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NUCLEOLUS-ORGANIZING REGIONS IN SALIVARY GLAND CHROMOSOMES OF DROSOPHILA MELANOGASTER.

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With 5 figures in the text.

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In the mitotic cell of *Drosophila melanogaster*, nucleoli are organized at specific regions in the proximal part of the X-chromosome and in the short arm of the Y-chromosome (KAUFMANN 1933, 1934; HEITZ 1933 b). In the salivary gland cell of this species the nucleolus is associated with the chromocentral region, but nucleolus-forming regions are not readily discernible because the Y-chromosome and the proximal third of the X are represented by only a few bands of heterochromatin which lie in proximity to heterochromatic portions of the autosomes. Critical information concerning the location of nucleolus-organizing regions is offered by various induced chromosomal alterations involving heterochromatic and euchromatic regions (KAUFMANN 1938). In the present paper there are presented some observations on X-ray induced alterations in which nucleolus-forming regions were transferred to new locations between euchromatic sections. Thus it has been determined that salivary gland nucleoli are organized in heterochromatic portions of the sex chromosomes.

The chromosomal rearrangements were secured in glands from first generation larval progeny of irradiated fathers. Although this procedure prevents the alteration from being perpetuated for supplementary analyses, it permits the study of some complex rearrangements which would not survive to adult stages. Slides were prepared by Miss RUTH BATE using BAUER's modification of the aceto-carmine technique. I am also indebted to Miss RACHEL PARKER for the photographs.

The nucleolus-forming region of the X-chromosome. The salivary gland nucleus of *D. melanogaster* contains a large nucleolus or plasmosome. It may be assumed that this nucleolus results from the fusion of two nucleoli originating independently in each of the sex chromosomes but brought into contact by their pairing. This is demonstrated in cases in which the sex chromosomes have failed to pair and two nucleoli are present. The pressure applied to the cover in spreading the glands for study may so disrupt the nucleolus that fragments of various sizes appear throughout the nuclear cavity, especially when the glands have been dissected out in aceto-carmine without previous fixation. Spreading, however, may serve the useful function of separating non-homologous

chromosomes from each other at the chromocentral region, so that the nucleolus-chromosome relationship is portrayed clearly.

This relationship is indicated in the cell from a normal female shown in figure 1. The nucleolus is associated with the heterochromatin of the paired X-chromosomes, which are detached from the other chromosomes. Some additional nucleolar material either abuts on or is connected with the proximal part of one of the homologues forming the right limb of the second chromosome (2 R), but it should be noted in this connection that nucleolus-like swellings may appear along the surface of any of the chromosomes, especially where they have been fractured, suggesting the welling out of some fluid content. The main nucleolus, however, is characterized not only by a definite place of origin but by the delicate intranucleolar chromatic strands connecting with the sex chromosomes (fig. 1).

