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The Assembly of the Synaptinemal Complex [and Discussion]

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The assembly of the synaptinemal complex

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[Plates 1–3]

The assembly of the synaptinemal complex in the ascomycete *Neottiella* was studied by three-dimensional reconstruction of a late zygotene nucleus. A single banded lateral component is formed between the two sister chromatids of each homologous chromosome prior to their pairing. The central regions are pre-assembled in organized form in folds of the granular part of the nucleolus and then converted into an amorphous transport form. The latter appears to move through the nucleoplasm to sites between the lateral components of synapsing homologous chromosomes. The central region material is reorganized into blocks with a recognizable central component and attached to one lateral component. The last step in the completion of the synaptinemal complex is the association of the free surface of the organized central region with the corresponding segment of the homologous lateral component. The findings are discussed in relation to mechanisms of chromosome pairing and chiasma formation.

Introduction

Meiosis provides for recombination of chromosomes as well as for crossing over, i.e. recombination of genes located on a single chromosome. Pairing of the homologous chromosomes at the microscopic, ultrastructural and molecular level is a prerequisite to the formation of chiasmata, the cytological counterpart of crossing over. In many, but not all, organisms the formation of chiasmata conditions regular disjunction.

The universality of four-strand crossing over is at the ultrastructural level matched by the universality in the dimensions of the synaptinemal complex, a structure which holds the paired homologous chromosomes of a pachytene bivalent in register, and from which the chiasmata originate.

Three-dimensional reconstructions from electron micrographs of serial sections through nuclei at various stages of meiosis in different organisms and in special cytogenetic situations have emphasized the importance of the synaptinemal complex in chromosome pairing and chiasma formation and solved several old cytogenetic problems. These aspects of the synaptinemal complex have been reviewed comprehensively in Westergaard & von Wettstein (1972) and in Gillies (1975*a*, *b*).

Lack of meiotic crossing over in *Drosophila melanogaster* males or in asynaptic mutants of *Drosophila melanogaster* females is related to blocks in the assembly of the synaptinemal complex (Rasmussen 1973, 1975). The absence of crossing-over and chiasmata in females of *Bombyx mori* is accompanied by provisions to retain and structurally modify the synaptinemal complex during stages after pachytene up to anaphase I (Rasmussen 1976*a*, *b*). These modified synaptinemal complexes which correspond to the classical elimination chromatin of female meiosis in butterflies and moths substitute for chiasmata and insure regular disjunction.

The ascomycete *Neottiella* offers several advantages for a study of the details in the assembly of the synaptinemal complex: the lateral components are readily observable at leptotene; the

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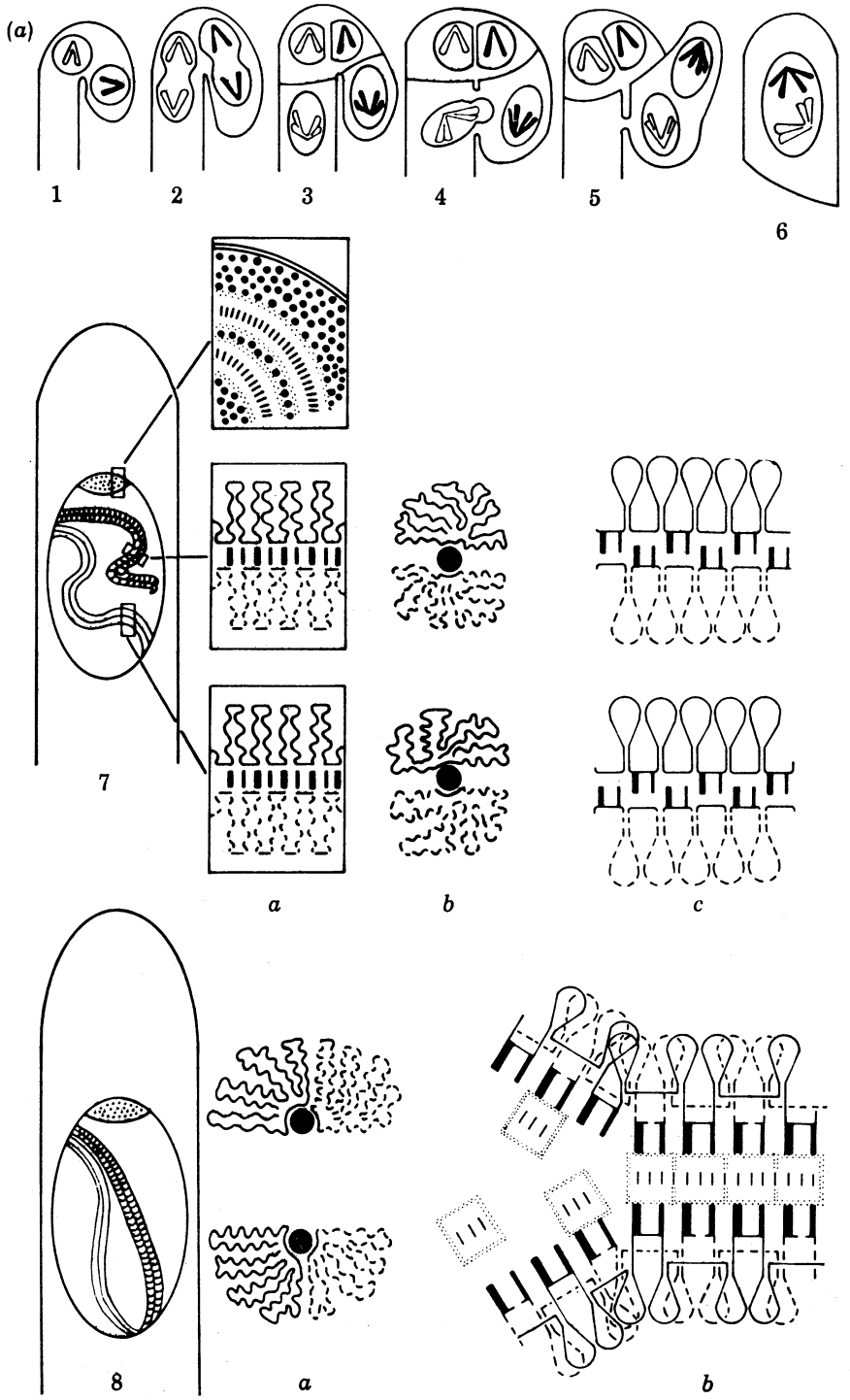

FIGURE 1. Diagram of the synaptinemal complex at different stages of meiosis in an ascomycete (*Neottiella*). (From D. von Wettstein 1971.) A single pair of homologous chromosomes is considered in the following stages:

(1) Two haploid nuclei in the tip of a bending ascogenous hypha.
(2) Telophase of the two synchronized mitoses in a crosier.
(3) Crosier with stalk cell nucleus and terminal cell nucleus after DNA replication of the chromosomes; the two nuclei in the penultimate cell are in G-1 phase.
(4) Migration of the nucleus from the stalk cell into the terminal cell.
(5) The chromosomes of the two prefusion nuclei in the outgrowing ascus consist of two chromatids.
(6) Young ascus after caryogamy.
(7) Leptotene; *a*, one lateral component between the sister chromatids of each homologue and preformed central regions in the nucleolus; *b*, cross section of the two homologous chromosomes; *c*, molecular interpretation.
(8) Zygotene; *a*, the lateral components are located lateral to the sister chromatids; *b*, formation of the synaptinemal complex by blocks of the central region.

