The Relation between the Axial Complex of Meiotic Prophase Chromosomes and Chromosome Pairing in a Salamander (*Plethodon cinereus*)

BY MONTROSE J. MOSES, PH.D.

(*From The Rockefeller Institute*)

PLATES 312 TO 314

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ABSTRACT

An investigation of the structure of meiotic chromosomes from primary spermatocytes of two salamanders, *Plethodon cinereus* and *Desmognathus fusca*, has been made using correlated light and electron microscopy. Feulgen squashes were compared with stained sections and these related to adjacent thin sections in the electron microscope. A transition from the familiar cytological preparation to the electron image was thus effected.

A linear complex consisting of three parallel strands has been observed with the electron microscope, passing along the central axis of primary spermatocyte chromosomes. The complex is similar to that found in comparable chromosomes from at least a dozen animal species. The structure in *Plethodon* is described in detail.

Synapsis has been positively identified as the stage of meiotic prophase at which the complex occurs. Thus the complex is a part of bivalent chromosomes. It has not been seen in other stages or other divisions and is thus thought to be exclusively of synaptic occurrence. The term *synaptinemal complex* is suggested for the entire structure.

By virtue of the material condensed around it, the complex is also seen in the light microscope where it appears as a fine, densely Feulgen-positive central core along the chromosome. The complex is thus closely associated with DNA, if not at least in part, composed of it.

In the stages studied, homologous chromosomes are not always completely paired. The lateral elements of the complex separate and follow the single chromosome axes at these points. The central element disappears and thus may be a phenomenon of pairing. It is concluded that the lateral elements of the synaptinemal complex may more correctly be a "core" of the single meiotic prophase chromosome, possibly being concerned with its linear organization.

Reports are currently accumulating that confirm the existence of a complex, linear structure along the axis of certain meiotic prophase chromosomes of animals. In accounts so far published, the structure has been reported in the primary spermatocytes of the crayfish (9, 10), rat (14, 10, 13; Y. Clermont, personal communication), pigeon, cat, and man (4), grasshopper (9, 5), *Xenopus* (10), a fish and a spider (13). In addition, I have learned that the complex also occurs in the clam *Spisula*, the snail, *Otala* (L. Rebhun, personal communication), and in the snail, *Viviparus* (6). In our laboratory, over the past year and a half, we have been studying this structure at length in the primary spermatocytes of two salamanders, *Plethodon cinereus* and *Desmognathus fusca*. Here, the complex appears as it has been most commonly observed, though it differs in detail from the more elaborate form in which it was first described (in crayfish (9, 10)). Despite such differences, the two forms are entirely homologous; this point is discussed elsewhere (11). The more usual appearance of the complex, as exemplified in Fawcett's description (4) and according to observations reported here, is of three filamentous ele-

ments, parallel, uniformly spaced and arranged in a single plane to form a ribbon. The lateral elements, which are symmetrical, are usually denser and larger than the central one which is often evanescent. As was demonstrated in the case of the crayfish, the complex (or "core") lies embedded in the axis of the chromosome (actually a bivalent, as will be shown) and is integral with the surrounding Feulgen-positive material (chromatin (10)).

Because the chromosome at early meiotic prophase is generally regarded to be in its most extended form, and because of the precise point by point pairing of homologous chromosomes during synapsis as demonstrated by both cytological and genetic observations, the significance of the complex to chromosomal organization in general is obviously intriguing. The purpose of this report is to establish the relationship of the complex to the chromosome by identifying the condition of the chromosomes in the meiotic stages in which the structure is found. A brief discussion of this and related problems has been presented (11) and more details will appear elsewhere.

Materials

Males of *Plethodon cinereus* were collected in the Palisades region of New Jersey, in early June. On the same day, their testes were dissected in cold, buffered 1 per cent OsO_4 (pH 7.4) containing 4.5 per cent sucrose (1), and were cut, caudad to cephalad, into four portions of equal length. Half of each portion was fixed in OsO_4 and embedded in methacrylate, while the corresponding half was fixed in acetic acid–alcohol (Carnoy), stained by the Feulgen procedure and squashed (2). Immediately adjacent thick and thin sections were taken from the methacrylate block with a Porter-Blum microtome (12), for light and electron microscopy. Sections 1000 to 1800 A (gold-purple) were found to be most useful for studying this phase of core-chromosome relationship. Thick (2 to 3 μ) sections were stained without removing the methacrylate, either by the Feulgen reaction or with iron hematoxylin.

Testes from *Desmognathus fusca* males, collected together with the *Plethodon* material, were prepared for light and electron microscope study in a similar fashion.

Light micrographs were made with Zeiss NA 1.3, 90 × apochromat and Zeiss NA 1.3, 90 × neofluar objectives, 7 × compens and 8 × projection oculars, on 35 mm. Adox KB 17 and microfile film. Electron micrographs were made with a modified RCA EMU 2C at magnifications of 4000 to 6000 diameters, and enlarged photographically as desired.

