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The Spatial Relationship of the X and Y Chromosomes during Meiotic Prophase in Mouse Spermatocytes

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Abstract. The ultrastructure of whole X-Y pairs has been reconstructed by serial sectioning and model building. Seven X-Y pairs were completely reconstructed and the lengths of the cores of the sex chromosomes were measured. These X-Y pairs corresponded to zygonema, early, middle and late pachynema. Special regions of the X-Y pair were reconstructed from thinner sections. — It has been shown that two cores exist in the sex pair during the cited stages, and that their lengths and morphology are rather constant in specific stages. The long core averages 8.9 μ in length and the short core is 3.5 μ long. Both cores have a common end region in which a synaptonemal complex is formed from zygonema up to mid-pachynema. This synaptonemal complex shortens progressively up to mid-pachynema and at late pachynema becomes obliterated. Each core has a free end touching the nuclear membrane. During mid-pachynema an anomalous synaptonemal complex is developed on most of the length of the long core. This complex is asymmetric and disappears at late pachynema. The meaning of the cores and the complexes are discussed, and the existence of a homologous region in the X-Y pair of the mouse is interpreted to be proved.

Introduction

Moses (1958) described a tripartite structure that develops simultaneously with the synapsis of homologues during meiotic prophase. The general occurrence of this structure, the synaptonemal complex, during synaptic stages in many organisms has been reviewed by Moses (1964) and its possible involvement in crossing-over was supported by Meyer's (1964) observations. However, the presence of identical structures in single chromosomes (Sotelo and Wettstein, 1964; Moses, 1968) and the occurrence of polycomplexes (Roth, 1966; Moses, 1968) outside the synapsed chromosomes, shows that the synaptonemal complex cannot be simply equated to a specific structure of synaptic chromosomes.

The study of a single, identified chromosomal pair during its whole meiotic evolution may show some interesting data on the function of the synaptonemal complex. Thus, the length and duration of this structure could be measured, as well as its changes, and they could be correlated with the light microscopical observations on the same chromosomal pair and with genetical data.

The X-Y pair of the mouse has been previously studied in this laboratory (Solari, 1964; Solari and Tres, 1967a; Solari, 1969a, 1969b; Reader and Solari, 1969) and thus this pair has been chosen for a three-dimensional reconstruction at several stages of meiotic prophase. The aim of this paper is to present the results of the three-dimensional reconstruction of the X-Y pair at zygonema and pachynema and to discuss the significance of these results in relation to synapsis in the sex pair.

Material and Methods

Albino mice, random bred, were supplied from different sources. Two stocks from our laboratories were mainly used in these observations. Squashed spermatocytes did not show any alteration of the normal X-Y pair.

Electron Microscopy. Small pieces of testes were fixed in 2.5% glutaraldehyde in 0.1 M phosphate buffer, pH 6.9, for two hours, washed in buffer and postfixed in Caulfield's fixative for one hour. The pieces were embedded in maraglas. Sections were cut at different thicknesses, mainly three ones: thin (silver coloured), nominally 500—750 Å thick; intermediate (nominally 1,000 Å thick) and thick (nominally 0.47 μ thick). Serial sections were made with each of the three thicknesses, but the complete reconstructions of the sex pair here presented were done exclusively with thick (0.47 μ thick) sections. These thick sections present several advantages over the thinner ones: smaller number of sections needed, completeness of the cores in single sections and smaller number of measurements needed to determine their length. Thick sections, however, do not show sharp images as the thinner ones, and they need to be examined with higher acceleration voltages (100 or 80 kV in the Siemens Elmiskop). Thus, the complete reconstruction of 7 sex pairs was done with thick sections, and the reconstruction of special parts of the sex pair, like the common end, were done with thin sections to achieve a sufficient resolution at these special points. The observations made with the thinner sections agreed completely with those made with the thicker sections and they gave some additional details.

Serial sections were picked in single-hole grids (LKB Produkter) 1×2 mm in diameter according to Sjöstrand's (1967) method. The sections were stained with uranyl acetate (saturated solution in methanol) and then with Reynolds' lead citrate stain. Micrographs were taken at the same magnification step in each series, and then a diffraction grid (28,800 lines per inch) was photographed to calibrate the magnification.

Model Construction. Each micrograph from a complete series showing the whole sex pair was copied with china ink on a celluloid sheet (0.6 mm thick). Once a set of plastic copies is obtained (only the outlines of the sex pair, the cores and the nuclear and cytoplasmic membranes are copied generally) they are sequentially ordered like the negatives, and the points of coincidence between adjacent sheets are looked for. Generally the nuclear and cytoplasmic membranes, large vacuoles and nucleoli are the most useful markers. After coincidence is obtained with at least three markers, each pair of sheets is bound together with plastic tape and with a sandwiched number of slide pieces to serve as a spacer in the same scale as the micrographs. The process is repeated with the following sheets. Once a complete model is assembled, guiding holes are drilled in the edges of the whole model (three guiding holes are sufficient) to permit a rapid assembly of the model. Then the model is disassembled and the lengths fo the cores are measured in each sheet.

Measurement of the Cores. Lengths of each section of a core in each sheet are measured with a flexible copper wire (or with a map measurer). When the core is split into two filaments, one of them was chosen for the measurements. The measured lengths actually correspond to the projection of the core on the plane of the photographic plate. Each measured length is then a projection P_i where i is the ordinal number of the section. The nominal section thickness is constant in all the sections, $t = 0.47\ \mu$, and when it is multiplied by the scale factor gives T, thickness in scale. Then the following formula is used to evaluate the length of one core (L = total length of the core): $L = \sum_{i=1}^{i=n} l_i$ where l_i is the calculated length per one sheet and n is the number of sections; each l_i is calculated with the formula: $l_i = \sqrt{P_i^2 + T^2}$ when the core goes across the sheet; if both ends of the core leave the sheet by the same face, this special sheet (a marginal one for this core) is calculated with the formula: $l_i = 2\sqrt{\left(\frac{P_i}{2}\right)^2 + T^2}$. The error inherent in this method of length calculation is a systematic error that will be the same for measurements in different cells thus permitting comparisons of measurements during different stages.