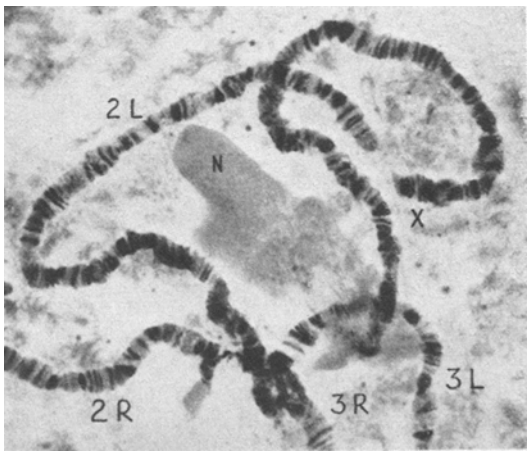
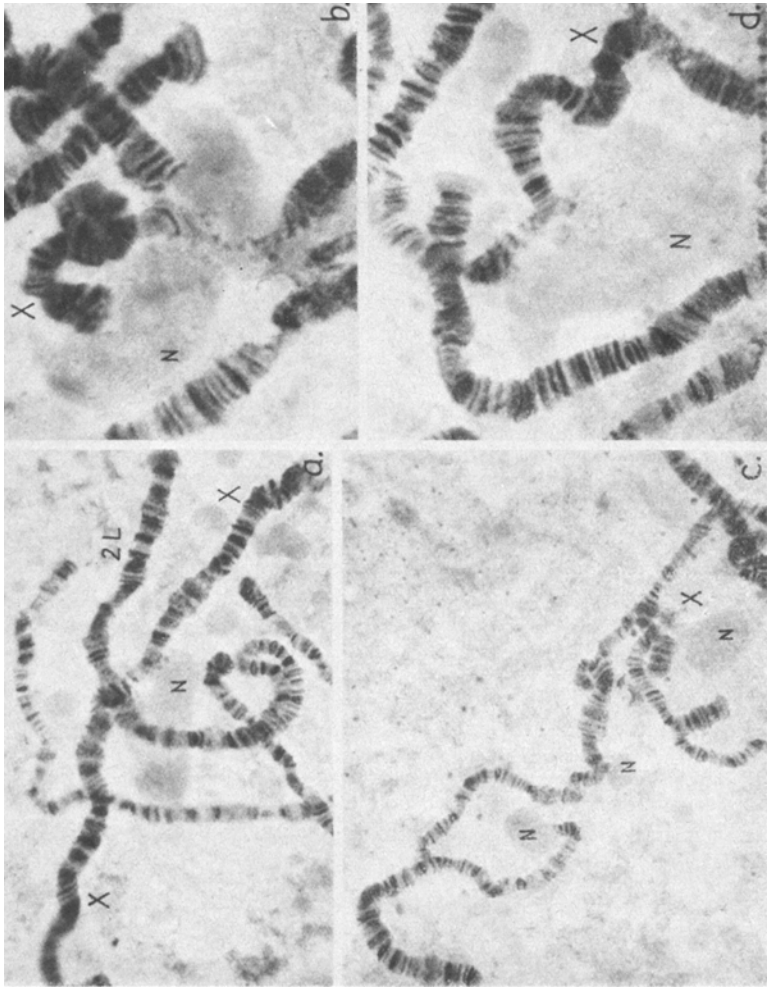


Fig. 1. *Drosophila melanogaster*, salivary gland chromosomes, female. 2 L, 2 R indicate left and right limbs of the second chromosome; 3 L, 3 R left and right limbs of the third chromosome; X the X-chromosome, here detached from the other chromosomes and connected with the nucleolus (N). Note the intranucleolar chromatic strands.

Additional evidence that a nucleolus-organizing region exists in the heterochromatic portion of the X-chromosome is furnished in figures 2a—2d. In this rearrangement the heterochromatic portion of the X from about 20 A 3 to near the spindle attachment region has been transferred to the euchromatic section 13 C, probably between the 13 C 4 and 13 C 5 bands, as determined from BRIDGES' 1935 salivary chromosome map. A nucleolus forms at this position (figs. 2a and 2d). Between 13 C 4 and 13 C 5, extending into the nucleolus, is a series of heterochromatic bands which represent the transposed section of the X-chromosome. At times this heterochromatic material traverses the nucleolus and lies in proximity to the heterochromatin of other chromosomes (fig. 2b) as is characteristic of chromocentral association. As the chromonemata spread out within the nucleolus, the heterochromomeres separate and may present the fan-like pattern shown in figure 2d. Since in this diploid complement there is in addition to the altered, paternal X, a normal maternal homologue, it should also participate in nucleolus formation. That

it does so is suggested in figure 2b, and shown clearly in figure 2c where the proximal regions of the two X-chromosomes are not paired. A large nucleolus is here attached to the normal X; parts of another