OBSERVATIONS

Light Microscopy.—Examination of the Feulgen squashes indicated that meiosis was just getting under way. *Plethodon*, like *Desmognathus* (7), undergoes a period of meiotic inactivity during the winter months, with most of the spermatogenic cells stopping at late spermatogonial interphase. In late spring, there is a wave of meiotic activity which results in a progression of stages from caudal to cephalic end of the testis. In the case reported, spermatogonial stages were found at the caudal level, while diakinesis, first division figures and a few second division figures were encountered at the cephalic end. In the second and third quarters of the testis, pairing (*i.e.*, synaptic) stages (zygotene, pachytene) predominated. All of the observations reported here were made on material from the third quarter, away from the caudal end. No presynaptic (leptotene) stages and only occasional stages of disjunction (diplotene and diakinesis) were found (Fig. 1). In most of the cells, chromosomes were in synapsis and arranged in characteristic "bouquet" formation with ends polarized and anchored at the nuclear membrane. This configuration persists through pachytene. The nuclei in Fig. 1, with the exception of No. *4*, reflect this arrangement, as seen in different aspects because the cells have been compressed and oriented in various ways during smearing and flattening. In nuclei *2* and *5*, the polarized chromosome ends are on the under surface of the nucleus, while the loops have been spread out peripherally. In nuclei *1* and *3*, on the other hand, the polarized ends lie against one side (arrows). The classical concept is that pairing between homologs generally occurs zipper-like from the ends and proceeds toward the loops, although the starting point and direction may vary (3). The rate and timing of pairing probably differs among chromosomes and hence both paired and unpaired segments may be expected within a nucleus. Indeed, it is common to find bivalents that are unpaired for part of their length (*e.g.* Fig. 1, nucleus *2*, arrow marked *Y*). After the acetic acid–alcohol procedure, chromosomes are condensed laterally into slender strands with bristly profiles. There seems to be less marked contraction in a longitudinal direction.

In 2 and 3 μ sections of osmium-methacrylate preparations, stained with the Feulgen reaction, the chromosomes are easily visible in transverse and longitudinal sections (Fig. 2). Their outlines are also fuzzy, but they are thicker and less condensed than in the squashes.

Polarization is indicated in nucleus *6*, where several chromosomes can be seen terminating at one side of the nucleus (arrow). (The illusion of heavy staining of the nuclear edge in this region is

due to the surface being perpendicular to the section at this point.) In nucleus *7*, cut near its equator, several chromosomes are seen longitudinally as they weave through the section. In nucleus *8*, cut to one side of its median, most of the chromosomes are transected. Although an accurate count is not feasible, about 24 to 30 cross-sectional profiles can be discerned. The diploid number is 24 in this species (8); if all the chromosomes were paired and looped on themselves in the nucleus, a section perpendicular to the chromosomes (on the side of center toward the terminations) would contain 24 cross-sections. The number would be higher, depending on how many unpaired chromosomes the sections transected. Counts of other similar sections generally revealed slightly more than 24 transverse profiles, indicating that in such nuclei pairing was usually not complete in all chromosomes. No evidence was found that pairing was incomplete in every or nearly every chromosome. Also, it cannot be said whether some of the chromosomes may not be entirely unpaired.

Electron Microscopy.—In electron micrographs the appearance of the nucleus in general and the chromosomes in particular (Figs. 3 and 4) is unfamiliar compared with more common Feulgen squash preparations (Fig. 1). There is sufficient similarity, however, between the appearance of the osmium-fixed, Feulgen-stained thick sections (Fig. 2) and both extremes to relate them. It is also clear that the nuclear structure, as far as can be seen in the light microscope, is intact after preparative procedures for electron microscopy. Comparisons with living preparations, furthermore, show that osmium fixation changes are small and that more extensive changes have occurred in the Feulgen squashes.

Fig. 3 is an electron micrograph of a relatively thick (1600 A) "thin" section of a nucleus similar to No. *7* in Fig. 2. The section contains a considerable portion of a chromosome in length, as well as at least three transverse sections. With adjacent thick and thin sections of such nuclei (not shown here), the Feulgen-positive regions can be easily identified, as was demonstrated in the crayfish (10). The fuzzy boundaries of the chromosomes, difficult to distinguish in the electron micrograph, are thus defined as the regions in which the fine textured fibrillar material of the chromosome begins to blend with the coarse, granular interchromosomal substance (Fig. *3'*, overlay). The dense axial complex (or "core") is clearly visible in both longitudinal and cross-sections.

In the longitudinal section in Fig. 3, the termination of the chromosome against the innermost nuclear membrane is a region of considerable density from which two dense lines emerge, with a suggestion of a third, central one in evidence (Fig. *3'*, overlay, *ce*). One or the other of the lateral lines (Fig. *3' le*) can be followed for about 5 or 6 μ, until the chromosome presumably bends and passes out of the section. The cross-section at *a* is of such a chromosome, in aspect-slightly oblique, showing three elements; two dense lateral ones, each about 300 A in width and a smaller, central one about 170 A in width. The lateral elements are separated by about 1000 A. Perfect cross-sections have been observed as three dense dots. Thus the "core" here consists of three parallel filaments of the sort described by Fawcett (4). The configuration in Fig. 3 suggests that the two lateral elements are twisted gently along the axis, making approximately 1½ full (360°) spirals before they are lost from view (see overlay). The central element, when it can be seen, is vague and often discontinuous. Three other chromosomes seen in a thinner section, are shown in Fig. 4; two (*a*, *b*) are cut obliquely by the section and the other (*c*) more longitudinally. The general appearance of the axial complex is similar; the separation of chromatin from interchromosomal material is more distinct. The chromosome at *c*, shown with its termination at the inner nuclear membrane, is comparable to one of those in the light micrograph (Fig. 2) of nucleus *6*.