Time Labelling of the Meiotic Stages. An adequate knowledge of the meiotic stage is needed for the analysis of the changing relationships of the XY pair. The time sequence was made as previously described (Solari, 1969a), that is, based on the stage of the spermatogenic cycle in each section as seen with low magnification and correlated with thick sections observed with the light microscope.

Results

1. Reconstruction of the X-Y Pair at Zygonema

Fig. 1 shows the characteristic stage 12 of mouse spermatogenesis with meiotic metaphases and anaphases in the upper spermatocyte layer. The lower spermatocyte layer shows cells in zygonema; the one selected for reconstruction is marked by the arrow. A series of thick (0.47 μ thick) sections of this cell showing the whole path of the cores of the sex pair is shown in Fig. 2a—g. Two cores are found in the sex pair (Fig. 2g). The long and the short cores are paired at one end, forming a rather long synaptonemal complex about 2,000 Å thick (Fig. 2b and c). The central element of this synaptonemal complex is found between the cores in the last half of this pairing region (Fig. 2b) but it may extend along most of this region. The synaptonemal complex thus formed is about 1.9 μ long and it is curved as an arc that lies approximately on a single plane. When both cores separate from each other, the short core has a short path that ends on the nuclear membrane. The long core goes across the central mass of chromatin of the sex pair (which is distinguished by its homogeneous degree of condensation) forming a large loop. The long core is thicker in this loop than where it forms the common end region; and in some parts of the loop it is clearly double, formed by two dense filaments about 300 Å each in thickness

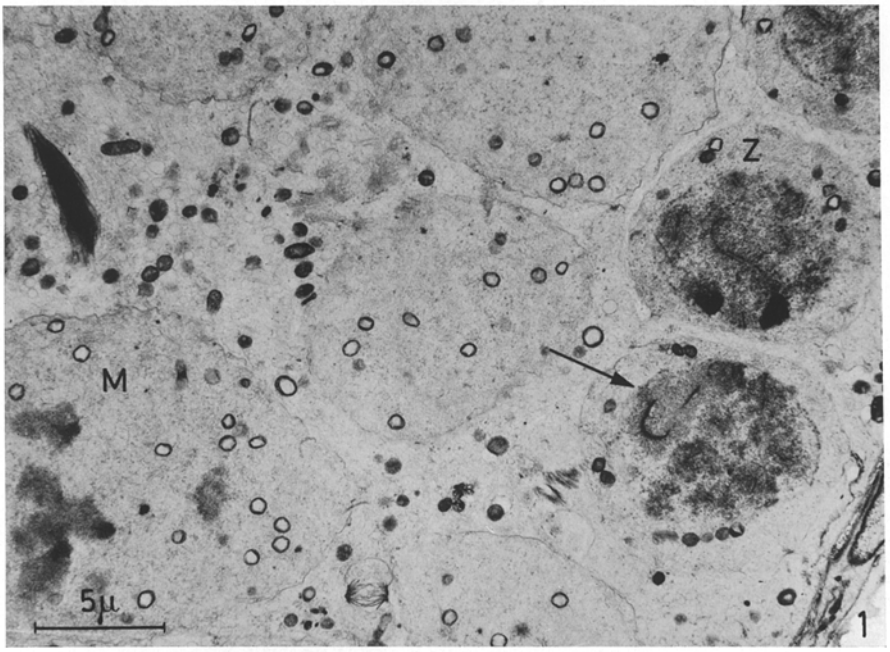

Fig. 1. Low-magnification electron micrograph showing the stage 12 of mouse spermatogenesis, with meiotic divisions (*M*) in the inner layer of spermatocytes; spermatocytes in zygonema (*Z*) are in the outer layer. The sex pair selected for reconstruction (Fig. 2) is marked by the arrow. × 3,400

(Fig. 2f). Then the long core curves towards the nuclear membrane and ends on it, surrounded by a mass of strongly condensed chromatin about 0.7 μ in diameter (Fig. 2a). Thus the general pattern of the two cores (Fig. 5) is already developed in zygonema. The two cores have a common end region forming a synaptonemal complex which is longest at this stage. Three regions can be distinguished in the chromatin of the X-Y pair at zygonema: the chromatin enclosed between the short core and the nuclear membrane, as well as the chromatin that surrounds the free end of the long core, are more packed than the main mass of chromatin (the one that corresponds to the large loop of the long core).

2. Reconstruction at Early Pachynema

In all the four cells reconstructed at early pachynema (stage 2—3 of the spermatogenesis) the pattern of the cores was similar to that of zygonema (see Fig. 3 in Solari, 1969b). However, the synaptonemal complex formed at the common end region is shorter than in zygonema