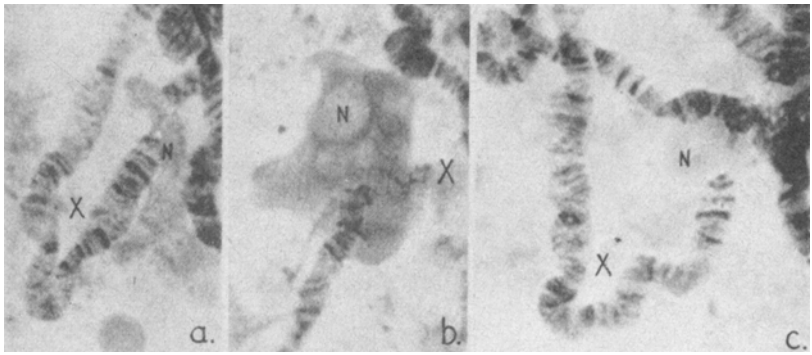


Figs. 2a—d. *D. melanogaster*, female. The nucleolus is formed between euchromatic bands 13 C 4 and 13 C 5 as a result of intercalation of the nucleolus-forming region. a Nucleolus in 13 C region of the X-chromosome; 2 L here overlies the distal 13 C 4 break. b and d show intranucleolar chromatic material; in b chromatic material traverses the nucleolus to associate with the heterochromatin of other chromosomes; in d spreading out of the chromonemata within the nucleolus reveals the chromomeres. c The lowermost of the 3 nucleoli is associated with the heterochromatin of the unaltered maternal X, the other 2 nucleoli adjoin the 13 C 4 and 13 C 5 bands of the altered paternal X.

nucleolus lie adjacent to the 13 C 4 and 13 C 5 bands which have been separated by the intercalation of the proximal region of the X-chromosome.

In another translocation a nucleolus was found at the 20 D end of a section of the X extending from 14 E to 20 D which is inserted in the 64 C region of the left limb of the third chromosome (3 L).

The foregoing observations indicate that nucleolus formation occurs in the heterochromatic portion of the X-chromosome, somewhere between the 20 A 3 and 20 D 1 bands. A more specific determination of the nucleolus-organizing locus has been possible in certain preparations in which formation of the nucleolus has separated parts of the chromosome (figs. 3a—3c). These three photographs are of males, so that the X-chromosome exists in the haploid condition. Nucleolar material lies between bands which have been interpreted as the 20 B $\widehat{1\,2}$ and 20 C $\widehat{1\,2}$ doublets. The 20 B 3 band of BRIDGES' map could not be identified in

