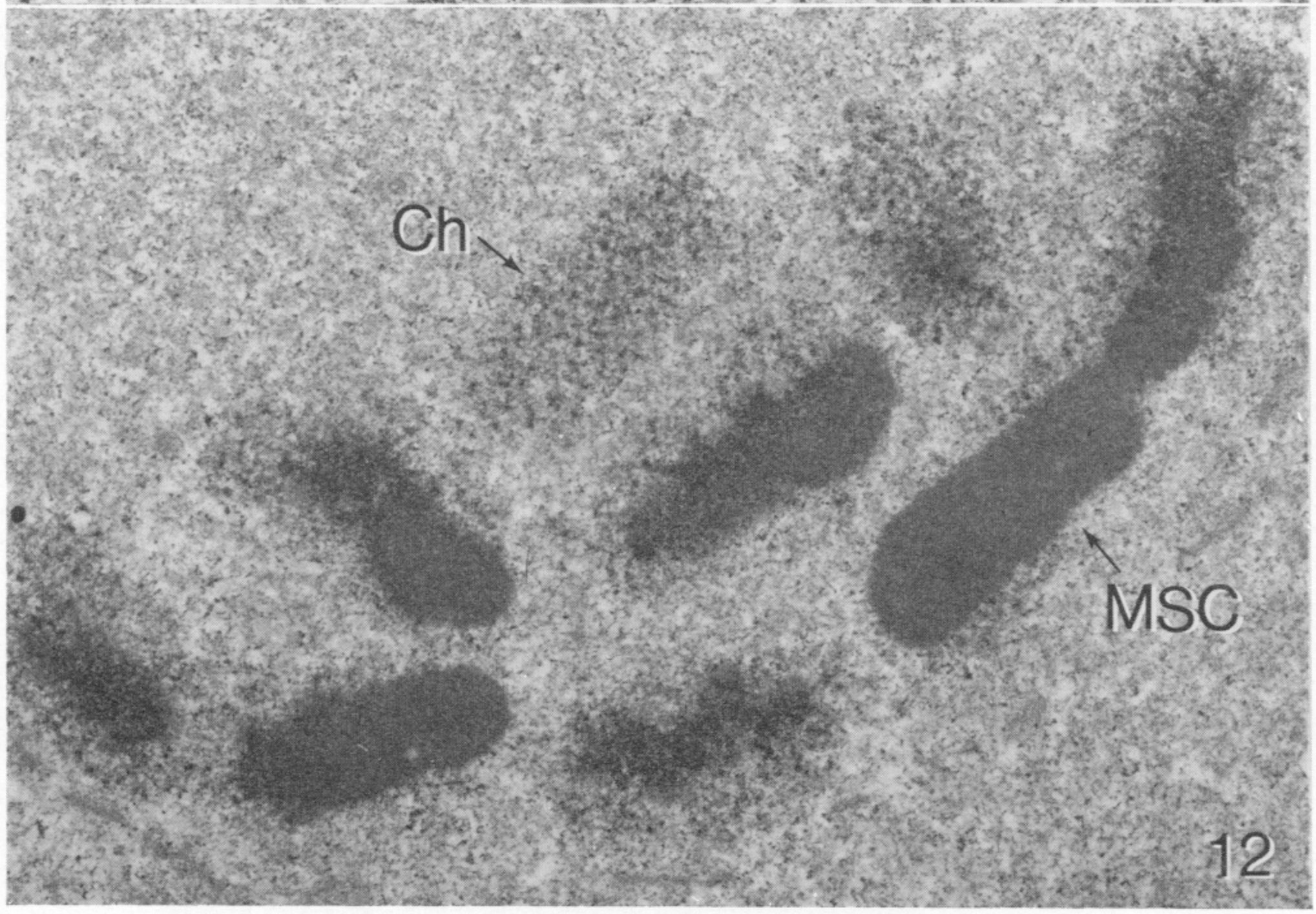
FIGURE 7. Cross section of a modified synaptonemal complex. (Magn. × 84000.)

FIGURE 8. Reorganized synaptonemal complex subunits of a post-pachytene nurse cell nucleus. (Magn. × 46000.)