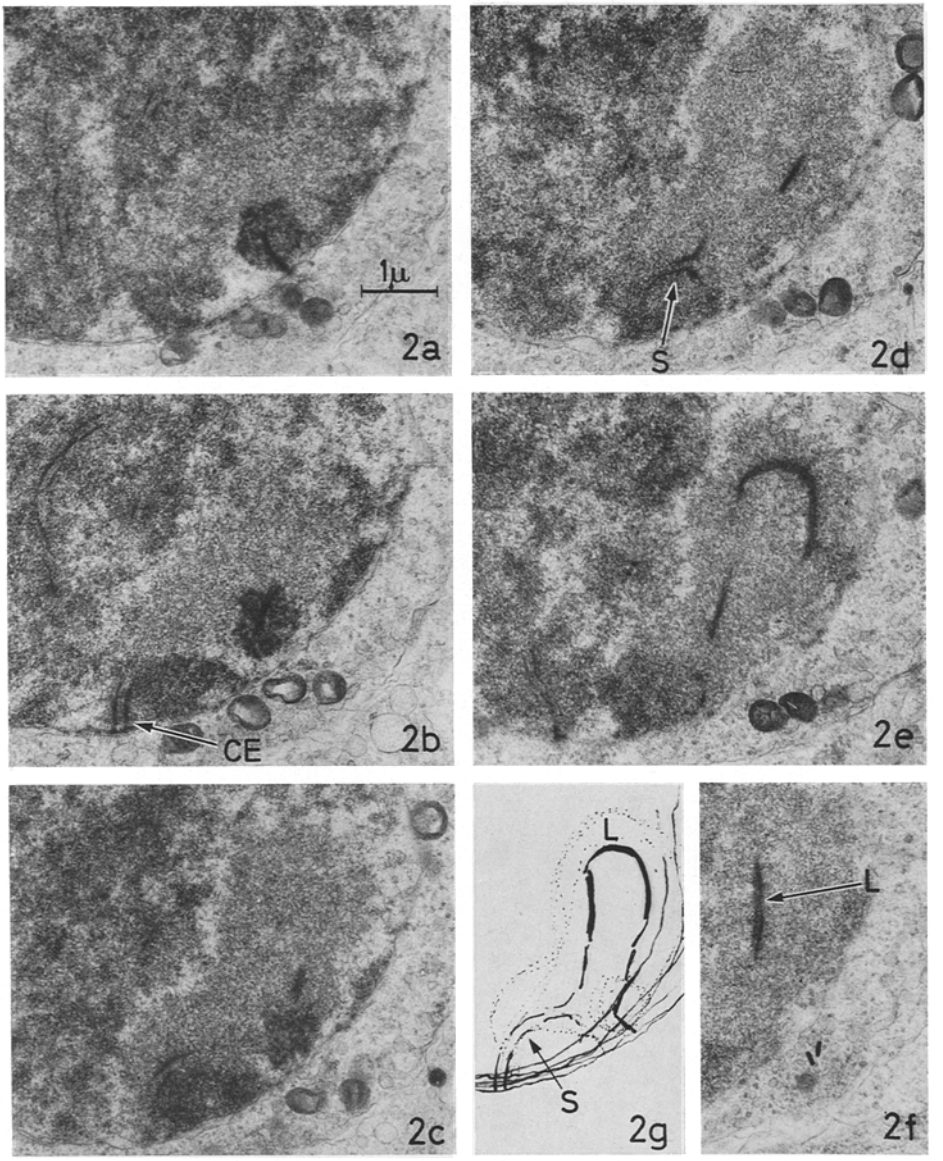

Fig. 2a—g. Serial electron micrographs from thick (0.47 μ) sections showing the whole path of the long (*L*) and the short (*S*) cores of the sex pair at zygonema. *CE* common end region. Fig. g is a photograph of the model. × 9,800

(see the Table, p. 225). The chromatin of the free end of the long core remains denser than the main mass of chromatin, but the chromatin related to the short core is no more distinguishable from the main mass.

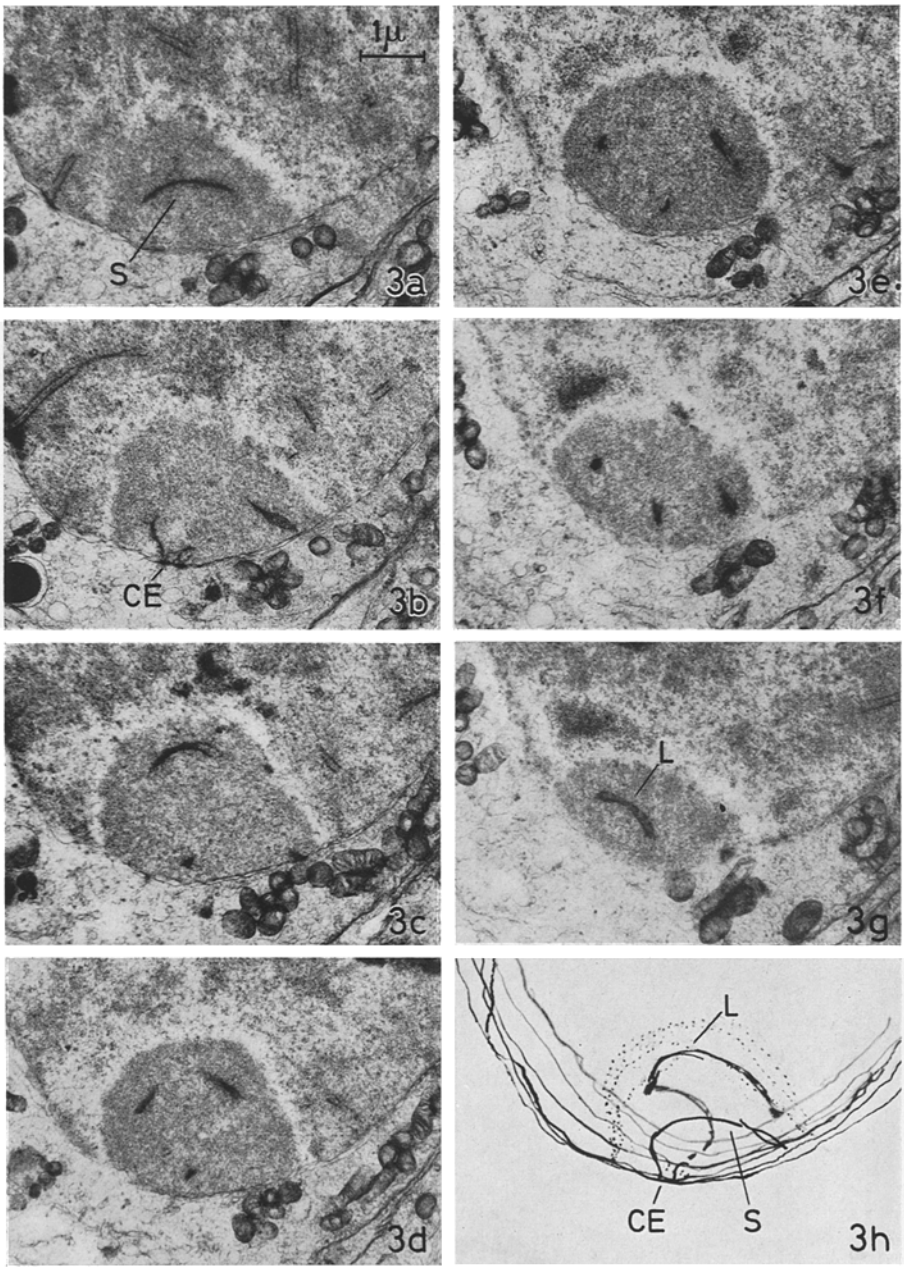

Fig. 3a—h. A series of electron micrographs from thick (0.47 μ) sections showing the whole path of the long (*L*) and the short (*S*) cores of the X-Y pair at the beginning of mid-pachynema. *CE* common end. The long core (*L*) is shown double at many places. Fig. h: photograph of the reconstructed model. × 8,400

3. Reconstruction at Middle Pachynema

A sex pair reconstructed at mid-pachynema (stage 6 of the spermatogenesis) is shown in Fig. 3a—h. The basic pattern of the cores is conserved but some significant changes have occurred. The long core is more convoluted and its two components are clearly separated in most of its length except at the common end (Fig. 3a—f). The distance between these two components equals the distance (about 1,000 Å) that separates the lateral elements of the autosomal synaptonemal complexes. Actually, a central element is visible at some points of the long core in the thick sections. This fact was confirmed with thin sections (Figs. 7 and 8) that showed the existence of an anomalous synaptonemal complex.