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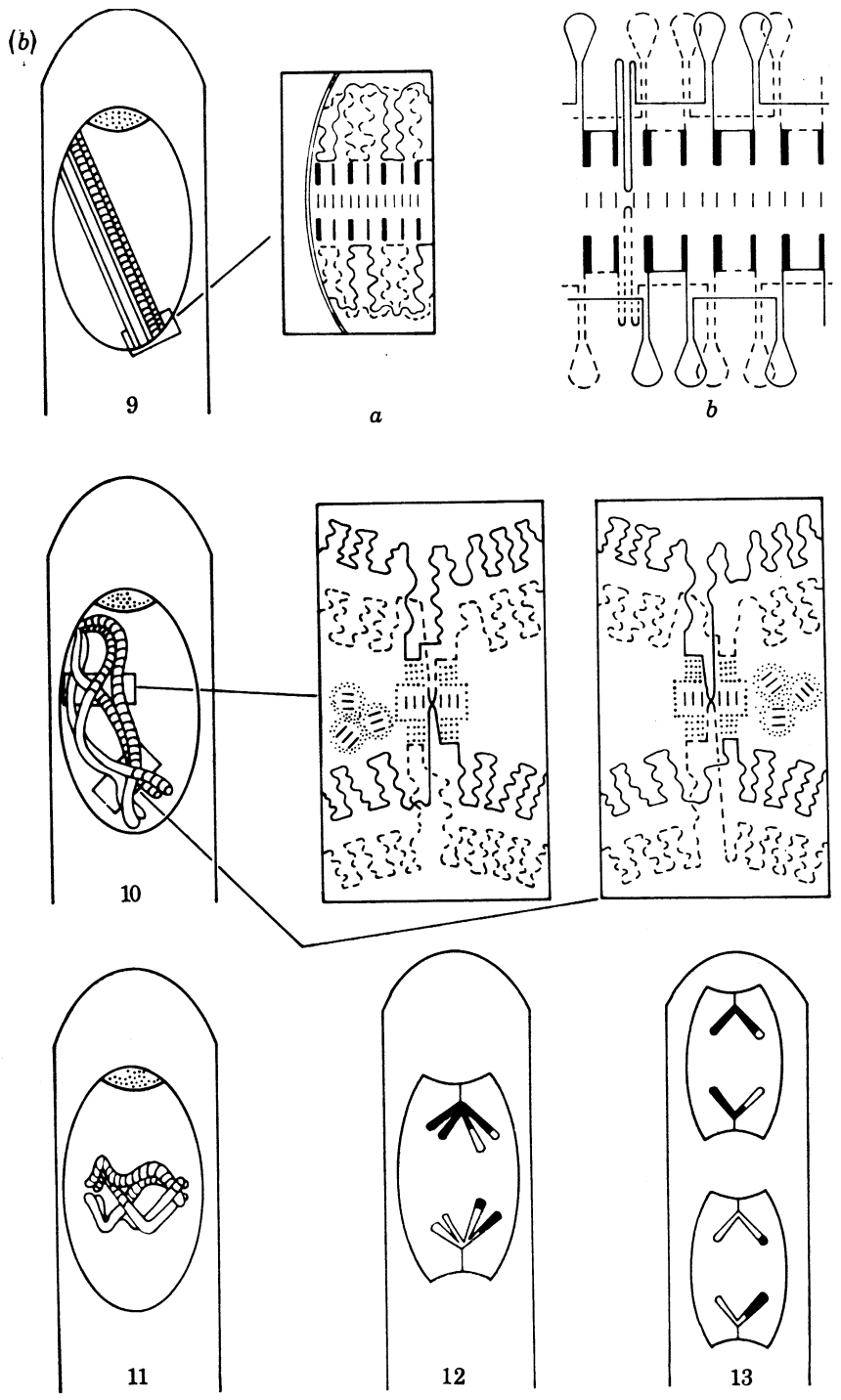

FIGURE 1—*continued.*

(9) Pachytene; *a*, synaptinemal complex at the attachment site of the bivalent on the nuclear envelope; *b*, molecular interpretation.
(10) Diplotene; the synaptinemal complex is stripped from the bivalent. The incipient chiasmata consist of retained short stretches of the synaptinemal complex.
(11) Metaphase I. (12) Anaphase I. (13) Anaphase II.

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chromatin of the homologous chromosomes is contracted and well defined in electron micrographs of all meiotic stages; preformed central regions of the synaptinemal complexes including the central component with its characteristic nodes are present in the granular component of the nucleolus prior to the precise pairing of the chromosomes (Westergaard & von Wettstein 1970*b*, 1972; von Wettstein 1971).

The latter observation suggested that the central regions are first formed in the nucleolus and then transported from the nucleolus to the pairing chromosomes and laid down between homologous chromosomes to join their lateral components. This further implied that the central regions cannot by themselves contain specific information for pairing of homologous chromosome regions. A major feature of the recently proposed preselection hypothesis for crossing over (Stern, Westergaard & von Wettstein 1975) is that preselected pairs of homologous DNA stretches are trapped within the synaptinemal complex during its assembly. To obtain more information on the assembly process of the synaptinemal complex, a late zygotene nucleus of *Neottiella* was serially sectioned and reconstructed. The results pertaining to the above questions are presented in this paper.

Material and methods

The material and methods of fixation are the same as described in Westergaard & von Wettstein (1970*a*). Serial sectioning and reconstructions were carried out as described by Gillies (1972, 1973), except that all 120 sections of the late zygotene nucleus were micrographed at a primary magnification of 10700 times and that also the chromatin was analysed in the reconstructions.

The stages prior to synapsis

The nuclear events which lead to the onset of meiotic prophase are summarized in stages 1–6 of figure 1. DNA replication takes place in the haploid nuclei before caryogamy (Rossen & Westergaard 1966). The zygote nucleus in stage 6 contains the 4*n* amount of DNA; each of its chromosomes consists of two chromatids. A single lateral component is formed *de novo* in the split between the two sister chromatids as drawn in stages 7*a* and *b* of figure 1. The nucleohistone fibril of one sister chromatid is shown as a continuous line, that of the other as a broken line. Central regions assemble in the granular part of the nucleolus (figure 1, stage 7*a* top). Micrographs of layers of organized central regions in this stage have been published in Westergaard & von Wettstein (1970*b*, figs. 14, 16, 58, 69, 78–81, 83; 1972, fig. 15).

Synapsis

After approximate alignment of the homologous chromosomes to within 300 nm the precise point-to-point pairing and stabilization of the paired homologues, via the synaptinemal complex was conceived to occur in the following way. The lateral component of the unpaired chromosome is relocated into a position lateral to both sister chromatids. This is accomplished by the rotation of the sister chromatids relative to the lateral component, whereby the space between the sister chromatids becomes eliminated (figure 1, stage 8*a*). The two lateral components of the homologous chromosomes are then arranged in register directly opposite each other, at a distance of 100 nm, with the aid of the central region material, as indicated in figure 1, stage 8*b*.