The associations between the chromosomes and the nuclear envelope are of considerable interest, but will be described only briefly here. They are of two kinds: (*a*) where the chromosome terminates almost perpendicularly against the nuclear surface (Fig. 1, nucleus *1*, *3*; Fig. 2, nucleus *6*, arrow; Fig. 3; Fig. 4); and (*b*) where the chromosomes lie against the inner surface and run parallel with it for a considerable distance (Fig. 2, nucleus *8*, peripheral chromosomes cut in cross-section). Both relationships can be seen with the light microscope in living as well as in fixed cells. The chromosome terminations appear as boutons, and in living cells there appears to be movement of these terminations over the inside of the nucleus. In the electron microscope, the boutons appear as masses of delicate fibrils and granules, similar to chromosomal material, that spread out from the chromosome ends. The strands of the axial complex seem to end abruptly at the inner membrane and may be somewhat denser at their terminations. Both inner and outer membranes of the envelope are intact; "pores" are never seen in the region of association. The spacing of the membranes is generally more

even in this area, and the membranes themselves appear to be straighter and presumably more rigid. The latter characteristics give the envelope the appearance of being thicker or denser (13), but this is not necessarily the case. No evidence has been found for direct association, continuity, or exchange between nucleus and cytoplasm at the points of contact.

Although the organization of the axial complex is generally tripartite or at least double, single elements are often seen. In longitudinal aspect it is difficult, without resorting to reconstruction of serial sections, to say whether such an element is truly single or whether another parallel strand may not lie above or below it, out of the section. In transverse sections, however, the singularity is clear. In Fig. 3, two of the cross-sections, *b* and *c*, contain only one dense structure, of similar dimensions as one lateral element of *a*. What may appear superficially as a second structure in *c* can be seen on close inspection to be an aggregation of large dense granules of the sort lying between the chromosomes, similar to the aggregation in *a* (Fig. 3′, *i.g.*). It is thus apparent that in some chromosomes at least, there are regions where the axial structure consists of a single unpaired strand resembling one lateral element.

Another such single profile is shown in Fig. 5, *c*. Those at *b* and *d* are less obvious. The section at *b* is probably a slightly distorted transverse view of the tripartite axial complex. The same may be true at *d*, but the presence of an extra dense element is unusual. The occurrence of both single and multiple axial structures in the same section is better understood in view of the structure shown in Fig. 5, *a*. A chromosome is cut here in longitudinal section. The tripartite axial complex is intact for a portion of the section, though the plane across the three elements is at a slight angle to that of the section, which accounts for the unequal density of the lateral elements. A bifurcation then occurs *wherein the lateral elements diverge and the central element disappears*. The separated lateral elements then presumably leave the section as they approach the nuclear envelope. Such a distinct forking of the "core" is rare in electron micrographs, but even if it occurred twice in every chromosome, the probability is quite low of finding such a region with all elements in the plane of a thin section for a sufficient distance. In the light microscope, chromosomes in Feulgen-stained sections occasionally do appear to bifurcate, but because of overlapping, very careful focusing is necessary. We have no evidence on which to state with certainty whether these are presynaptic or precocious disjunctive regions, though it is generally thought that such chromosomes are apt to be incompletely paired (presynaptic) in places. In any case, it is likely that some, if not all of the single axial elements seen in cross-section are actually lateral elements of the tripartite complex, which are separate.

The results reported above stem from one block of tissue from which control of cytological staging and careful comparison among acetic acid–alcohol Feulgen squashes, thick sections for light microscopy, and electron microscope observations of the same piece of testis could be maintained. However, it should be emphasized that similar observations have been made repeatedly on tissue from other individuals, some of which were collected at different times of the year, and from another species, *Desmognathus fusca*. They are thus not special, but rather of a general nature, at least in the species studied.

DISCUSSION

There can be little doubt of the presence in electron micrographs of a complex, linear structure along the axis of primary spermatocyte chromosomes from a number of animal species representing a variety of phyla. Whether the structure is to be found in all such meiotic chromosomes is problematical, but it is reasonable to predict it for most species. The exceptions, if they appear and if they are proven beyond doubt, will be of the greatest interest in shedding light on the role of this complex. At the moment, neither the functional significance of the structure nor its relationship to chromosome organization in general has been established. This core has so far been reported exclusively in meiotic prophase chromosomes of primary spermatocytes. It seems likely that it is also to be found in oocytes. Nothing resembling it has yet been seen in chromosomes of secondary spermatocytes or of mitotic prophases. Thus, the structure, in its present form, must be regarded as a phenomenon of meiosis and specifically of the phase in which chromosome pairing occurs (first division). In previous published reports (9, 4, 10, 13) it could not be said with certainty whether the core was of presynaptic, synaptic, or postsynaptic (disjunctive) occurrence. The unfamiliar appearance of most nuclei in the electron microscope makes diagnosis of meiotic stages difficult and even such broad classifications as early or late prophase are dubious without close correlation with light microscopy. And even here, the appearance of the nucleus after osmium fixation may sometimes be

deceiving. In the present paper the point is established that the axial complex is associated with the period of synapsis, that it is a part of the bivalent chromosome, and that when the chromosome is unpaired, the lateral elements of the complex are also separate. This is consistent with the fact that the complex has not been observed in clearly presynaptic, in postsynaptic (disjunctive), or in any other meiotic or mitotic stages of this and other material. It is therefore concluded that the complex is exclusively of synaptic occurrence, though the component elements may exist individually in unpaired chromosomes.

When such a thread-like complex axial to the chromosome is observed, it is tempting to speculate about its relation to the chromonema. But this is premature at the moment. The chromonema is classically defined as that fundamental linear element of the chromosome, somatic as well as meiotic, which is responsible for its continuity. The complex described here, on the other hand, has so far been associated with only one kind of chromosome. It is, of course, conceivable that this structure is actually but one form, easily visible, of an underlying organization that may be fundamental to all chromosomes, but which for various reasons has yet to be discerned in other chromosomes. Until experimental evidence is obtained for what this basic organization may be, such speculation is groundless and the identification of elements of the complex with the chromonema must be held open. For the purposes of this paper, then, the axial structures are considered here only as they have actually been observed; *i.e.*, in the chromosomes at synapsis.