The common end is very shortened, but it is clearly distinguishable (Figs. 3b and 6a and b). Its structure is described below. There are no longer special parts of the chromatin mass distinguishable by a special condensation. Thus, during zygonema and early pachynema the regional condensations dissapear. During this stage a mass of dense, 200 Å thick granules begins to cover a part of the inner side of the X-Y pair, always in relation with the chromatin that surrounds the long core.

4. Reconstruction at Late Pachynema

During this stage the pattern of the cores remains the same, but some changes are reversed. Thus, the long core does no longer show the structure of a synaptonemal complex that appeared during mid-pachynema; both filaments composing the long core have now approached each other, and the cross-section of this core has often an oval profile suggesting a coiling between these filaments. The nucleolus is strongly developed around the chromatin that is centered by the long core (Fig. 4a and b). This relationship between the long core and the nucleolus is enhanced by the presence of invaginations of nucleolar material that come near, but do not touch the long core (Fig. 4b).

The common end region exists as a very changed part of the cores (Fig. 4a). It is very short (about 0.3 μ) and the ends of the short and the long cores have fused together in a dense rod (Fig. 4a) where four denser lines are seen (in the thin section shown in Fig. 4a only two lines appear). From this fused common end region both the short and the long core come out straightly and almost orthogonally to each other (Fig. 4a).

5. General Features of the Cores of the X-Y Pair

As seen in all of the reconstructions, there are two cores running inside the chromatin part of the sex pair ("sex vesicle"). These cores never enter the nucleolar part when it is developed during middle and late pachynema. The two cores have constant differences thus permitting