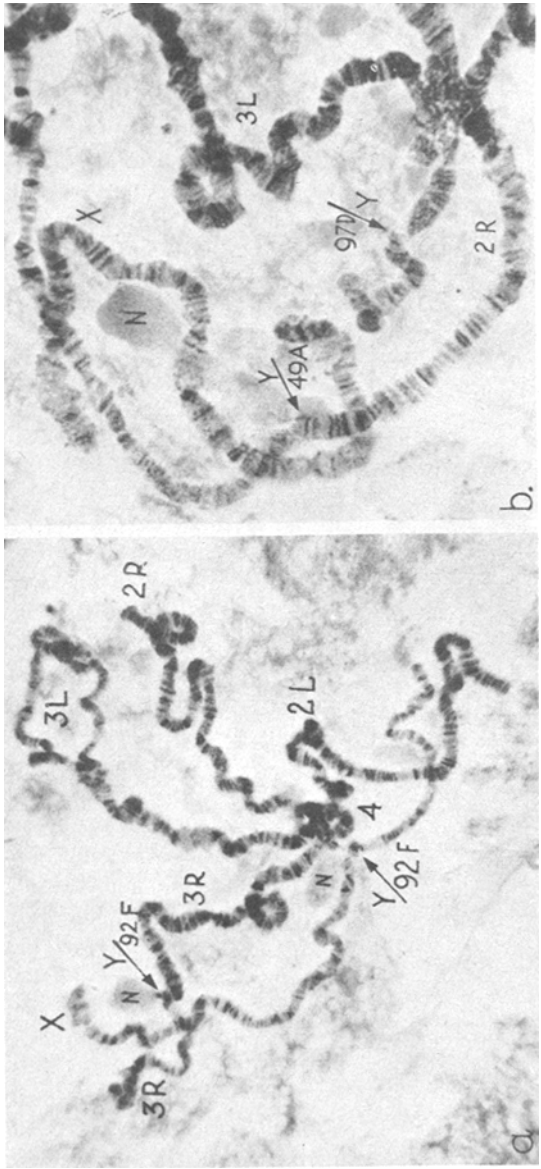


Figs. 3a—c. *D. melanogaster*, male. Separation of heterochromatin of X-chromosome between 20 B $\widehat{1\,2}$ and 20 C $\widehat{1\,2}$ bands by formation of nucleolus. In c only the distal (20 B $\widehat{1\,2}$) bands show clearly.

these preparations, so that it is uncertain whether the B 3 band is associated with the proximal or distal section of the separated chromosome. In figures 3a and 3b the proximal and distal bands bordering the nucleolus are apparent; in figure 3c the B $\widehat{1\,2}$ doublet shows clearly, but the proximal region of this chromosome is associated so intimately with autosomal heterochromatin that the C bands are indistinguishable. Similar observations of the intercalation of nucleolar material between the 20 B $\widehat{1\,2}$ and 20 C $\widehat{1\,2}$ bands have been made on cells of female larvae.

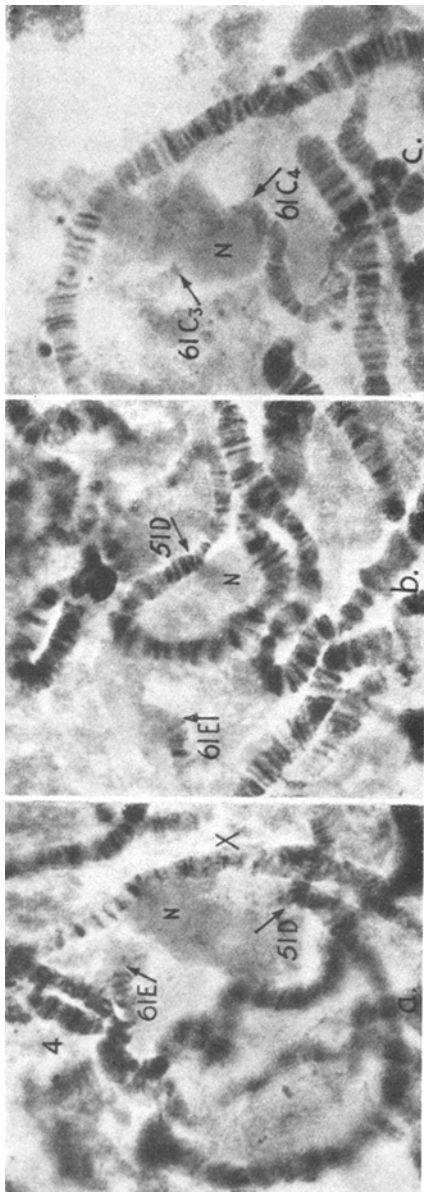
Some evidence has been accumulated which indicates that the nucleolus-forming portion of the chromosome lies proximal to 20 B. Several glands were observed in which the nucleolus is associated with this region, and in a few of the glands only with the 20 C and D bands. Moreover, in an X—3 L reciprocal translocation having breakage points in 20 C and 67 E, a nucleolus is associated with the 20 C portion of the X/3 L recombination (centromere-20 C/67 E-tip of 3 L) but not with the 3 R · 3 L/X combination (100—81 centromere 80—67/20 C-tip of X). The symbol / is used to indicate the position of breakage and reattachment points.