The term "chromosomal core" was applied to the axial complex when it was first described (9). Though the structure is in a sense core-like, being both central and intimately involved with the chromosomal material, the chief virtue of the word as a descriptive one is its brevity. Unfortunately, the term also implies a generalization to all chromosomes, and certainly at the moment this is unwarranted. Also, it is likely that only one of the lateral elements may more correctly constitute a chromosomal core. A more precise term would, in the light of results reported here, indicate that the structure is associated specifically with chromosome pairing, and that it is thread-like. Unwieldly though it is, *synaptinemal complex* is more accurately descriptive.

From the electron microscope evidence presented here, it is concluded that each lateral element of the synaptinemal complex is a part of a single chromosome. The fine textured material of the chromosome surrounds the element and is integral with it. The whole complex is thus a reflection of the pairing of two homologous chromosomes wherein the lateral elements are situated near the apposing faces of the individual chromosomes, close to and parallel with each other. The third, central strand is transient and sometimes non-existent. It may well represent a "condensation" product of the pairing (4).

The chemical identity of the elements of the synaptinemal complex has yet to be determined. In the crayfish the complex was shown to be intimate with the chromosomal DNA (10). In the present material, chromosome cross-sections seen in light micrographs of Feulgen-stained sections (neighboring those used for electron microscopy) show central areas of higher stain concentration (Fig. 2, nucleus *8*, arrows; inset). Almost every cross-section shows such a central density, depending on how obliquely the chromosome has been cut. Usually a gradient of increasing dye concentration from the periphery of the chromosome to the center is apparent. It can be seen from Fig. 3 in both longitudinal and cross-sections that a similar gradient of electron dense chromosomal material also occurs. The implication is thus strong that in the chromosome the electron dense and Feulgen-positive materials are one and that a major component is DNA. Assuming that the synaptinemal complex contains DNA, the structure should be visible in Feulgen preparations with the light microscope under favorable optical conditions. Its width is about 0.2 μ, just at the limits of light optical resolution, and in cross-sections it is seen in depth for 2 or 3 μ. Even a single element, because of the gradient of material surrounding it should be visible. In the complex, the lateral elements lie too close together to be resolved separately with the light microscope. Further, measurements of their width in light micrographs cannot be used to distinguish unpaired segments from those in the paired condition since variations in chromosome thickness and indistinct boundaries render such measurements meaningless. However, one should occasionally encounter sections through chromosomes in regions where the two homologues are unpaired and where their elements are sufficiently separated to be resolved in the light microscope but at the same time lie close enough together to be identified as parts of a bivalent. Indeed, there are places where two closely separated central densities can be distinguished (Fig. 2, nucleus *8*, arrows marked *x*); in one case their

centers are about 0.7 μ apart, in the other about 1 μ. They probably represent regions where the chromosomes are not closely paired. However, a majority of the chromosomal transections contain single densities as would be expected when either the entire complex or more rarely, an individual element is involved. In longitudinal sections the complex would be more difficult to see since its thickness is hardly sufficient to cause an appreciable increment in optical extinction. Nevertheless, suggestions of it do occasionally appear (Fig. 2, nucleus *7*, arrows); these are presumably regions where the DNA is more concentrated around it.

Despite this presumptive evidence, it can be stated only that it is likely that the strands of the complex contain DNA. Proof of their composition must await other methods. It is also almost certain that other substances, especially proteins, are present to a considerable extent both in the complex and around it. In any case, whatever the composition of the complex, it is undoubtedly the structure around which chromatin condenses after the more common acetic acid–alcohol fixation and Feulgen staining as shown in Fig. 1. It follows that the same is also true of the lateral elements in regions where the chromosome is unpaired. Thus it is reasonable to assume that these components of the compxel (*viz.* the lateral elements) are intimate with, if not actually responsible for the linear continuity of the individual synaptic chromosomes of which they form an integral part.

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Explanation of Plates

Legend

ce	central element of axial complex	*m*	mitochondrion
chr	chromosome	*ne*	nuclear envelope: two membranes
cv	cytoplasmic vesicles	*nu*	nucleolar material
ig	interchromosomal granules	*se*	single axial element
le	lateral element of axial complex		

Plate 312

Fig. 1. Feulgen squash of Carnoy-fixed testis of *Plethodon*. This small piece, of which these cells are a sample, was immediately adjacent to the piece used for electron microscopy. All nuclei are from primary spermatocytes. Nuclei *1* and *3* are at zygotene, Nos. *2* and *5* are at late zygotene-pachytene. All four depict stages of synapsis and typify the cells in this piece. No. *4* is at diplotene; very few of the cells were as far advanced in prophase. Arrows in Nos. *1* and *3* point to chromosome terminations of bouquet stage. Arrow marked *V* in No. *2* indicates point at which paired chromosome becomes unpaired. (90 × N.A. 1.3 Apo. + 7 × ocular, Wratten No. 74 filter.) × 1050.