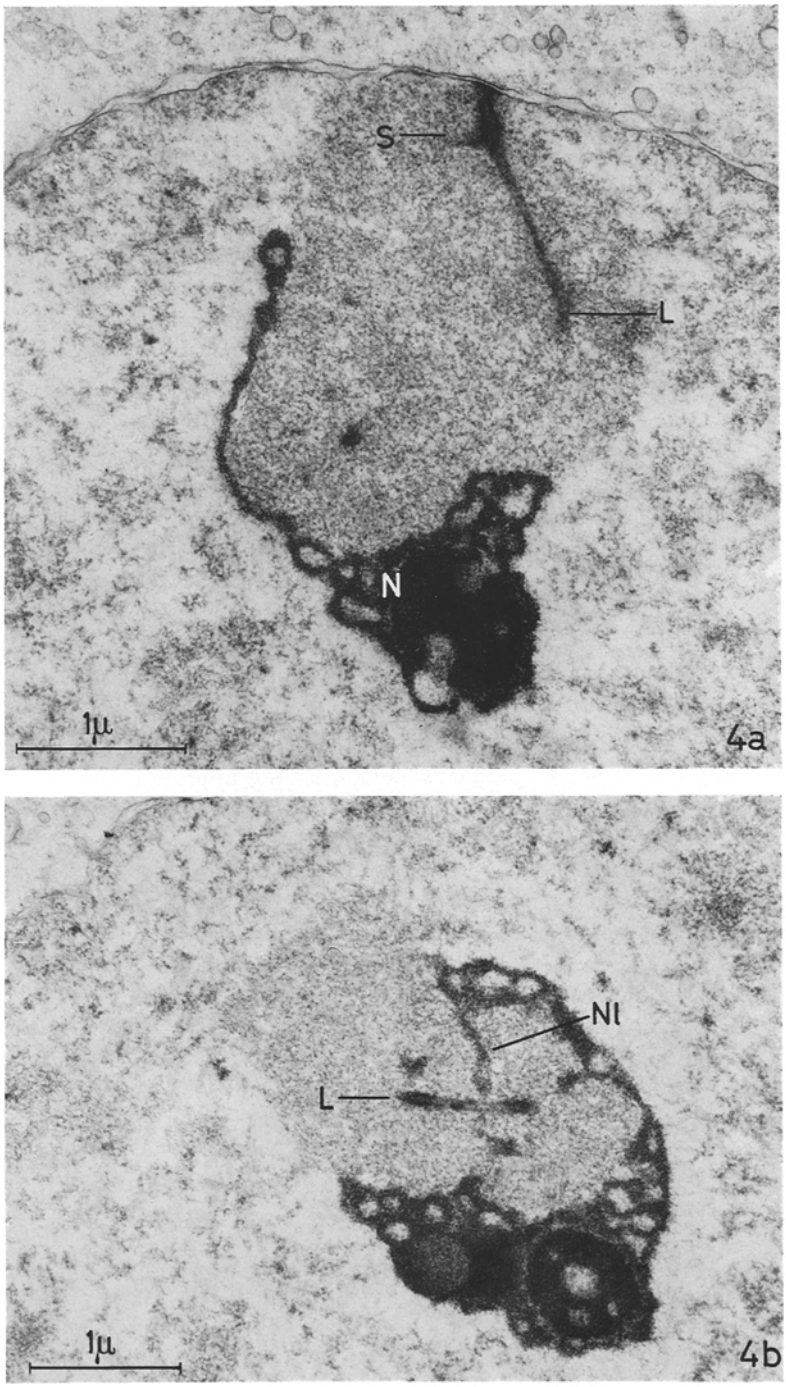

Fig. 4a and b

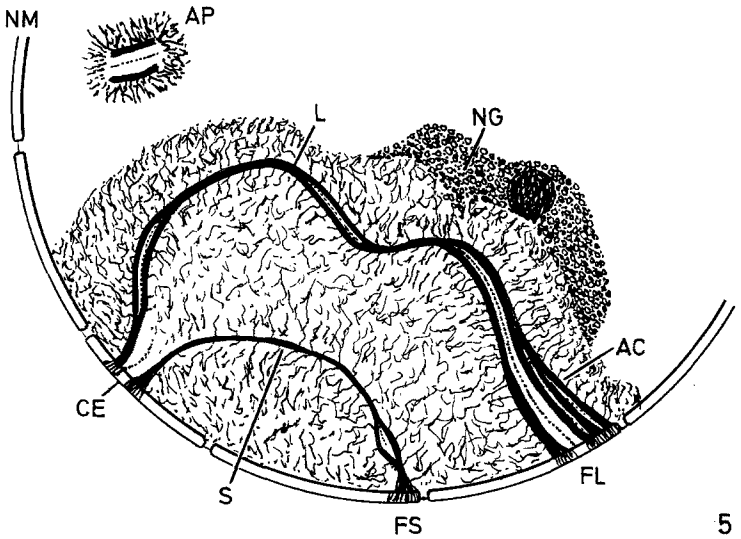

Fig. 5. Schematic drawing showing the X-Y pair during mid-pachynema. *L* and *S* long and short cores respectively. *CE* common end with a short synaptonemal complex. *FS* free end of the short core; *FL* free end of the long core; *AC* anomalous synaptonemal complex developed on the long core; *NG* nucleolar granules, *AP* autosomal pair; *NM* nuclear membrane

their identification. As they differ greatly in length, they are identified as the *long* core and the *short* core (Figs. 5, 2g and 3h). The length ratio of the short versus the long core, 1:2.5, is rather constant during prophase (Table). The absolute lengths of the cores do not show great

Table. *Measurements of the cores of the X-Y pair at several stages*

Model No.	Stage	Long core (μ)	Short core (μ)	Length ratio (long/ short)	Common end length (μ)
1	mid-pachynema	8.3	3.7	2.2	0.2
2	zygonema	8.2	3.4	2.4	0.95
3	early pachynema	8.6	3,1	2,7	0,54
4	early pachynema	9.7	3.6	2.6	0.43
5	early pachynema	9.9	3.9	2.5	0.40
6	late pachynema	8.2	—	—	—
7	zygonema	9.9	3.2	3	1.9
Average		8.9	3.5	2.5	

Fig. 4a and b. Electron micrographs of thin (700 Å thick) sections of the X-Y pair at late pachynema. The nucleolus region (*N*) is completely developed and shows invaginations (*NI*) towards the long core (*L*). In Fig. a the common end region is a short, dense rod ending on the nuclear membrane, from which the short (*S*) core and the long (*L*) core come out straightly. × 22,500; × 20,000

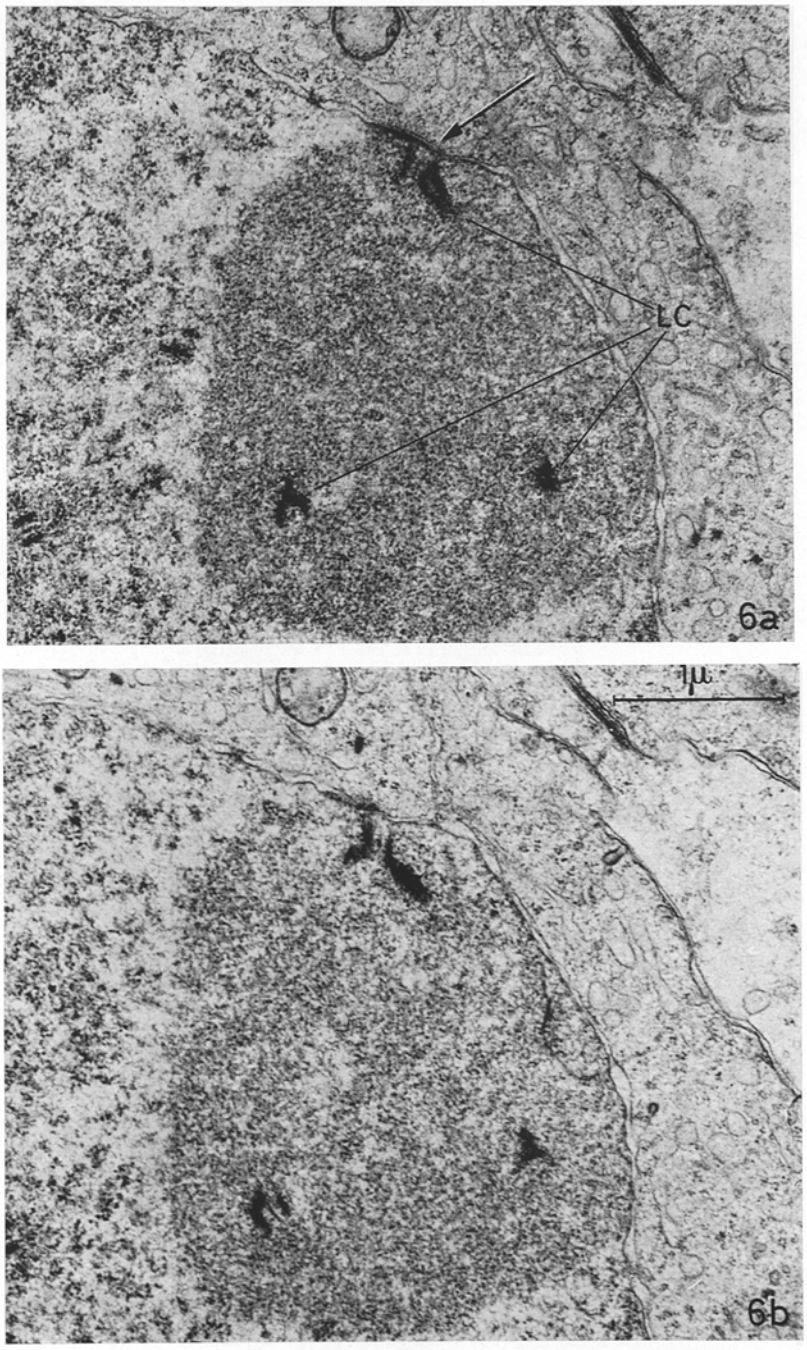

Fig. 6a and b. Electron micrographs of two serial sections showing the common end and its short synaptonemal complex (arrow) at mid-pachynema (section thickness, 1,000 Å). The long core (*LC*) is double from the common end. × 22,500

changes during the examined stages, although the measurements suggest that a little shortening of the long core can occur during these stages. Both cores begin and end on the nuclear membrane, like the autosomal synaptonemal complexes.