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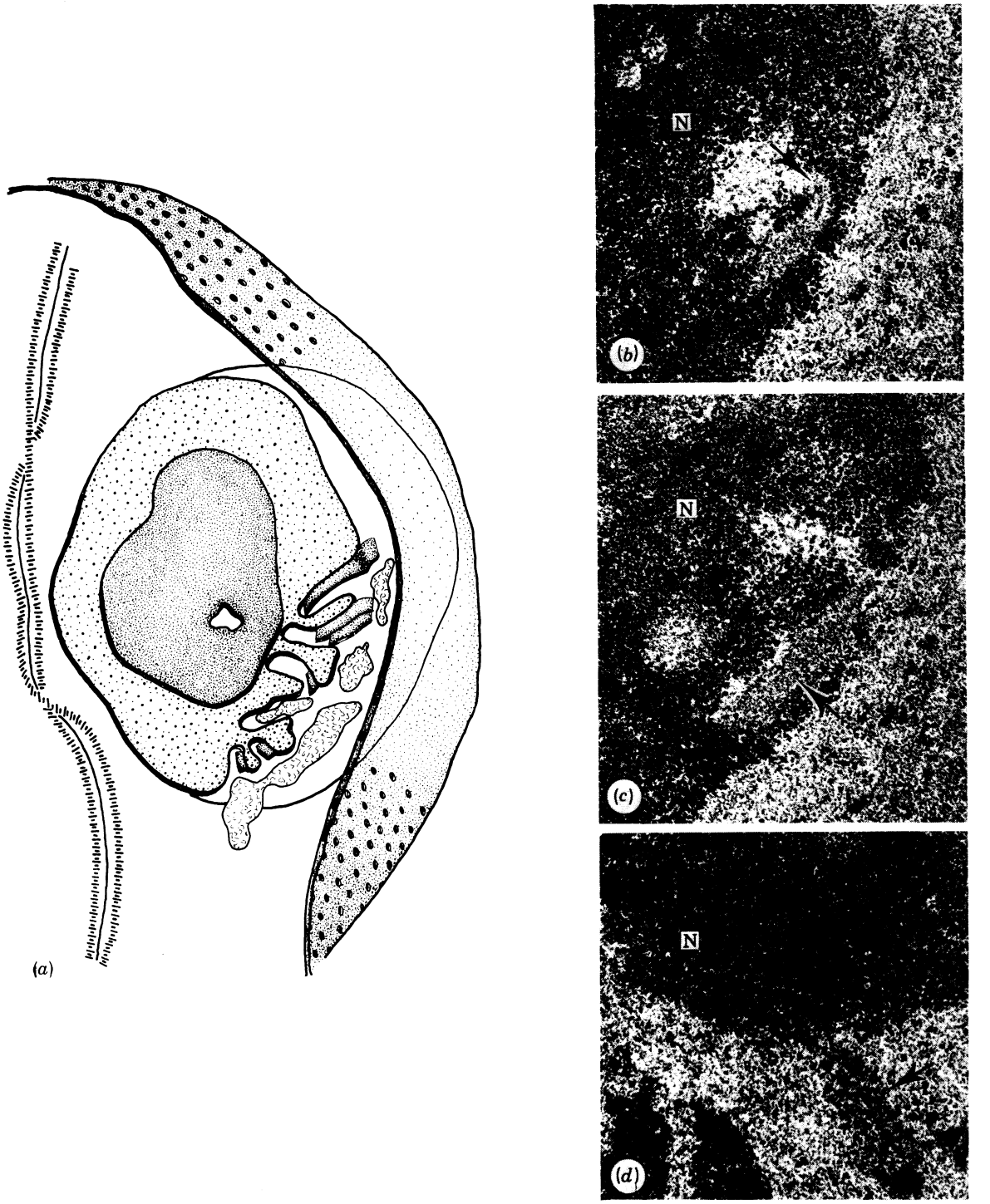

FIGURE 2. Three-dimensional reconstruction of nucleolus in late zygotene nucleus of *Neottiella*. (*a*) Sheets of central regions of the synaptinemal complex in the granular component of the nucleolus. These sheets are converted into an amorphous form, which is found extending into the nucleoplasm. (*b*) Section 59 of the series with organized central region (arrow). (*c*) Section 58 with amorphous central region (arrow). (*d*) In section 50 the amorphous material extends into the nucleoplasm (arrow). (Magn. × 40000.)

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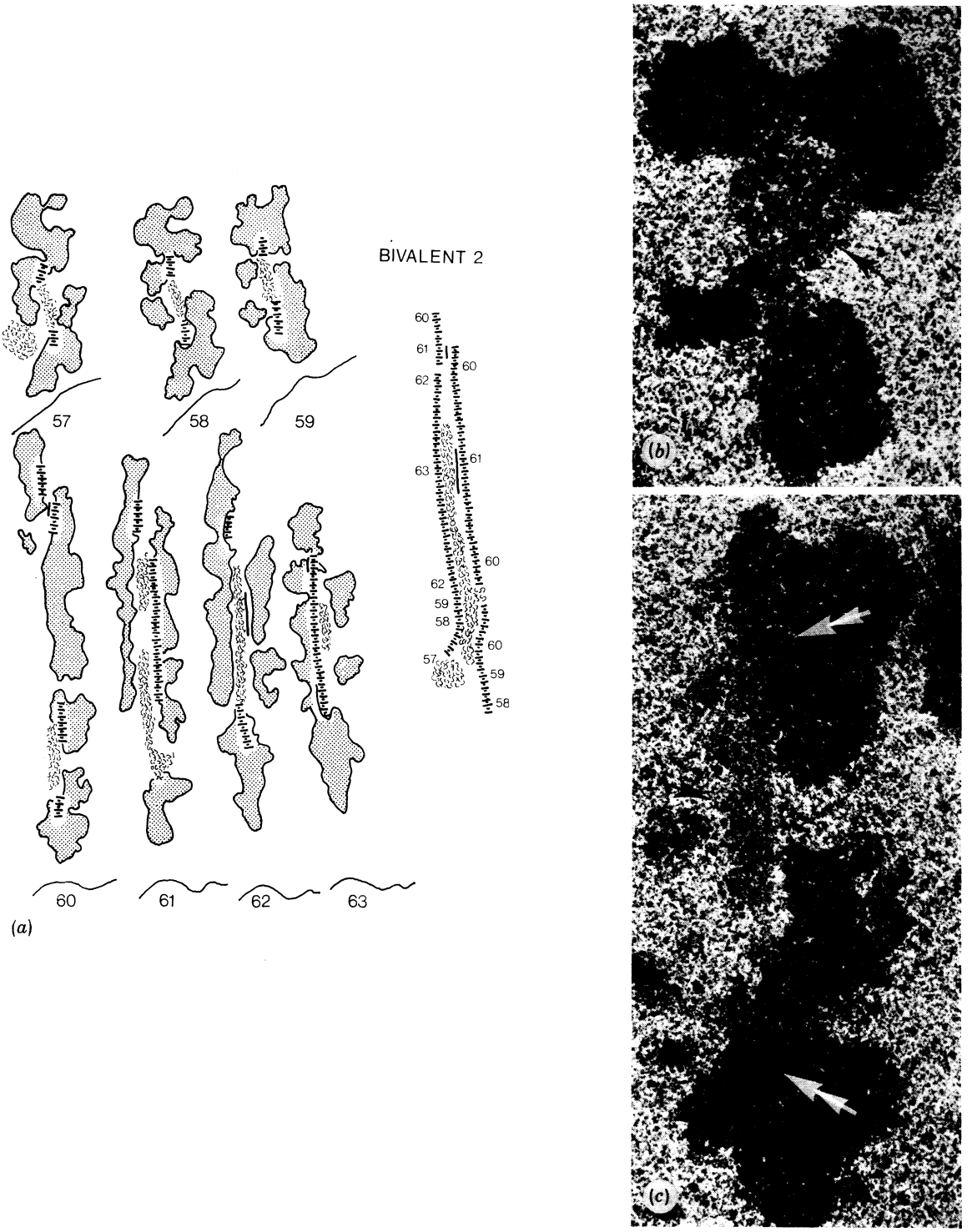

FIGURE 3. (*a*) Portion of bivalent 2 reconstructed from the tracings in sections 57–63. It illustrates the presence of the amorphous form of the central region between the lateral components at synapsis. (*b*) Cross section of bivalent at synapsis with amorphous central region (arrow) between homologous chromosomes. (*c*) Bivalent 2 in section 60 with amorphous central region marked by single headed arrow and the lateral component of one homologue with double headed arrows. (Magn. × 60 000.)

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The non-specific ribonucleoprotein blocks of central region material arrive from the nucleolus. When a given segment of the lateral component associates with the surface of such a block, its opposite surface is patterned by conformational change into a structure fitting only to the segment's counterpart in the homologue.

Direct evidence supporting this view of synaptinemal complex assembly was obtained from the three-dimensional reconstruction of a late zygotene nucleus. Figure 2*a* (plate 1) consists of a reconstruction drawing of the cut-open nucleus in the region of the nucleolus. At left is a portion of a bivalent with the completed synaptinemal complex, at right the perforated nuclear envelope. The nucleolus contains the centrally located fibrillar component surrounded by the granular component, which on one side is folded and pervaded by nucleoplasm. In the folds are found single or double layers of organized central regions and amorphous material. On the one side, the amorphous material is continuous with the organized central regions and on the other it extends freely into the nucleoplasm outside the nucleolus. It will be shown below that amorphous material of identical structure occurs in the space between the synapsing chromosomes of this nucleus. The amorphous material is therefore interpreted as the transport form of the central regions, when these move from the folds in the granular component of the nucleolus through the nucleoplasm to the assembly site of the synaptinemal complex. In figure 2*b* is depicted a portion of section 59 containing a piece of organized central region (arrow) in direct contact with the amorphous transport form. An illustration of the opening of a fold containing the amorphous central region into the nucleoplasm outside the nucleolus is found in the adjacent section 58 (figure 2*c*), whereas a portion of the amorphous central region located freely in the nucleoplasm is depicted from section 50 (figure 2*d*).