The nucleolus-forming region of the Y-chromosome. The existence of a nucleolus-forming region in the Y-chromosome of the salivary gland



Figs. 4a—b. *D. melanogaster*, male. a A 3 R-Y reciprocal translocation with breakage point in 3 R in region 92 F. The section of 3 R from the tip to 92 F is attached to the proximal part of the Y-chromosome which is paired with the heterochromatic region of the X-chromosome (the lower Y/92 F). The nucleolus which forms where the distal section of the Y is attached to 3 R in 92 F (the upper Y/92 F) suggests the translocation of a nucleolus-forming region to that location. b A 2 R-3 R-Y rearrangement. A nucleolus forms where the Y is attached at 49 A in 2 R, suggesting the translocation of the nucleolus-forming region to this location.

has been inferred from a series of translocation configurations. In these a section of the Y is transferred to an autosomal region where a nucleolus



Figs. 5a—c. *D. melanogaster*, male. a and b Two nuclei showing a rearrangement in which the nucleolus forms between 51 D in 2 R and 61 F in 3 L. Th is interpreted as resulting from the insertion of the nucleolus-forming region of the Y between these two loci. In a note the chromomeres within the nucleolus following 51 D. c A rearrangement in which the nucleolus-forming region is inserted between the 61 C 3 and 61 C 4 bands of 3 L.

is then organized. Since it is not always possible to identify the bands representing the Y-chromosome in these nuclei, interpretations of Y-chromatin have depended to a considerable extent on pairing relations with the proximal region of the X-chromosome. When the bands of the Y-chromosome can be identified they are paired with the region of the X proximal to 20 A, as PROKOFYEVA-BELGOVSKAYA (1937) has determined. An illustration of pairing between the X and the proximal portion of the Y is represented in figure 4a of a 3 R–Y translocation. The distal section of the Y is attached to 3 R at 92 F, where it forms a nucleolus. Although the distal section of the Y is not paired with the X in this figure, it frequently does so in such translocations. Of the 44 glands showing rearrangements of Y-chromosome material, which were obtained in another study (KAUFMANN and DEMEREC 1937), several had similar reciprocal translocations involving transfer of nucleolus-forming regions to autosomes.

Among more complex rearrangements from male larvae, two showed the nucleolus between sections of autosomes. In one of these (figs. 5a, 5b) the nucleolus occurs regularly between a 51 D break in 2 R and a

61 F break in 3 L. This has been interpreted as resulting from the insertion of Y-chromatin into this position. Another complex alteration (fig. 5c) shows a nucleolus between the 61 C 3 and 61 C 4 bands of 3 L. This likewise has been interpreted as resulting from the translocation of nucleolus-forming, Y-chromosome material into the left limb of the third chromosome. In the photographs of these alterations, poorly defined chromatic material may be seen within the nucleolus.

Rearrangements such as have just been described suggest that the Y-chromosome of the salivary gland contains a nucleolus-forming region homologous with that of the X-chromosome, although actual identification of the bands involved has not been determined.

Discussion.

Nucleolus-forming regions. Since HEITZ (1931) focussed attention on the relationship which exists between the nucleolus and specific chromosomes in certain plants, there has been an increasing number of similar observations. They indicate the widespread occurrence of nucleolus-forming chromosomes in both plants and animals from thallophytes to spermatophytes, and from protozoa to vertebrates. A review of the recent literature pertinent to this subject may be found in papers by MCCLINTOCK (1934), HEITZ (1935), CHEN (1936), SATO (1937), EMMENS (1937) and GATES (1937).

The dividing cells of several species of *Drosophila* have revealed a relationship between the nucleolus and specific chromosomes (HEITZ 1933a, 1933b; KAUFMANN 1933, 1934, 1936, 1937). Studies of the salivary glands of *Drosophila* have furnished, however, varying interpretations. This may be attributed in part to the fact that in those species with a distinct chromocentral region the position of the nucleolus is obscured because the enlarged chromosomes, differentially elongated in euchromatic and heterochromatic regions, are compactly aggregated at their spindle attachment regions. The pressure applied to the cover in spreading the glands for study helps moreover to distort the normal aspect. BRIDGES (1935) has stated briefly that in *D. melanogaster* the nucleolus is attached to the base of the X at the bands in 20 C and B. BAUER (1936b) records in his figure 5 of *D. pseudoobscura* a connection between the loose heterochromatin of the X-chromosome and the nucleolus. TINIAKOV (1936) reported that in *D. funebris, D. obscura* and *D. melanogaster* the nucleolus is connected with the X-chromosome, usually by an aggregate of chromatic threads. EMMENS (1937) observed a nucleolus-forming chromosome in *D. subobscura*. Other interpretations deny a constant relationship between any chromosome and the nucleolus, or suggest that all of the chromosomes are associated with the nucleolus

through a common chromocenter formed by an aggregation of proximal chromomeres[1].