There are three ends of the cores: one common end of both cores and one free end from each of them.

6. The Common End

This region of the cores is formed by the approachment and the association of the long and the short cores a little before ending against the nuclear membrane (Figs. 6a, b, and 5). During zygonema, early and middle pachynema this common end region is a synaptonemal complex in which each lateral element is formed by each core. After the common end region both cores separate from each other almost in perpendicular directions. The length and structure of this common end varies during prophase but it is present from zygonema to diplonema (it has not been identified after diplonema). The length of the common end shortens progressively from a maximum of about 1.9 μ to a minimum at late pachynema of about 0.25—0.35 μ, that remains during diplonema. The common end shows the three elements of a synaptonemal complex up to mid-pachynema (Fig. 6a and b), the only characteristics being the duplication of one of its lateral elements as soon as it begins to separate from the other (the double core is the long core) and some variations in the path of the central element, which becomes curved or oblique and can deviate towards the end of one of the lateral elements. After mid-pachynema the space separating both lateral elements and the central element disappears (Fig. 4a).

7. The Free End of the Long Core and the Anomalous Synaptonemal Complex

The double structure of the long core becomes more evident during mid-pachynema when the two filaments composing this core become more separated (up to 1,000 Å) and a central element appears between them (Figs. 7 and 8b). This separation occurs at several places of the long core, possibly in most of its length except the common end region, but it is more evident at the free end (Fig. 7). At this point, and exclusively during mid-pachynema, a long stretch of the long core forms a very curious, asymmetrical structure: the anomalous synaptonemal complex (Fig. 7). While one of the lateral elements of this synaptonemal-complex-like structure is similar to the normal ones, the other is thicker, about 1,500 Å wide. This thicker lateral element is composed of at least three dense filaments about 300 Å wide surrounded by a fibrillar matrix. The

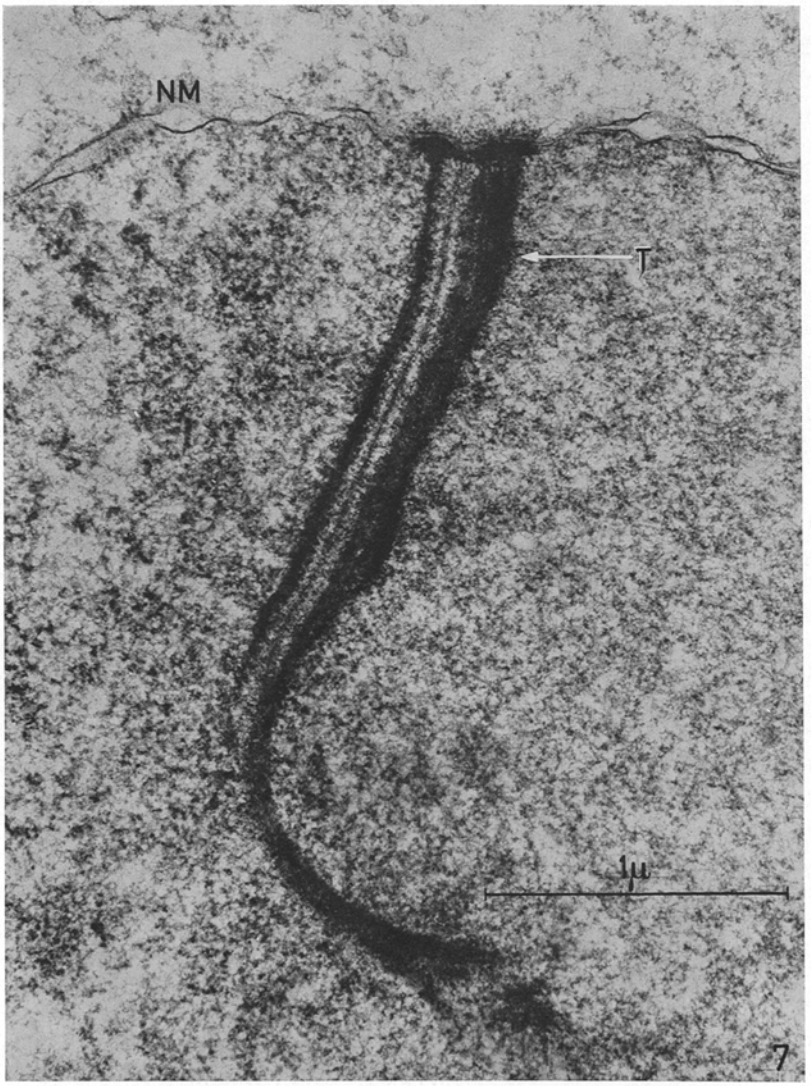

Fig. 7. Electron micrograph of the free end of the long core at mid-pachynema showing a long stretch of the anomalous, asymmetric synaptonemal complex with its thick (*T*) lateral element. × 40,000

central element is similar to that of an autosomal synaptonemal complex. This asymmetrical structure is more easily seen at the free end but it is present at least in the final third of the long core. The thicker element of this anomalous synaptonemal complex faces the nucleolar mass and