The presence of amorphous central regions between the lateral components of synapsing homologous chromosomes is evident from figure 3 (plate 2). In *a* tracings of bivalent 2 in the sections 57–63 are reproduced indicating the chromatin, the lateral components, the amorphous material and the few places, where a central component has been organized. At right the reconstruction of this portion of bivalent 2 is drawn, revealing the amorphous material between the two lateral components. The micrograph in figure 3*b* depicts a cross section of a different bivalent. The space between the two pairing homologous chromosomes is spanned by amorphous central region material. Figure 3*c* is the micrograph corresponding to the lower portion of the tracing of bivalent 2 in section 60. The amorphous material is in direct contact with the lateral component.

The final stages in the assembly of the synaptinemal complex are revealed by the reconstruction of bivalent 22 (figure 4, plate 3). The right-hand portion of the bivalent is found in sections 76–95 and has a completed synaptinemal complex which is attached to the nuclear envelope in sections 90–95 (figure 4*a*). At the other end of the bivalent the homologous chromosomes are approximately aligned, the lateral components being 300–400 nm apart and attached to the nuclear envelope in sections 73–75. The central regions are present at many places in organized form, i.e. consisting of the electron scattering central component of standard dimension embedded in a little electron scattering structure 100 nm wide. However, the organized central regions are attached to a lateral component on one side only. In the portion of the bivalent closest to the telomere in section 73 (figure 4*a*) the organized central regions are attached to the right lateral component, whereas in the adjacent portion of the bivalent the organized central regions are attached to the left lateral component, i.e. that of the homologous chromosome. In figure 4*b* are the tracings of the chromatin, the lateral components, and the organized central

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regions for the relevant portion of the bivalent covering sections 64–70. It is noteworthy that the organized central regions are attached to stretches of banded lateral components located lateral to the chromatin, whereas the unattached homologous stretches of lateral components are embedded in chromatin, i.e. located between the two sister chromatids. The micrographs in figures 4*c* and 4*d* correspond to the tracings of section 65 and section 66. In the former an

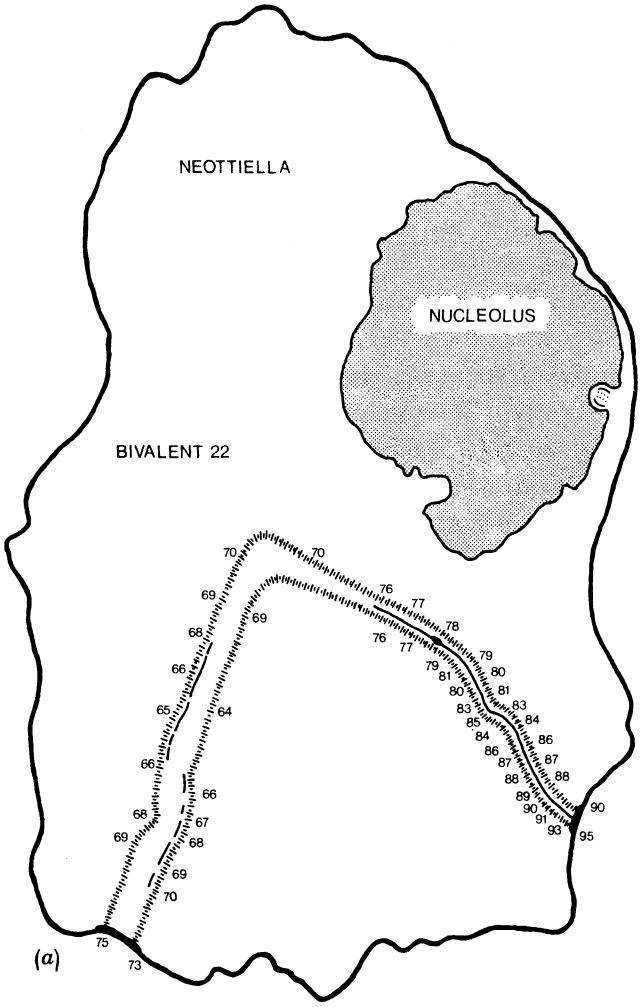

FIGURE 4. (*a*) Reconstruction of bivalent 22 at synapsis. The right-hand portion of the bivalent (sections 76–95) has a completed synaptinemal complex. In the left-hand portion, which is in the process of synapsis, central regions with the central component are attached to the lateral component of one homologue only. (*b*) Tracings of chromatin, lateral components and central regions in sections 64–70. (*c*) and (*d*) Sections 65 and 66 with lateral components (L) and central components (C) marked. (Magn. × 60000.)

organized central region is attached to the left lateral component, whereas that of the homologue is located between the sister chromatids. In the lower part of section 66, the situation is the reverse, the organized central region is there attached to the right lateral component. The last step in the completion of the synaptinemal complex is the association of the free surface of the organized central region with the corresponding segment of the homologous lateral component.

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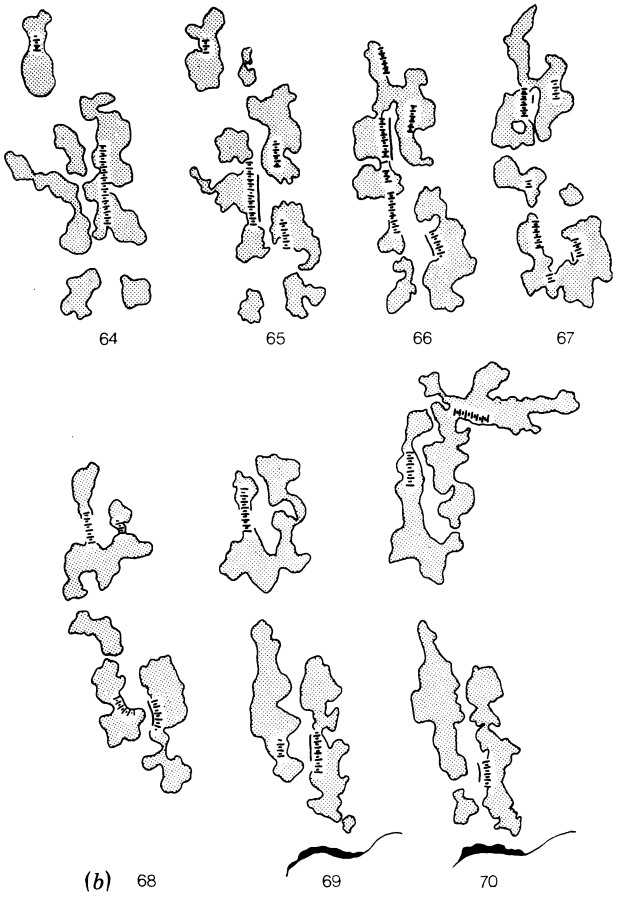

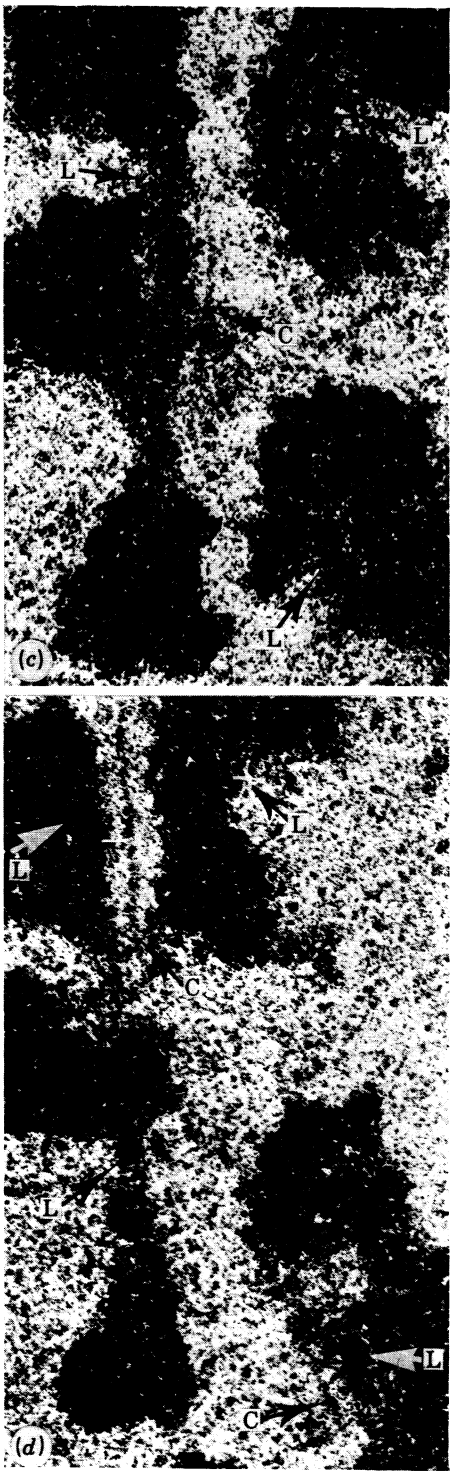

FIGURE 4(*b*)–(*d*). For description see opposite.