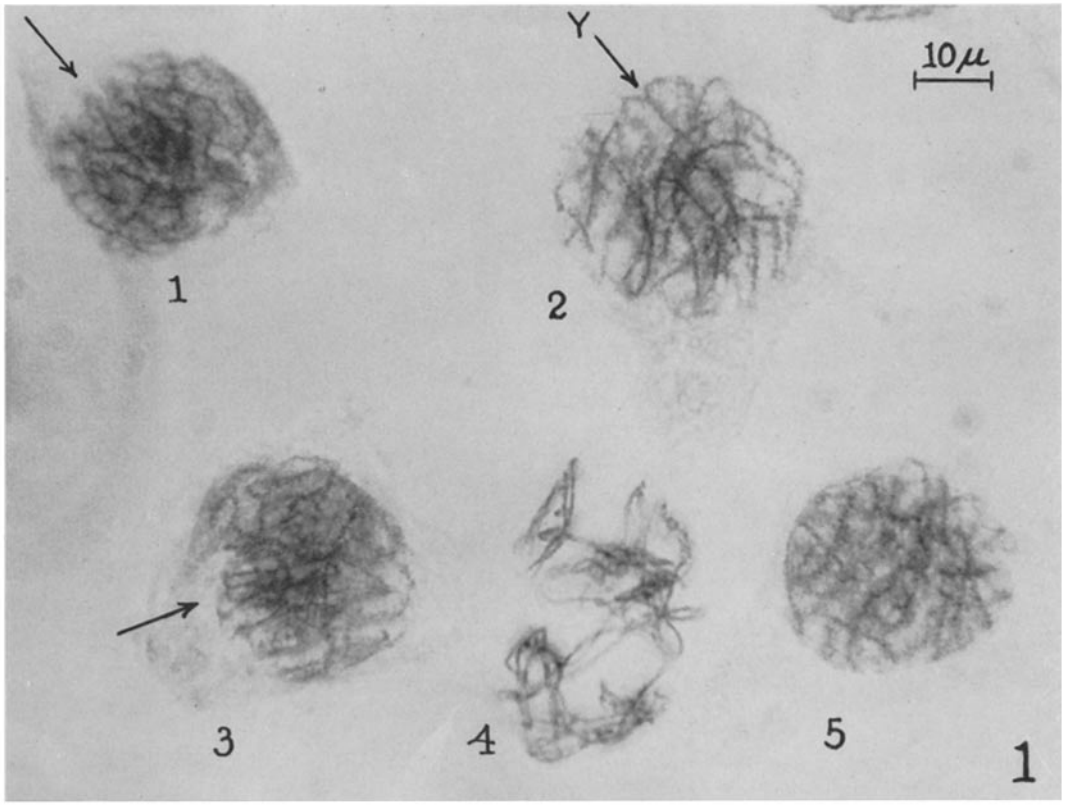
Fig. 2. 2 to 3 μ section of osmium-fixed testis, Feulgen-stained. This piece was adjacent to that shown in Fig. 1. The section is closely adjacent to those shown in Figs. 3, 4, and 5.

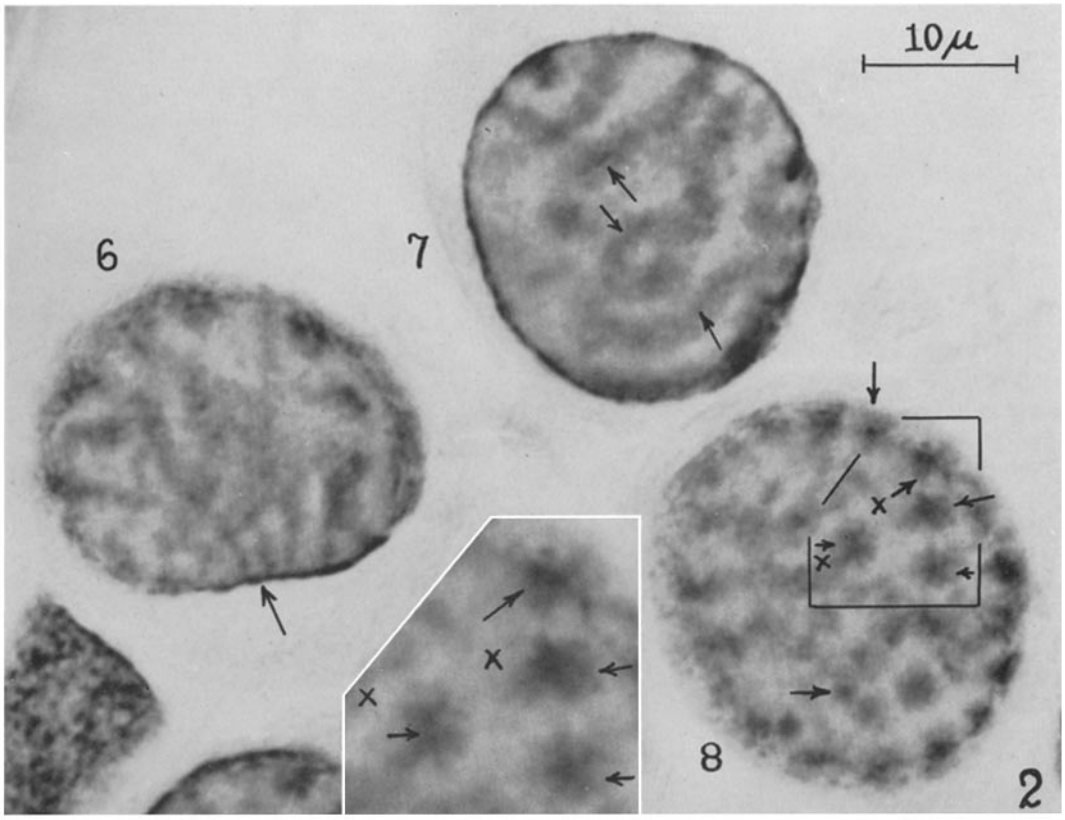
Nucleus *6* shows bouquet stage; chromosomes terminate at nuclear envelope (arrow).