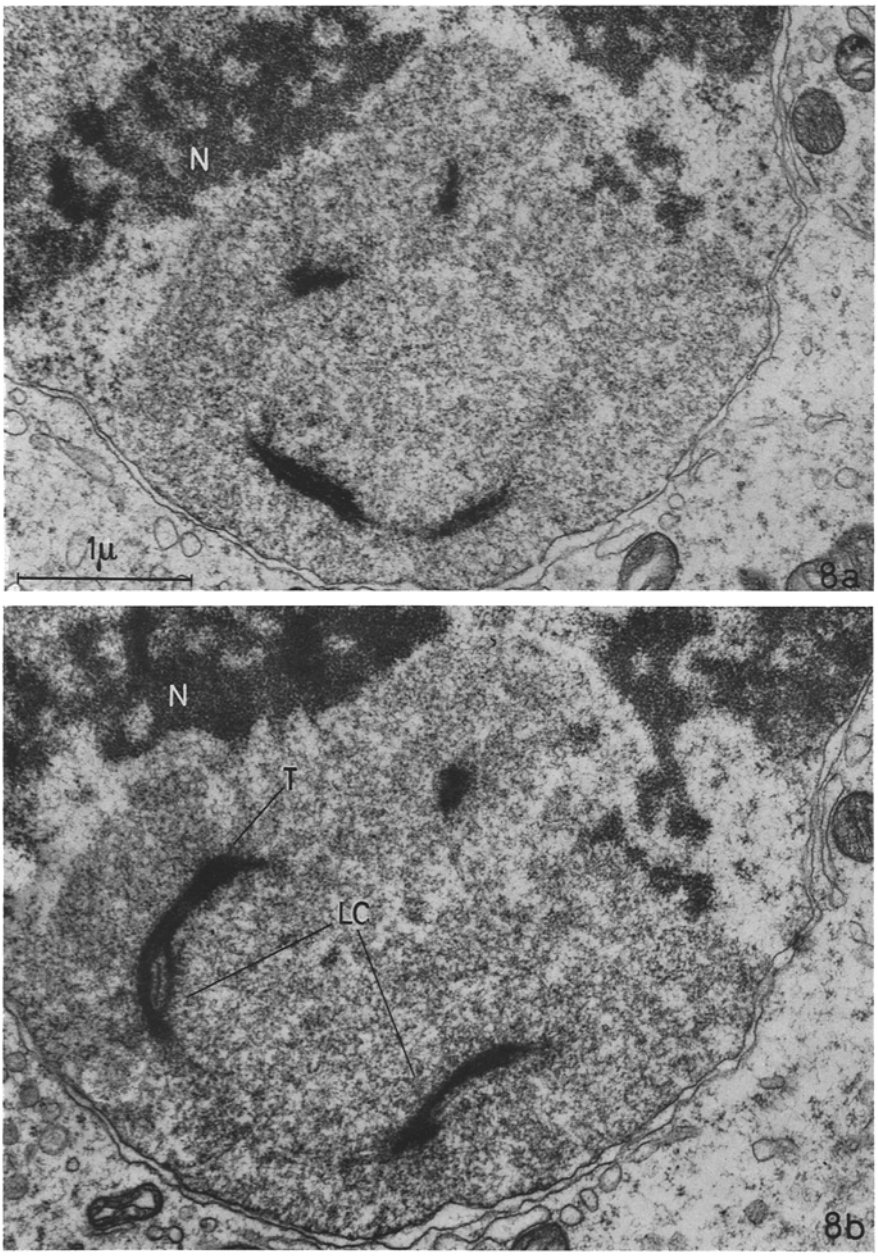

Fig. 8a and b. Two serial thin sections showing the anomalous synaptonemal complex of the long core (*LC*) at advanced mid-pachynema, and the relationship of the thicker lateral element (*T*) with the developing nucleolus (*N*). × 23,000

some nucleolar invaginations come near to it (Fig. 8a and b). The chromatin fibers that join both lateral elements are indistinguishable from each other.

While the short core does not form any synaptonemal complex by itself at any stage, it is split into two filaments that rejoin after a short distance near its free end during mid-pachynema, forming an "eye-like" zone (Fig. 3b).

Discussion

1. The Meaning of the Cores of the Sex Pair

As shown previously (Solari, 1969b) and in this paper, the long and the short cores are constant and characteristic elements of the sex pair of the mouse during meiotic prophase. In the human (Solari and Tres, 1969), and in the rat (in preparation) the same two cores (with different and specific length ratios) have been found. The length ratio of the cores remains rather constant during zygonema and pachynema, although the cores become more folded and suffer other changes. This constancy suggests that the cores represent — or that they are involved with — some fixed structure of the chromosomes.

During early zygonema the long core is axial to a rod-like mass of chromatin, that is connected by one end with a smaller mass of chromatin. The short core is axial to this smaller mass of chromatin (Solari, 1969b; in some cells this disposition of the cores is observed up to the beginning of pachynema).

At late pachynema the cores separate straight from each other as if pulled from their free ends. Thus, the characteristics and the behaviour of the cores are similar to those of a hypothetical chromosomal axis of each chromosome. Besides, the length ratio of the cores is nearly the same as the length ratio of the Y and X chromosomes observed with the light microscope (Ohno and Lyon, 1965). From these data we conclude that the cores are axial structures of each sex chromosome during zygonema, pachynema and diplonema.

The formation of the cores in the sex pair seems to be simultaneous to the appearance of cores (lateral elements) in the autosomes during early zygonema (Solari, 1969a). During leptonema well-defined cores are not present in the mouse, but they have been described in other species (Moens, 1968).

However, the evolution of the cores of the sex chromosomes differs from those of the autosomes. While the cores of the sex chromosomes become paired only at the common end region, synaptonemal complexes are formed all along the paired autosomes, as shown in *Gryllus* by Wettstein and Sotelo (1967) and in the mouse by Woollam, Ford and Millen

(1966). In this respect, the cores of the X-Y pair behave like the cores of the unpaired sections (univalents) of the chromosomes in the triploid *Lilium tigrinum* (Moens, 1969). The cores of the sex pair remain thick and dense during diplonema, when the autosomes offer a different picture.

In Searle's X-autosome translocation, the core of the translocated segment of the X chromosome combines itself with the core of one autosome outside the sex pair (Solari, 1969b), thus mirroring the behaviour of the axes of the chromosomes involved in that translocation.

Thus, the available evidence suggests that the cores are axial structures of the sex chromosomes, formed in the same way as the lateral elements of autosomal synaptonemal complexes (this suggestion was advanced earlier, Solari, 1964).

2. The Cores and the Structure of the Sex Bivalent

While the cores can be related to the linearity of the sex chromosomes, their position with respect to the two chromatids composing each homologue shows further complexities. Both the X and the Y chromosomes are composed of two chromatids at diplonema as seen with the optical microscope (Ohno, Kaplan and Kinosita, 1959). DNA synthesis at premeiotic interphase duplicates the DNA content of the nucleus (Rhoades, 1961), thus showing that the essential part of the chromosomes is already double at meiotic prophase. A small quantity of unreplicated DNA, as that described in *Lilium* by Stern and Hotta (1969) (0.3% of the genome) would probably not be sufficient to prevent the expression of chromosome doubleness.