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The presented ultrastructural results in *Neottiella* strongly support the previous notions that the central regions are preassembled in the nucleolus, transported to the site of synapsis in amorphous form and there reorganized by attachment to one lateral component. The subsequent association with the other lateral component is consistent with a specific site to site recognition between the lateral components of homologous chromosomes. The mode of assembly of the synaptinemal complex in *Neottiella* can easily accommodate the postulated trapping of preselected pairs of homologous DNA stretches in its central region.

Chiasma formation

At pachytene the two homologous chromosomes in a bivalent are paired throughout their length by a continuous synaptinemal complex, spanning from one telomere to another on the nuclear envelope (stage 9 in figure 1). When pairing of the homologous chromosomes is replaced by their repulsion, the synaptinemal complex is shed from the bivalents, except at places where the homologous chromosomes are held together by chiasmata (figure 1, stage 10) (Westergaard & von Wettstein 1968, 1970*b*). These consist of short retained regions of the synaptinemal complexes with an altered fine structure. The synaptinemal complex bridge is subsequently replaced by a chromatin bridge. The shed synaptinemal complexes which are eliminated via the nucleoplasm have an amorphous structure not unlike the transport form of the central regions as they leave the nucleolus at zygotene. A three-dimensional reconstruction of a diplotene nucleus has not yet been made in *Neottiella*. A quantitative determination of the number of synaptinemal complex remnants at early diplotene in maize by Gillies (1975*b*) gave an average of 5.6 per bivalent. Darlington (1934) found for maize 3.65–1.95 chiasmata per bivalent in light microscopic analyses of late diplotene stages a figure in agreement with the genetic estimate for crossing over frequencies. This comparison reveals the number of synaptinemal complex remnants at early diplotene to be of the same order of magnitude as the number of chiasmata observed at late diplotene. The surplus of synaptinemal complex remnants may represent latent chiasma sites which are eliminated or – as suggested by Sotelo, Garcia & Wettstein (1973) – simply points of delayed shedding of the synaptinemal complexes.

A major portion of this work was done at the Institute of Genetics, University of Copenhagen. I am indebted to Ms Ulla Edén for the serial sectioning and taking the electron micrographs. For expert assistance I wish to thank Mss Bibi Andersen, Ann-Sofi Steinholtz and Nina Rasmussen. Financial support by grant GM-22051 of the National Institutes of Health, U.S. Public Health Service, is gratefully acknowledged.

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Discussion

MARJORIE P. MAGUIRE (*Zoology Department, University of Texas, Austin, Texas* 78712, *U.S.A.*). In Gillies' publication (*Chromosoma* **43**, 145–176 (1973)) it appears that the K10-bearing parent (of maize plants which were heterozygous for the inversion and for K10) was from a stock known to have longer chromosomes at pachytene than the KYS stock of the inversion-bearing parent. Since those plants which were heterozygous for the inversion and did not carry K10 were of pure KYS background, the greater length at pachytene in those inversion heterozygotes which also carried K10 should not be attributed directly to the presence of K10 without further observations, since genetic background for chromosome length differed in the two cases. The conclusion that greater crossover frequency in the presence of K10 can be attributed to greater pachytene chromosome length does not seem justified at this time.

D. VON WETTSTEIN. The seeds for the maize plants studied by Dr Gillies were provided by Dr M. M. Rhoades, who informs me that it is not known if KYS stocks have shorter pachytene bivalents than other stocks. The seeds were from the same material, which Rhoades & Dempsey used for analyses of crossing over frequencies and pairing at the light microscopic level. They could establish in sib plants that the presence of K10 leads to more intimate pairing at the light microscopic level (as confirmed by Gillies at the electron microscopical level) and to increased crossing over frequencies in the chromosome regions studied. An influence of the KYS background was not noticeable. The number of reconstructions of the nuclei at the electron microscopical level are of course limited, but I think the measurements strongly hint that greater crossing over frequency in the presence of K10 is related to greater pachytene bivalent length. We are continuing to determine synaptinemal complex length for meiocytes known to differ in crossing over frequencies.

K. JONES (*Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey*). Today it is common to see in major textbooks diagrams of simple facts of mitosis and meiosis erroneously portrayed.

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Some of this is due to an incorrect appreciation of the new discoveries relating the time of DNA synthesis and its implications. It is therefore important that we need to fully appreciate how these new discoveries should be interpreted from the point of view of student education.

I would therefore like to ask whether, in fact, in view of your findings, diagrams of meiosis should show that each parent chromosome is already separated into its sister chromatids at pachytene. It seems to me from what you have said, that although DNA replication has certainly taken place at this time, the sister chromatids have not yet been fully individualized in a way comparable to that seen at mitosis. In fact the sister chromatids, which you have shown in your talk, are still joined to a synaptinemal complex at pachytene upon which they are hinged and which allows them to come back into intimate contact for pairing. This leads me to draw a distinction between DNA replication and the individualization of the chromatids, and I think one would, therefore, prefer to see pachytene diagrams showing the pairing of single, rather than double, strands. I would appreciate your comments on this.

D. von Wettstein. As shown in figure 1, I consider that the sister chromatids during meiotic prophase are as individualized as during mitotic prophase. I tried to point out that the presence of the lateral component between the sister chromatids at leptotene and the arrangement of sister chromatids with respect to the synaptinemal complex at pachytene make the chromosome appear as a single strand. Since a diagram of meiosis should incorporate the information that crossing over occurs at the four strand stage, the leptotene, zygotene and pachytene chromosome is best portrayed to consist of two sister chromatids.

K. R. Lewis, (*University of Oxford*). I would like to ask Professor Wettstein a peripheral question regarding the nuclear membrane.

We tend to talk rather glibly of nuclear fusion yet a genuine fusion of nuclei rarely, if ever, occurs in higher plants and animals. What seems to happen at fertilization is that the still separate male and female nuclei proceed through a synchronized prophase and, following nuclear membrane break-down, both chromosome sets congregate on a common spindle – that of the first cleavage division. In other words, at no stage of the sexual cycle is there a single diploid nucleus surrounded by a membrane; rather two haploid nuclei, by mitosis on a common, or fused spindle, produce two diploid nuclei.

In haplontic organisms, of course, a true fusion is obligatory because fertilization is followed by meiosis. It must occur also in heterokaryons when somatic recombination is involved. Can Professor Wettstein tell us something of the fusion process which, though often assumed, has, so far as I am aware, never been described in diplontic or haplodiplontic organisms?

D. von Wettstein. In ascomycetes the nuclear envelope is retained without breakdown throughout mitosis and meiosis. In the outgrowing ascus the fusion of the nuclear envelopes of the two prefusion nuclei has been observed by electron microscopy. After fusion of protoplasts from pea leaf and *Vicia* cell cultures fusion of interphase nuclei have been documented by electron microscopy. Nuclear fusion during mitosis has, however, also been observed in this material. (Gamborg, personal communication.)