The various chromosomal rearrangements described in the present paper furnish evidence that the salivary glands of *D. melanogaster* contain nucleolus-forming regions homologous with those of mitotic cells. A similar situation exists in *D. ananassae*. In both of these species the nucleoli are organized in portions of the chromosomes which are heteropyknotic in the prophases of dividing cells and which are represented in the salivary gland nucleus by only a few bands of heterochromatin. The existence of nucleolus-forming regions within this heterochromatin attests to its specific organization. Because of such organization the chromocentral region of the salivary gland nucleus cannot be regarded as an amorphous mass, designated as a "magma" by KOLLER (1935). Moreover, apart from the translocations pertinent to the present study several were observed involving breaks in the heterochromatin of the second and third chromosomes. The resulting chromosomal rearrangements which will be described in another publication demonstrate the individuality of heterochromatic regions of the autosomes. Induced chromosomal alterations of these types serve to confirm the interpretation previously inferred from nuclei showing dissociation of the component chromosomes, that the chromocentral region results from the close approximation of proximal regions of the chromosomes of the complex (cf. BAUER 1936a, 1936b; FROLOWA 1936; TINIAKOV 1936; EMMENS 1937; KAUFMANN 1937). Because of this close association the nucleolus normally occupies a position in the chromocentral region and may simulate thereby a direct attachment to all of the chromosomes.

Observations that the nucleolus-forming regions are restricted to the sex chromosomes of *D. melanogaster* stand at variance with FROLOWA's interpretation (1936a, 1936b) that the nucleolus is connected directly with an aggregate formed by the centromeres of all the chromosomes. TINIAKOV (1936), although recognizing the association of the nucleolus with the sex chromosomes, likewise has reported the existence of an aggregation of granules ("chromatin nucleoli", which he regards as independent from the spindle attachment regions) frequently centering on the nucleolus and uniting with the proximal regions of the various chromosomes by chromatic threads. The transposition shown in figure 2 of the present paper demonstrates that the centromere of the X-chromosome has no direct connection with the nucleolus. The organization of this altered X-chromosome may be designated as follows, using the lettering of BRIDGES' 1935 map; tip of X-13 C 4/20 A 3-20 F/13

[1] In Diptera other than Drosophila, nucleolus-forming chromosomes have been found in the salivary glands or the structurally similar Malpighian tubule cells in *Bibio* (HEITZ and BAUER 1933); *Simulium* (GEITLER 1934); *Chironomus* (KING and BEAMS 1934; BAUER 1935).

C 5-20 A 2/20 F-centromere. The nucleolus invariably develops from the heterochromatic region (20 A-20 F) inserted between 13 C 4 and 13 C 5, and not from the region adjacent to the centromere. This is shown best in those nuclei in which the proximal regions of the two X-chromosomes do not pair (fig. 2c). FROLOWA's further assumption that the nucleolus should be associated most intimately with the chromosome containing the greatest amount of inert chromatin is in harmony with the situation in *D. melanogaster*, but this relationship is not dependent on the quantity of inert material, as FROLOWA suggests (1936b), but on the existence of nucleolus-organizing regions within the inert material.

Intranucleolar chromatin. A conspicuous feature of the *Drosophila* salivary gland nucleus is the intranucleolar chromatic material. Its existence has been reported in other publications (HEITZ 1934; KAUFMANN 1934, 1937; FROLOWA 1936a, 1936b; TINIAKOV 1936). KAUFMANN (1936, 1937) suggested that in *D. ananassae* the distinctly banded intranucleolar heterochromatin represents the paired satellites of the fourth or nucleolus-forming chromosomes. The banded portion is connected with the bulk of these chromosomes by chromatic strands.