Thus, the cores of the sex pair may be related in one of the two following ways with respect to chromatids: either the cores can be related to the axis of each of the chromatids, or they are related to the axis of the whole chromosome. The first alternative seems less probable, as the short core is not clearly double along its whole length. Furthermore, the doubleness of the long core, that is enhanced during mid-pachynema, is lessened during late pachynema and diplonema, contrary to what could be assumed to happen according to the light microscope image of the chromosomes. The most significant proof of the relationships between chromatids and cores would be given by their involvement in chiasmata formation. However, this question requires further genetical and structural data. On the whole, the second hypothesis seems more probable. The place that can be occupied by the core if it is co-linear to the whole chromosome but is not axial to each chromatid, can be the interface between chromatids. If the cores are placed at that interface, they do not need to be double, and they can remain in place after

separation of the homologues during diplonema while the chromatids remain approached to each other. According to this hypothesis the cores do not necessarily take part in the formation of chiasmata.

A second question remains about the relationship of the cores with the basic structure of the chromosomes, that is, the chromatin fibrils. The core can be interpreted as a part of the fibrillar components of the chromosome, packed in a special array and density. The apparent continuation of the chromatin fibers with the substance of the cores seems to support this idea. However, Coleman and Moses (1964) and Moses (1968) have shown that the denser part of the lateral elements of synaptonemal complexes (which are similar to the cores of the sex pair) is deceptively poor in DNA to mirror a packed array of DNA-containing fibers. Furthermore, the cores of the XY pair diminish in staining affinity by extraction with cold perchloric acid, a treatment which does not affect DNA but extracts RNA and some basic proteins (Solari and Tres, 1967a). Evidence has been provided by Sheridan and Barrnett (1969) about the richness in basic protein in the lateral elements of synaptonemal complexes. In agreement with those observations, alcoholic PTA stains intensely the cores of the XY pair. Furthermore, optical observations with histochemical tests for DNA do not show DNA-containing condensations comparable to the cores; instead, "negative" filaments have been observed, which could be related to proteinaceous axes (Solari, 1964).

Thus, the present evidence supports the idea that the cores are not mainly formed by chromatin fibrils, but by some added material, part of which may be basic protein. However, this added material seems not to be unconnected to chromatin components; it is rather specifically deposited on some parts of the chromosomes at a specific moment, as Moses has suggested (1968). The autoassembly of a synaptonemal-complex-material (Schin, 1965), if it exists, would seem to be a rather rare event, and in any case, the involvement of extrachromosomal DNA in that assembly has not been discarded.

3. The Anomalous Synaptonemal Complex of the Long Core

If the core material is deposited at the interface between the two chromatids of the X chromosome, then the doubleness of this core may be related to an enlargement of this interface, and the deposition of that material on parallel sides of both chromatids. The organization of a synaptonemal complex at mid-pachynema would then be the result of the attainement of a "critical distance" of about 1,000 Å between two surfaces having homology, as suggested by Wolstenholme and Meyer (1966). However, the asymmetry of both lateral elements is a singular

feature that is probably related with functional differences between sister chromatids. In relation with this asymmetry, Peacock (1965) has shown in *Plethodon cinereus* that the presumptive nucleolus-organizer region in the lampbrush chromosomes is asymmetric; one chromatid bears large loops related to nucleolus development and the other none.

In the present results it has been shown that the "redundant" or thicker lateral element of the anomalous synaptonemal complex was the one facing the developing granular zone of the nucleolus, with the intermediate chromatin which is probably connected to the thicker element. It can be suggested that the enlargement of chromatid interface and the excessive, asymmetrical deposition of synaptonemal material on one of the sides of this interface may be related to the synthesis of nucleolar components by one of the chromatids; when such a synthesis ends, as in late pachynema (complete development of the nucleolus), the anomalous synaptonemal complex becomes obliterated and the asymmetric array of the long core disappears. Experimental methods to test this hypothesis are available.

4. The Partial Synapsis of the X-Y Pair

The existence of synapsis in the X-Y pair of mammals has been doubtful according to most of the cytogenetical work (Sachs, 1955; Ohno, Kaplan and Kinosita, 1959). With the exception of a few species like the chinese hamster (Ohno and Weiler, 1962), there was no positive evidence either of synapsis inside the "sex vesicle" or of chiasmata in the sex bivalent. A hypothetical material of the "sex vesicle" was supposed to join both chromosomes by their ends.

The ultrastructural (Solari, 1964, 1969a) and histochemical (Solari and Tres, 1967a) analysis of the X-Y pair ("sex vesicle") showed the non-existence of materials other than the chromatin fibrils and the associated nucleolus in the case of the mouse [in which species the nucleolus organizer is carried by the X chromosome (Ohno, Kaplan and Kinosita, 1957)]. In the first ultrastructural study of the X-Y pair (Solari, 1964) no synaptonemal complexes were observed, mainly because full-size sex pairs during late pachynema were mainly studied (when the common end is obliterated) and no serial sections were used. However, the possibility of a *short, partial* synapsis was not excluded, and indeed it was soon observed that synaptonemal complexes were present in the X-Y pair (Solari and Tres, 1967b; Solari, 1969b). Ford and Woollam (1966) confirmed the ultrastructural description of the X-Y pair made by Solari (1964) and found a partial synaptonemal complex in the golden hamster.

As shown by the present results, the formation of a synaptonemal complex in the common end region between the two cores is a constant feature in every sex pair examined before late pachynema. A similar complex exists in man (Solari and Tres, 1969) and in the rat (in preparation), and probably in the golden hamster.

The restriction of the formation of the synaptonemal complex to the common end region may represent the lack of homology of the remaining part of the Y chromosome. The decrease in length of this synaptonemal complex during pachynema may be interpreted as a precocious repulsion of the X and Y chromosomes. However, the final 0.2 μ of this region remain joined up to diplonema. This fact is in agreement with cytological observations which show that the sex pair as soon as it is unravelled from the "sex vesicle" is already joined at the very tip of their ends. However, the functional significance of the apparent melting of the inner sides of the cores at the common end region must await further investigation.

Thus, lateral approachment and joining by the common end region has been proved in the X-Y pair, and synaptonemal complexes develop in that region as well as in paired autosomes. The presence of a synaptonemal complex is a prerequisite (Moses, 1968) for the formation of chiasmata but it is not in itself sufficient for that formation. Thus, although the existence of chiasmata and genetic recombination is suggested by the present results, further work is needed for its proof.

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