FIGURE 9. Synaptonemal complex in a progressed state of modification. Note the less electron-dense material inside the dense complex. (Magn. × 22400.)

FIGURES 10*a* AND 10*b*. Two consecutive sections through an advanced modified synaptonemal complex. Note the dense material inside the complex. (Magn. × 28000.)





FIGURES 11 AND 12. Section through an almost mature egg. The chromosomes in the meiotic nucleus are still paired with a modified synaptonemal complex. MSC, Modified synaptonemal complex; Ch, chromatin; Bv, bivalent. (Magns: figure 11, $\times 3000$; figure 12, $\times 13800$.)

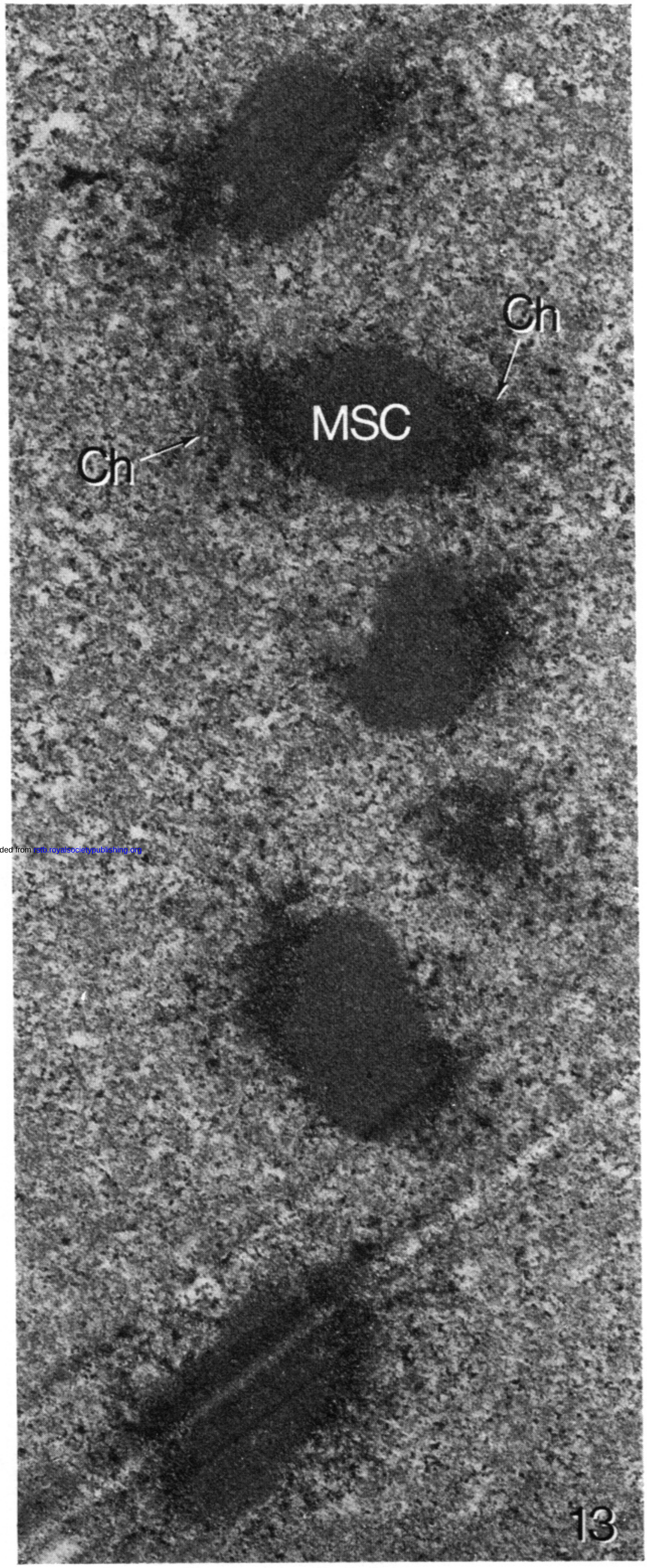


FIGURE 13. Section through a metaphase plate of a mature egg of *Bombyx mori*. MSC, Modified synaptonemal complex; Ch, chromatin. (Magn. ×22800.)