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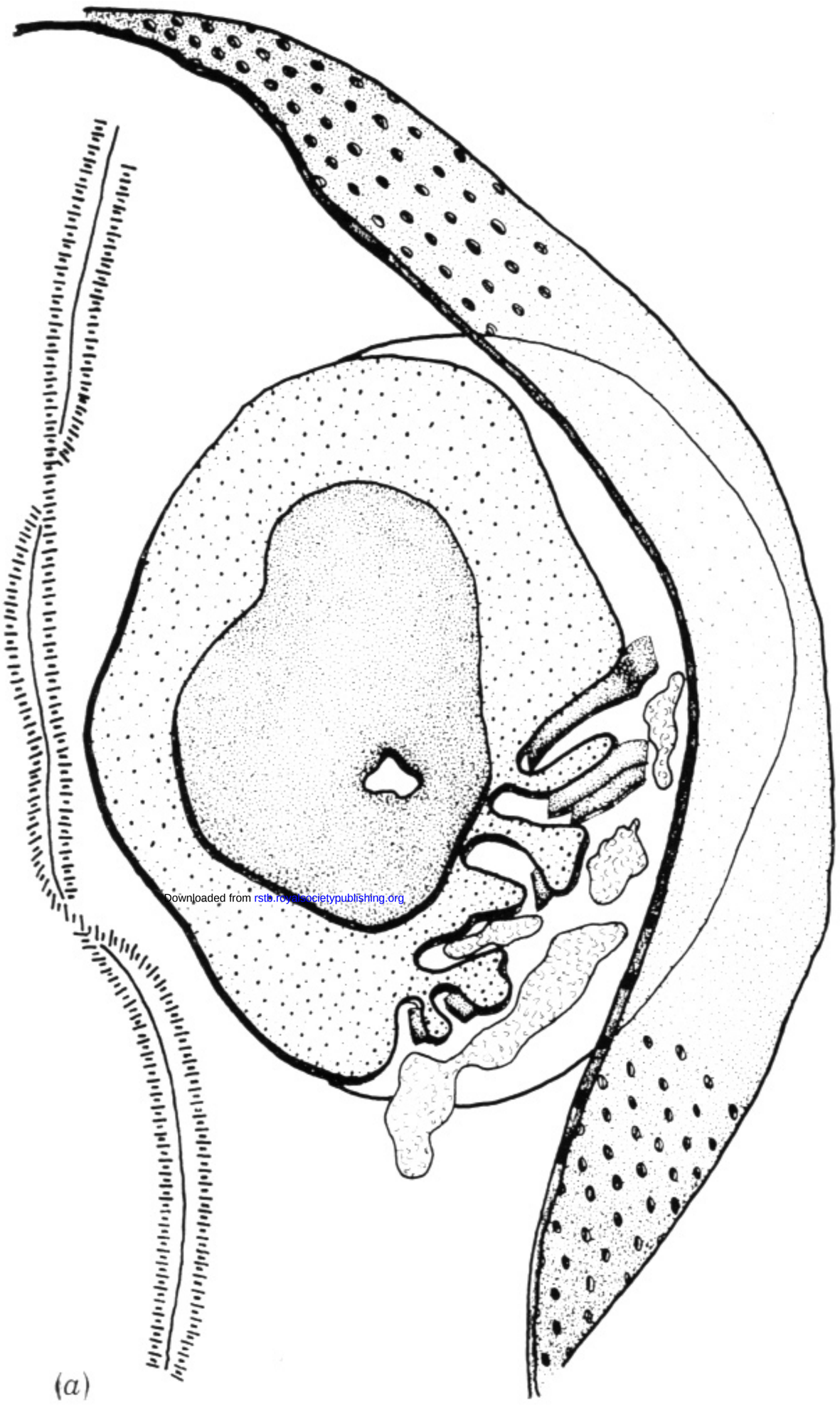