Nucleus *7* contains several chromosomes in longitudinal view. Arrows point to Feulgen-positive regions along axis of chromosomes.

Nucleus *8* is sectioned so that all chromosomes are cut transversely (each chromosome is cut twice as it loops back in itself). About 27 cross-sections can be counted. In the center of almost every one is a densely staining Feulgen-positive spot (arrows). In some places the spot is double (arrows marked *x*). Evidently the spot represents the axial complex in cross-section. (100 ×, NA 1.3 neofluar + 8 × proj. ocular, Wratten No. 74 filter.) × 2000.

Inset.—Higher magnification of chromosome sections indicated in nucleus *8*. × 3750.





(Moses: Meiotic prophase chromosomes and chromosome pairing)

PLATE 313

FIG. 3. Electron micrograph of a *ca.* 1600 A section of a nucleus similar to that in Fig. 2, No. *6*. The dense axial complex ("core") of a bivalent chromosome originates at the nuclear envelope and lies in the plane of the section for a considerable distance. Two dense lines (lateral elements) twist about each other and flank an indistinct central line. The fine textured material of the chromosomes is quite dense near the complex and merges with the granular interchromosomal component.

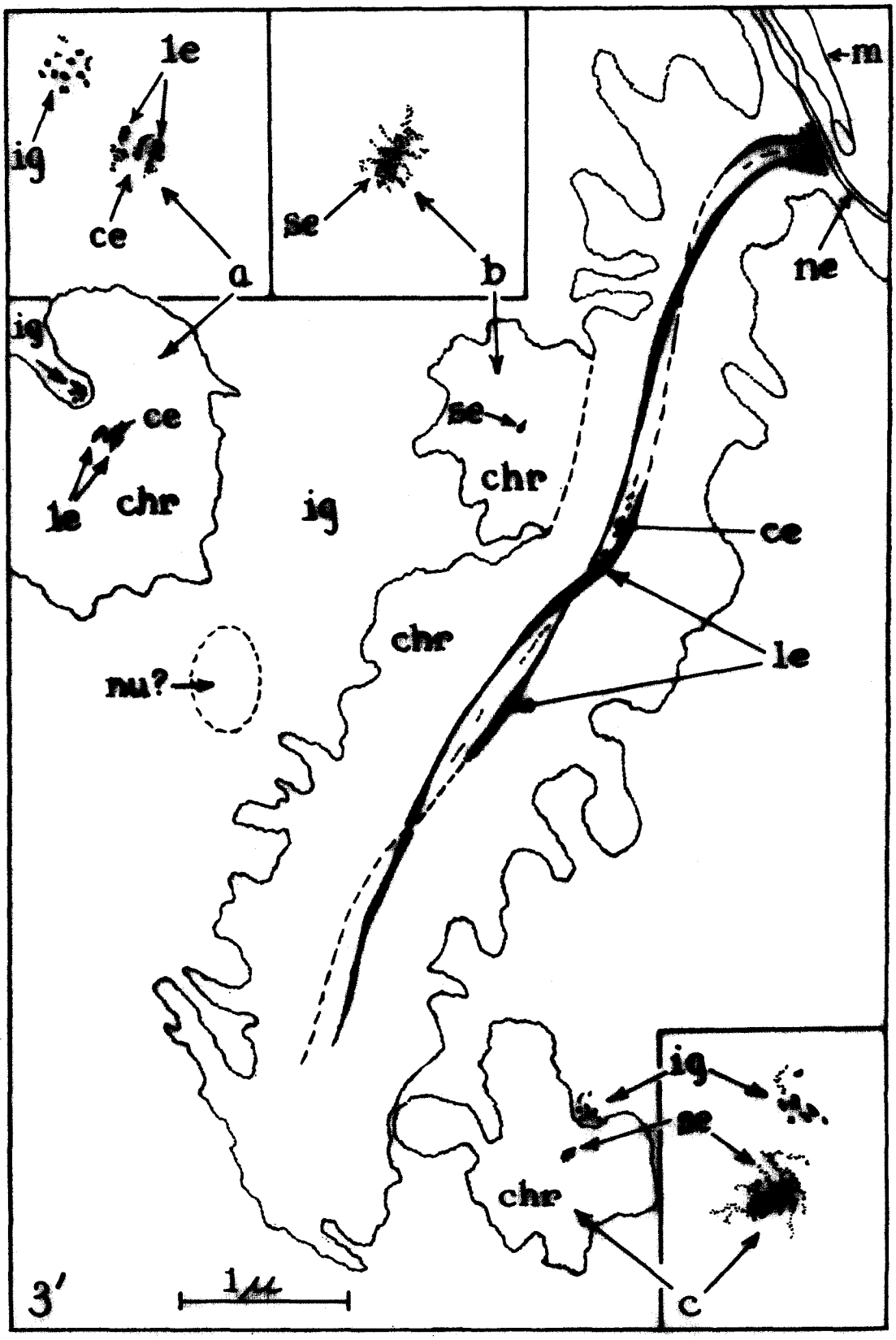
Three cross-sections are seen at *a*, *b*, and *c*; these are shown at higher magnification in the insets.

In *a*, the three elements of the complex are seen in slightly oblique section. They appear continuous with the delicate filamentous material of the chromosome.

b is a slightly oblique section showing only one element of dimensions about that of a single lateral element as shown in *a*.

c is a similar section to *b*, more nearly transverse. Only a single element is seen. The nearby dense clustered granules probably are an aggregation of interchromosomal material. × 27,000; insets, × 53,000.