In the mitotic cells of *D. melanogaster* delicate strands traverse the nucleolus connecting the dissociated parts of the X- and Y-chromosomes. Similar strands may also traverse other secondary constrictions not associated with nucleolus formation, as is well illustrated in the left limb of the second chromosome (KAUFMANN 1934). It has been assumed that such connections represent attenuations of the chromonemata, probably of regions possessing little nucleic acid (cf. HEITZ 1935, who describes these fibrillae as "anukleal"). The question arises, therefore, whether the strands within the salivary gland nucleolus are similar structures. Frequently they seem to terminate in the nucleolus rather than connect dissociated parts (fig. 1), but this may be the result of the nucleolus surrounding the chromosome, as occasionally occurs in neuroblast cells. When the nucleolus separates parts of the chromosome (fig. 3) there is evidence of intranucleolar connecting strands. Such strands, however, bear chromatic granules, which are not evident in the "anukleal" fibrillae of the constriction regions of dividing chromosomes, but this contrast in appearance may result from the difference in the amount of nucleic acid in the two types of nuclei, for the chromosomes of *Drosophila* when in an attenuated state, as in early mitotic and oocyte prophase, do not give a distinct Feulgen reaction (cf. GARDINER 1934).

Whatever the merits of such attempts to determine homologies, there is good evidence that the strands within the salivary gland nucleolus are continuous with those of the associated sex chromosomes. This is shown in figures 1, 2b, 2d, 3b, 5a, 5b and 5c. In figure 5c there is shown a zone of chromatic material which traverses the nucleolus between the dissociated 61 C 3 and 61 C 4 bands. Since this chromatic material is not part of the left limb of the third chromosome it probably represents

intercalated Y-chromosome material. The chromonematic axis is to be regarded, therefore, as more or less continous from the proximal part of 3 L through the intercalated Y-heterochromatin, around which the nucleolus develops, into the tip of 3 L. A similar situation with respect to X-chromosome heterochromatin is shown in figure 2d.

Within the nucleolus the chromomeres along the chromonemata which form the salivary chromosome may become conspicuous. A distinct fan-like aspect shows clearly in the preparation illustrated in figure 2. A similar appearance is visible in figure 5a, adjacent to the 51 D break in the right limb of the second chromosome. At such places the individual chromonemata become widely separated, and the homologous chromomeres correspondingly conspicuous. The diffuse mass of threads sometimes seen within the nucleolus may result from such wide separation. This is not meant to imply, however, that the material of the nucleolus is itself banded, but merely that the nucleolus presents a medium in which the opening out of the constituent chromonemata of the chromosome may occur (cf. BAUER 1935). Widening out of chromatids within the nucleoli of dividing cells has been reported by DEARING (1934) for *Ambystoma,* by CHEN (1936) for the opalinid, *Zelleriella,* and by PÄTAU (1937) for the peridinian, *Merodinium.*

The observations of the present paper concern primarily the main nucleolus of *D. melanogaster.* No effort has been made in the present study to determine either the origin of accessory nucleolus-like bodies sometimes seen along the chromosomes (cf. KING and BEAMS 1934; BAUER 1935) or the significance of the "puffs" and other localized swellings which appear to be associated with the accumulation of fluids within the salivary gland chromosomes (BRIDGES 1935; METZ 1937).

It is recognized also that the method of the formation of nucleoli may differ greatly in different species of Drosophila, since EMMENS (1937) has indicated that there is variability in the organization of the chromocentral region within the genus, and BAUER (1936a) has shown differences in the location and nature of the nucleolus-forming regions of the genus Chironomus.

Summary.

The nucleolus of the salivary gland nucleus of *Drosophila melanogaster* is formed by nucleolus-organizing regions which exist in the heterochromatin of the sex chromosomes. This interpretation is supported by the discovery of a series of induced chromosomal alterations involving transfer of nucleolus-forming regions to euchromatic sections of the chromosomes.

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