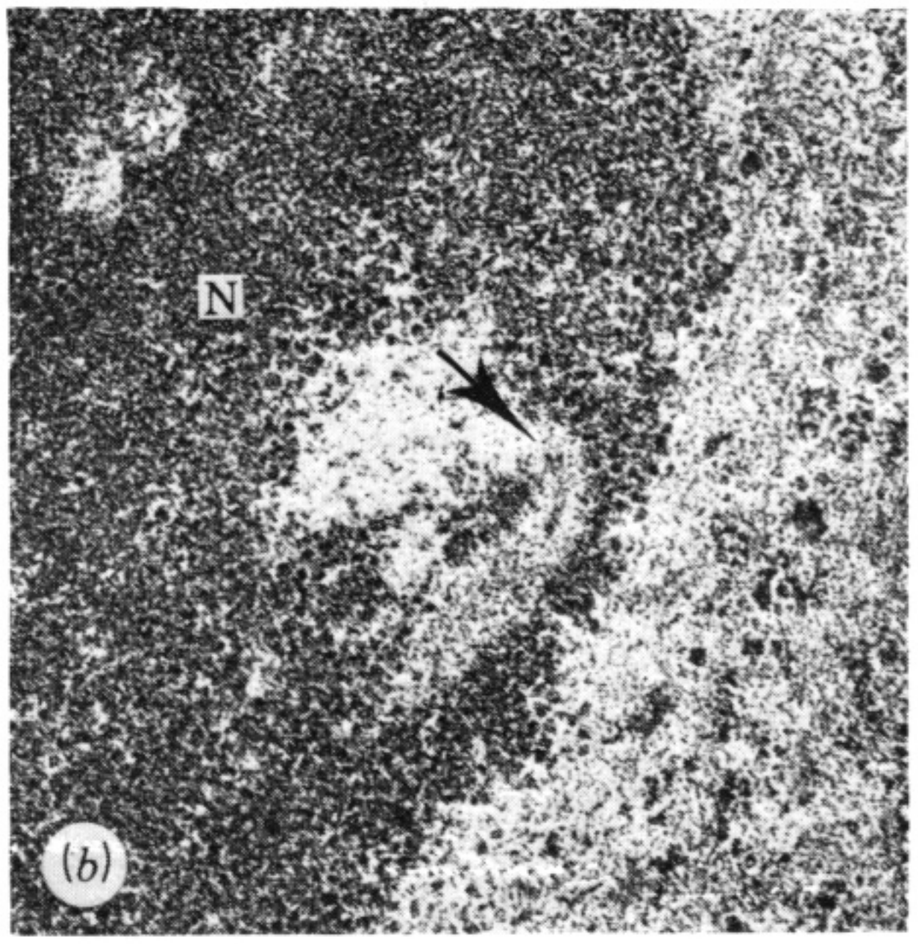

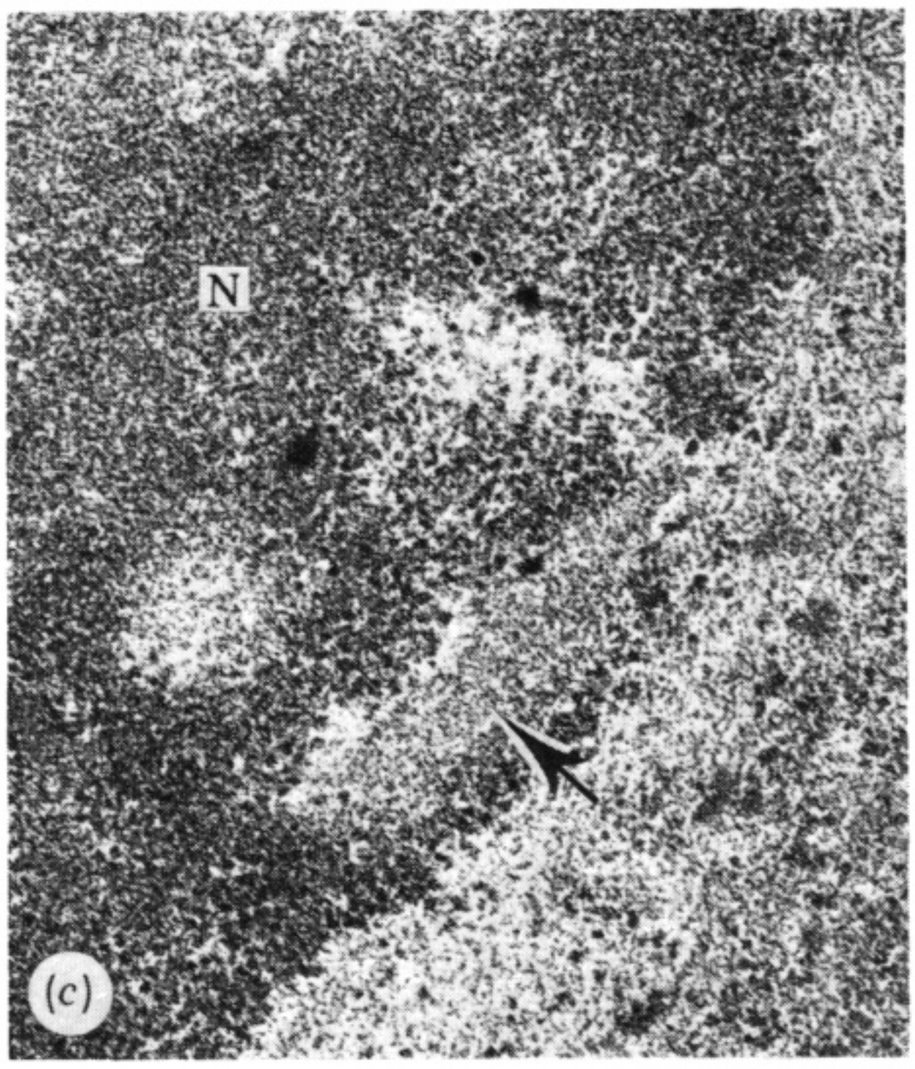

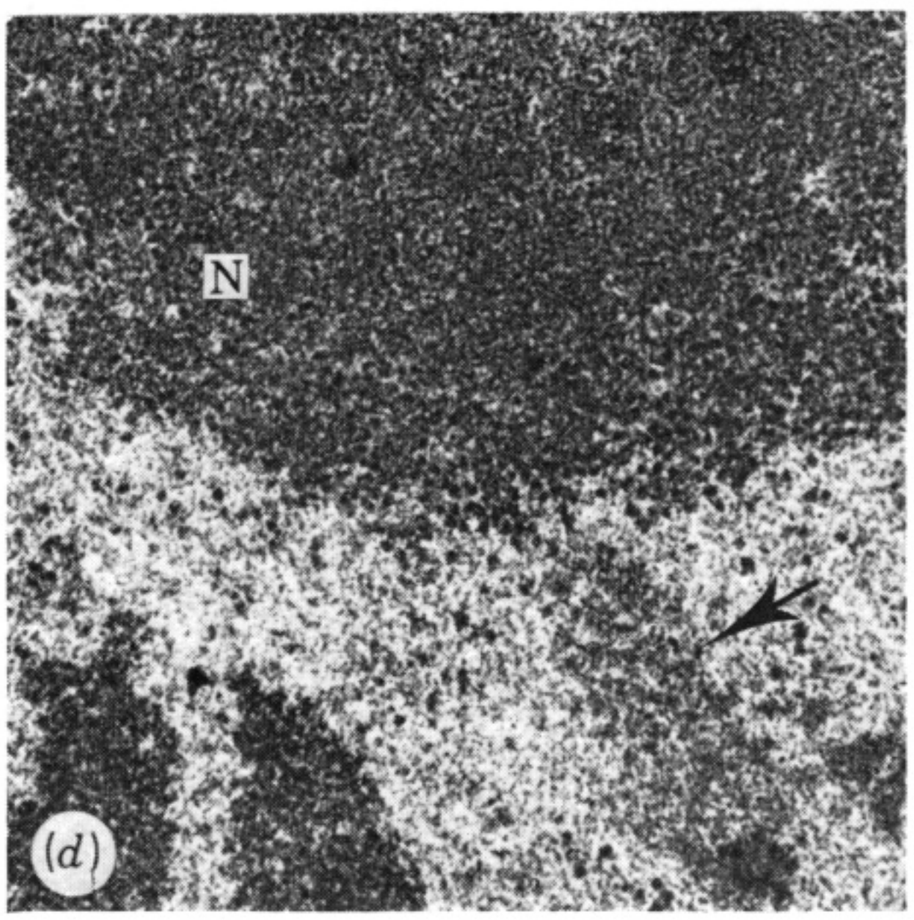

FIGURE 2. Three-dimensional reconstruction of nucleolus in late zygotene nucleus of *Neottiella*. (*a*) Sheets of central regions of the synaptinemal complex in the granular component of the nucleolus. These sheets are converted into an amorphous form, which is found extending into the nucleoplasm. (*b*) Section 59 of the series with organized central region (arrow). (*c*) Section 58 with amorphous central region (arrow). (*d*) In section 50 the amorphous material extends into the nucleoplasm (arrow). (Magn. × 40000.)

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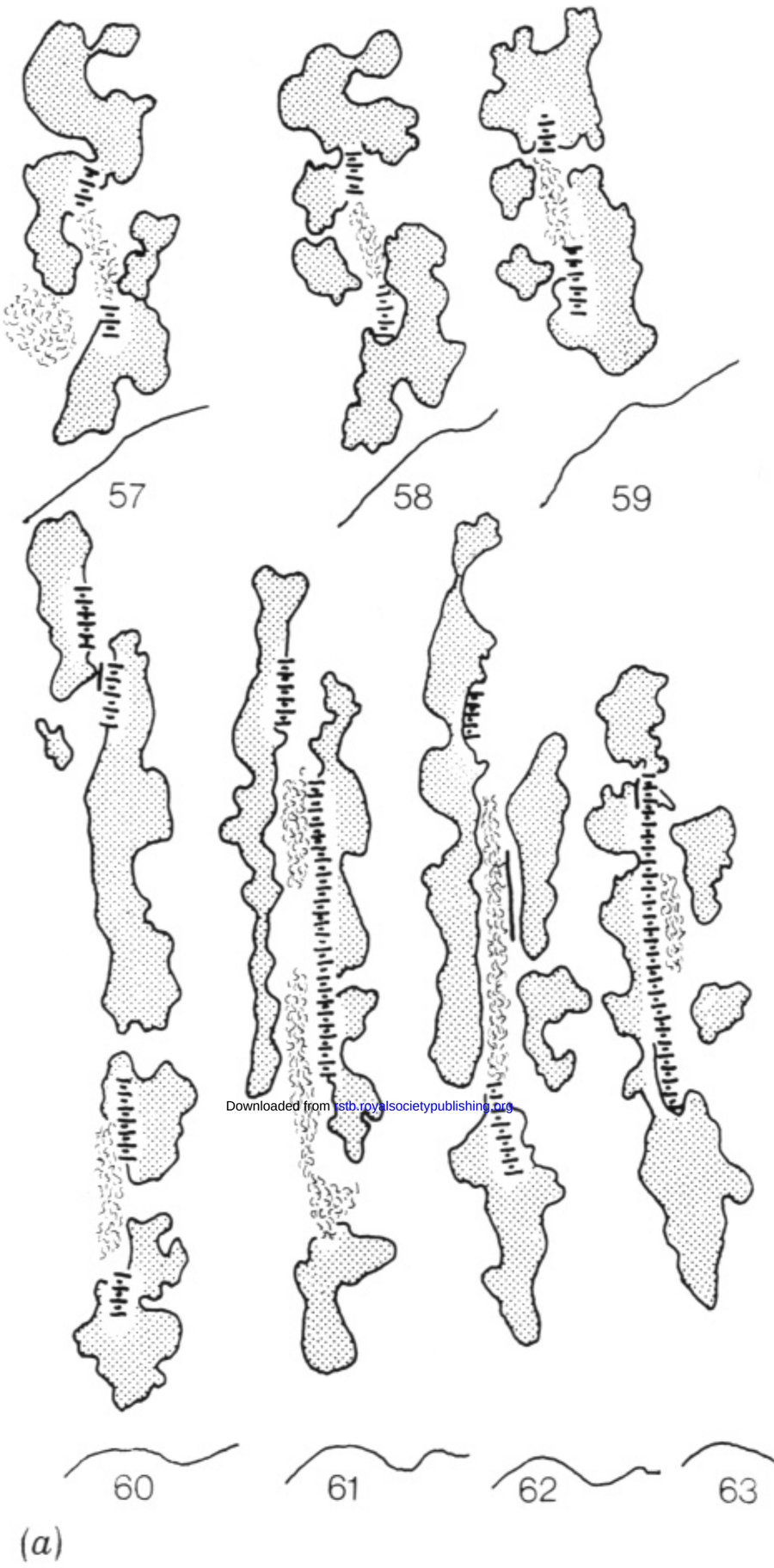