FIG. 3′ is an overlay on which the essential details interpreted in Fig. 3 are drawn. The approximate boundaries of the chromosomal profiles are indicated by dotted lines. The axial complex is shown making 1½ complete twists.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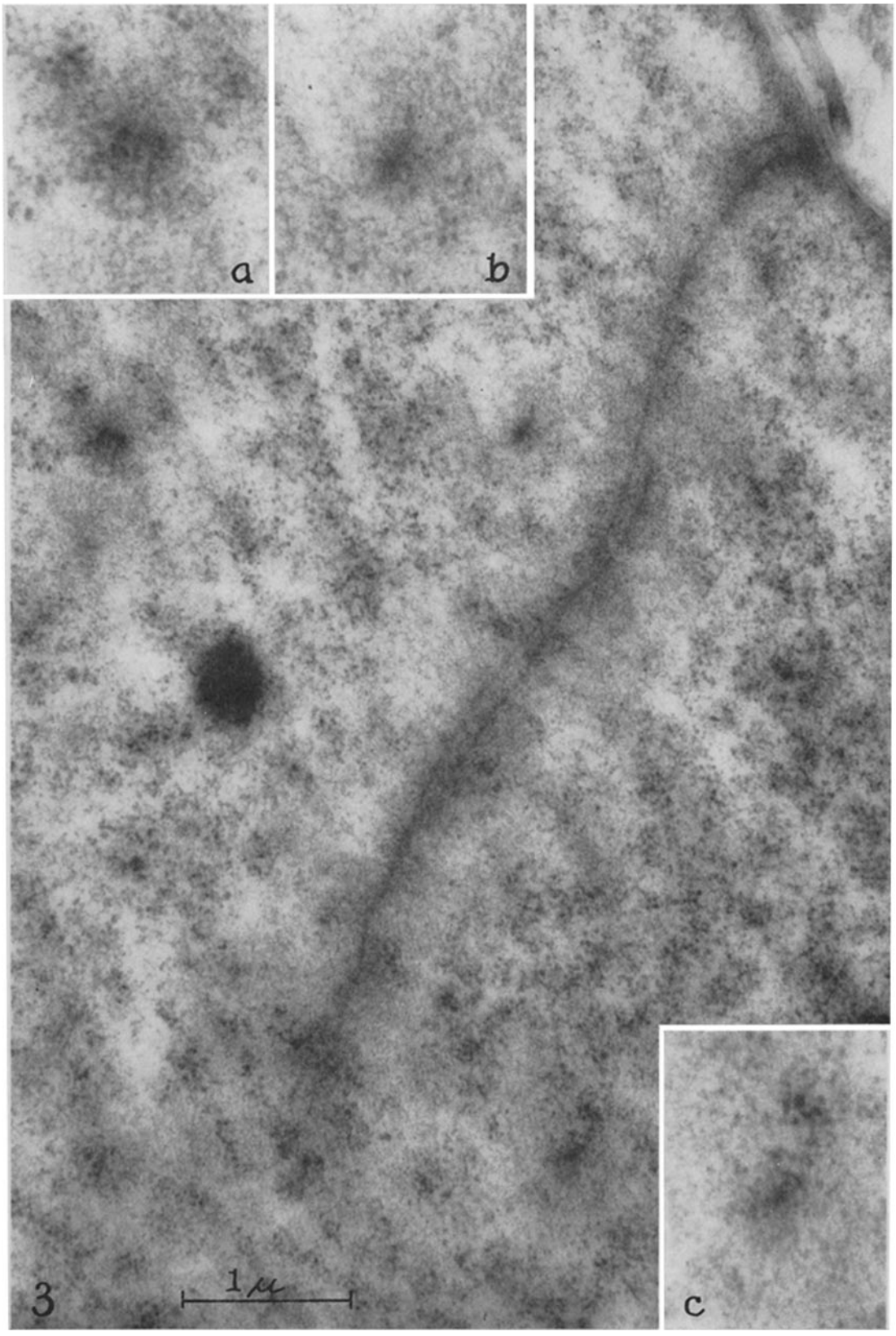


(Moses: Meiotic prophase chromosomes and chromosome pairing)

PLATE 314

FIG. 4. Electron micrograph of a 1000 A section near the edge of a nucleus similar to that in Fig. 2, No. 6.

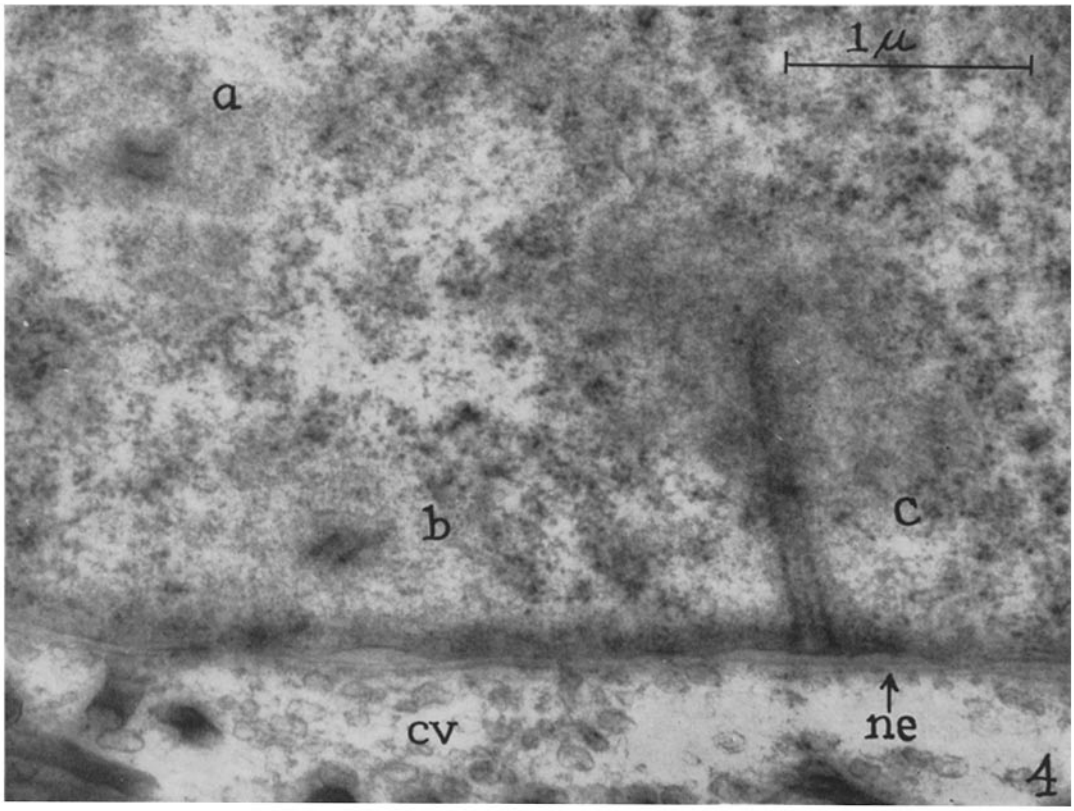
a and *b* are oblique sections through chromosomes. The dense lateral elements with their associated fine chromosomal material are clearly visible, but the central element is faint. The coarse interchromosomal granules surround the fine textured chromatin.

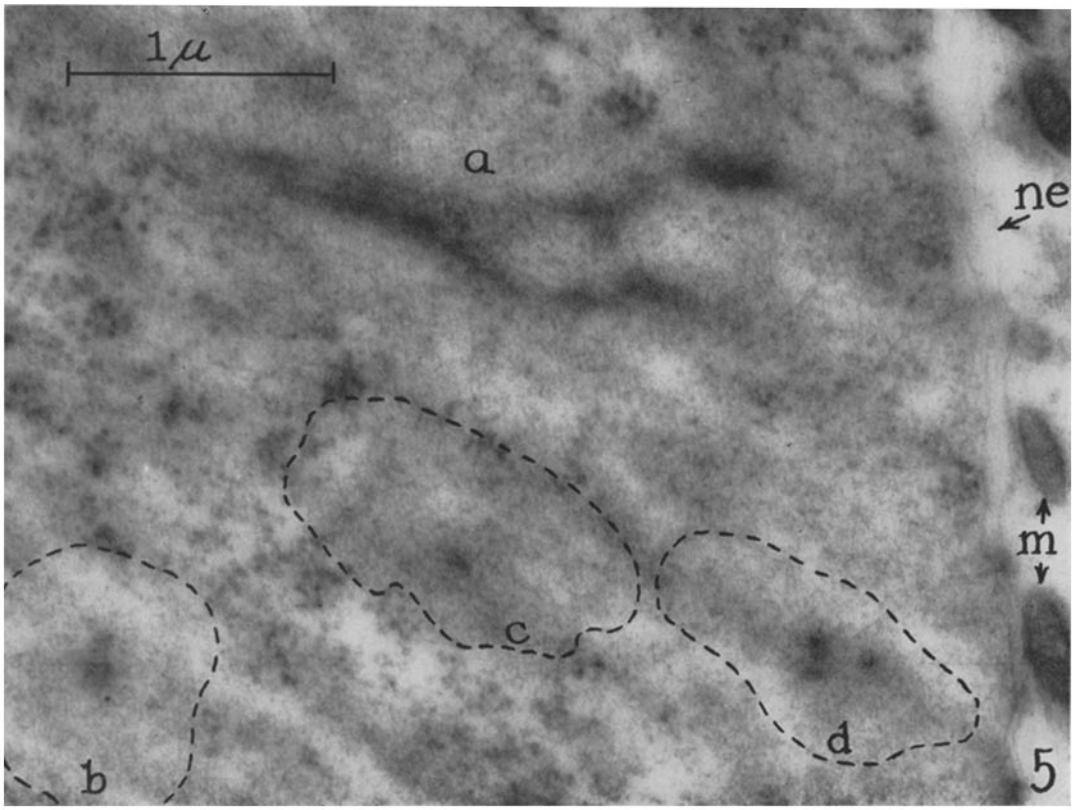
c is a longitudinal section of a short length of chromosome showing its termination against the inner membrane of the nuclear envelope. The parallel strands of the axial complex end on the membrane. × 32,000.

FIG. 5. Electron micrograph of a *ca.* 1600 A section near the edge of a nucleus

A portion of the axial complex is seen in longitudinal section at *a*; three parallel elements are visible. The complex bifurcates and the lateral elements separate; they can be followed for a short distance until they leave the section. The central element cannot be followed beyond the fork.

b, *c* and *d* are cross-sections: paired lateral elements with central strand are seen at *b* and *d*, while a single element, presumably a section of a single lateral element from an unpaired portion of a complex is seen at *c*. The fourth dense body at *d* is not understood. × 35,000.





(Moses: Meiotic prophase chromosomes and chromosome pairing)