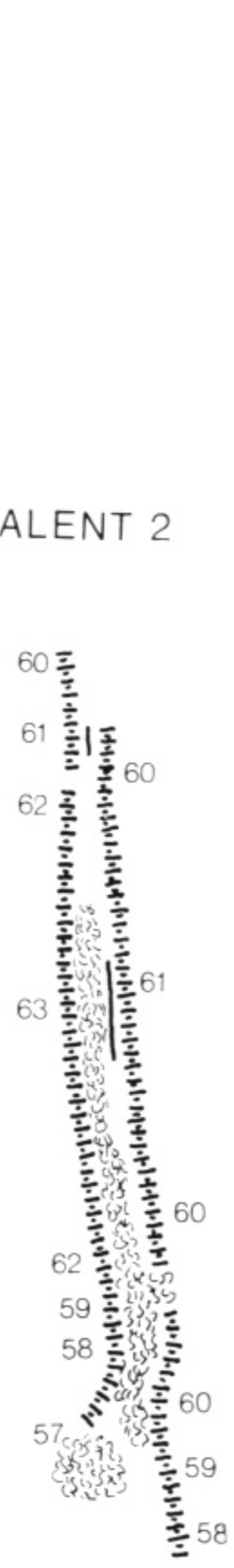

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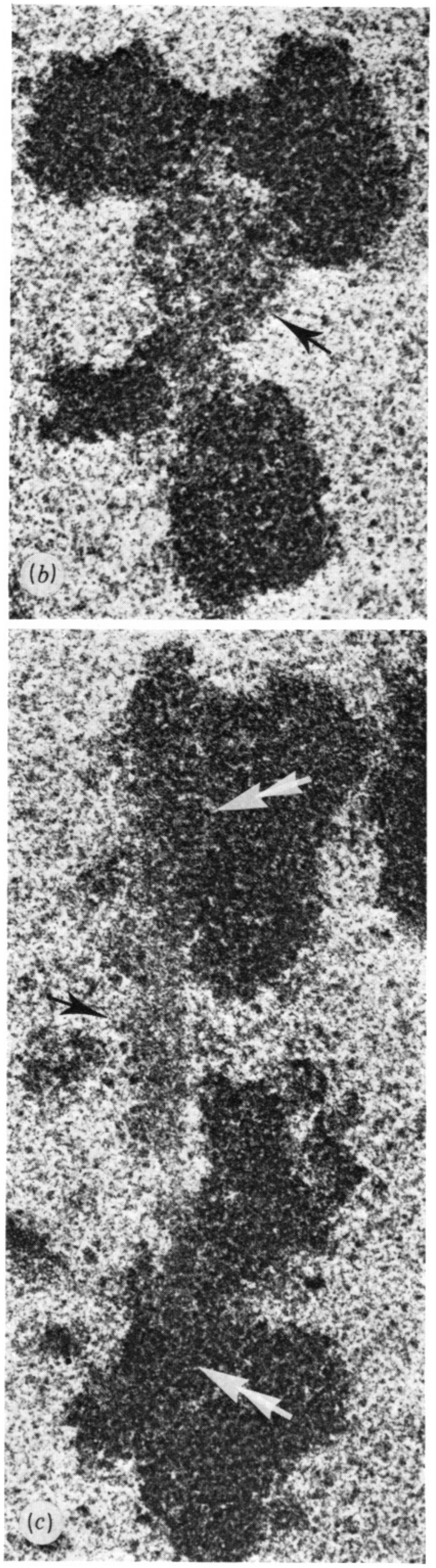

FIGURE 3. (*a*) Portion of bivalent 2 reconstructed from the tracings in sections 57–63. It illustrates the presence of the amorphous form of the central region between the lateral components at synapsis. (*b*) Cross section of bivalent at synapsis with amorphous central region (arrow) between homologous chromosomes. (*c*) Bivalent 2 in section 60 with amorphous central region marked by single headed arrow and the lateral component of one homologue with double headed arrows. (Magn. × 60000.)

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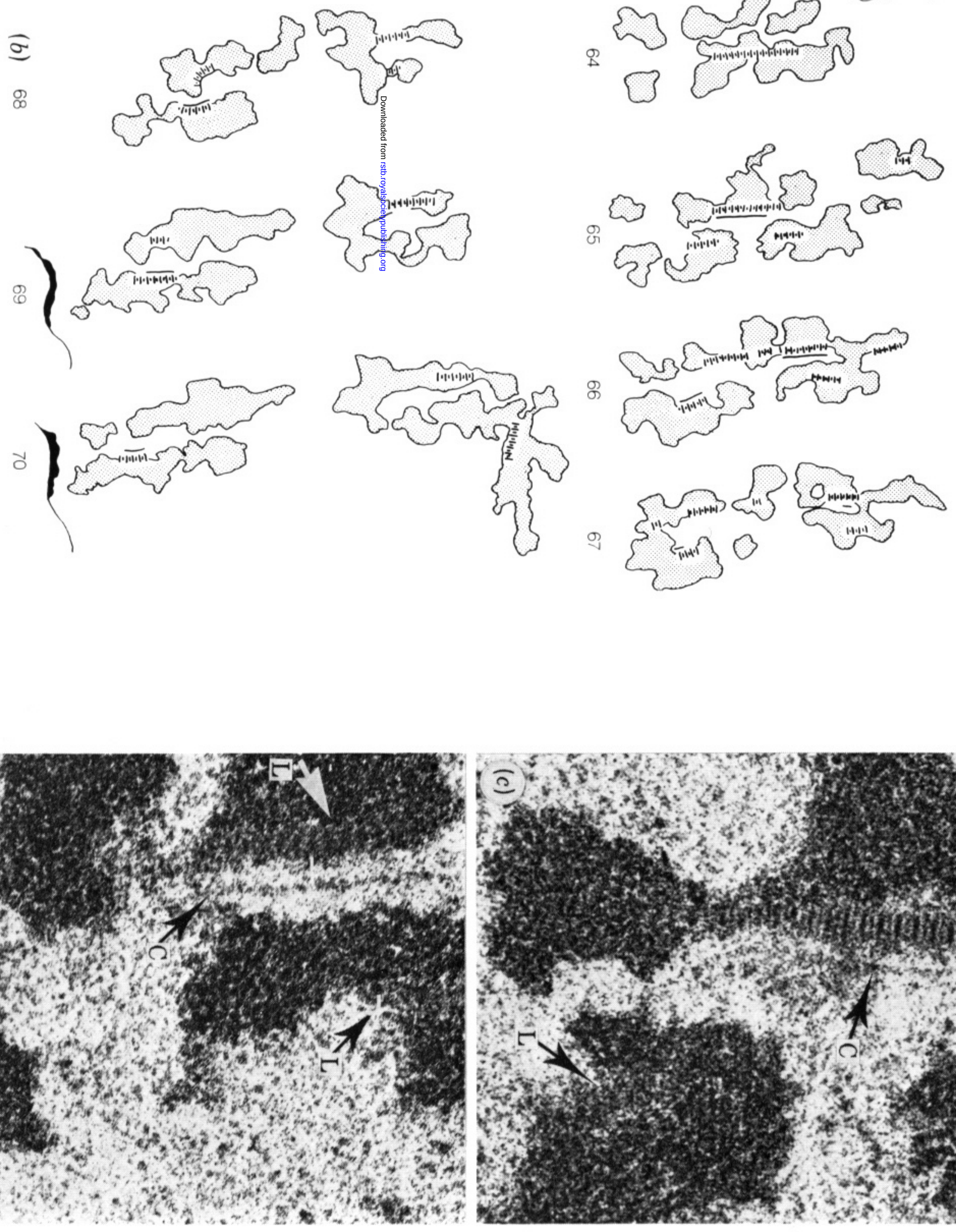

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FIGURE 4 (*b*)–(*d*). For description see opposite.