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Inversion Polymorphism in Two Populations of *Drosophila melanogaster* in Lagos State, Nigeria

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ABSTRACT

Two different natural populations of Drosophila melanogaster were surveyed to determine the types of inversions present by examining the salivary gland chromosomes of third instar larvae. Seven different inversions were detected in populations, Tejuosho market and Bariga market (Lagos, south-western Nigeria) populations. All inversions detected were single, paracentric and autosomal. The inversions observed were distributed in the arms of the chromosomes as follows: two in the left arm of chromosome 2 (2L), one in the right arm of chromosome 2 (2R), two in the left arm of chromosome 3 (3L) and two in the right arm of chromosome 3 (3R). Some inversions occurred together with other inversions in the same larva and this occurrence was probably just due to chance but also indicates that such conditions were not lethal.

Some of the inversions detected in this study had been recorded by earlier researchers in some parts of south-eastern Nigeria and south-western Nigeria. The occurrence of similar inversions in these regions may be evidence that the inversions are not recent. This similarity in inversions also suggests that there is or had been migration from one place to the other or the inversions originated somewhere else and had been transported to other places.

***Key words**: Inversion, Drosophila melanogaster, populations, migration, lethal*

INTRODUCTION

Chromosomal inversion polymorphism is a common characteristic of the genome in the *Drosophila* genus. Inversions have been said to be the most common form of chromosomal rearrangement in the evolutionary history of *Drosophila* (Gupta and Bihari, 1987; Aulard, 1986; Das and Singh, 1990; Aulard *et al*., 2002; Balanyà *et al*.,

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2004). Paracentric inversions are the most common types of inversions in nature (Das and Singh, 1990; Aulard *et al*., 2002; Balanyà *et al*., 2004). Pericentric inversions and inversions involving the X-chromosomes are very rare because of aneuploid eggs produced by recombination in female karyotypes and possible deleterious effects in hemizygous males respectively (Aulard *et al*., 2002). Over 42,000 paracentric inversions have become fixed during the evolution of the species and about 28,000 paracentric inversions are currently segregating in natural populations. About three-quarter of *Drosophila* species have been found to be polymorphic for paracentric inversions in natural populations (Navarro *et al*., 2005). Apart from *Drosophila* species, paracentric inversions are common in other dipterans, such as midges and mosquitoes in the species complex of *Anopheles gambiae* (Hoffmann *et al.,* 2004). These paracentric inversions are presumed to have resulted from the homologous recombination of repetitive elements such as transposons because transposable elements have been found at breakpoints in *Drosophila* and mosquitoes (Aulard *et al.,* 2002; Hoffmann *et al*., 2004).

Several evolutionary consequences of inversions have been reported. Inversions have been regarded as a device for holding together co-adapted genes, and therefore an outstanding adaptation of organisms, because of the low rate of successful recombination within the inverted region (Gupta and Bihari, 1987; Balanyà *et al.,* 2004; Hoffmann *et al*., 2004). The inversion process sometimes serves to produce a record of the evolutionary history of a group of species. As species evolve, breaks for new inversions can occur within preexisting inversions. This therefore leads to very complex rearrangements of loci as compared to the original arrangement. Since certain arrangements can only come about by a specific sequence of inversions, it is possible to know in such cases, which species evolved from which other species (Gupta and Bihari, 1987; Balanyà *et al.,* 2004; Hoffmann *et al*., 2004). Within the same species, it is possible to determine the history of colonization of different areas by the species (Gupta and Bihari, 1987; Hoffmann *et al.,* 2004).

Drosophila melanogaster, a cosmopolitan and domestic species, is highly polymorphic and over 500 inversions have been described from different regions of the world (Aulard *et al*., 2004). The extent of chromosomal variability varies from one species to another and from one population to another of the same species (Gupta and Bihari, 1987; Das and Singh, 1990; Aulard *et al*., 2002; Aulard *et al*., 2004). For instance, *D. melanogaster* is known to be highly polymorphic while *D. simulans* is known to be a monomorphic species (Aulard *et al*., 2004). Also, the Afrotropical populations of *D. melanogaster* have been found to be more polymorphic than populations of *D. melanogaster* from other regions, such as India and America (Aulard *et al.,* 2002; Hoffmann *et al*., 2004). Some inversions also tend to occur in higher frequency in one climatic condition than the other. Apart from ecological and climatic factors, other factors that affect the presence and frequency of particular inversions in a population include: food availability, distance between sites, human

traffic between sites, natural boundaries, level of urbanization and industrialization as well as population size (Akpabio, 2000; Aulard *et al.,* 2002; Iriarte *et al*., 2003).

The objective of this research was to study inversion polymorphism in the two populations of *D. melanogaster* under investigation.

MATERIALS AND METHODS

Samples of *Drosophila melanogaster* were collected from Tejuosho market and Bariga market in Lagos, Nigeria. Tejuosho market and Bariga market are about 12km apart from each other. Tejuosho market seems to be a bigger market in terms of the human traffic, the level of urbanization, the population size and the general size of the market. The two markets get supplies from the same markets, Mile-12 market and Ketu market; Tejuosho market however seems to have increased food availability because of the bigger size of the market.

Samples were collected between July and October, 2007. Flies were trapped using bottles containing fermenting oranges and bananas kept at strategic places in the markets for about 24 hours. Male and female flies were raised in culture bottles on the same type of medium used by Williams and Akpabio (1993) and the bottles were placed on shelves in the laboratory at about 25^{o}C. Mass cultures were used in this research because isofemale lines rarely survive in this part of the world. Frequencies of inversions were therefore not taken. After 3 days, the culture bottles were transferred to an incubator at 22^{o}C. The reduced temperature was to retard the rate of larval development that results in the development of larger larvae. On the 4th day of transfer of flies to culture bottles, about 3 drops of yeast suspension were added to the medium in order to ensure a yield of relatively large larvae.

Salivary gland chromosome preparations were made, using third instar larvae, by the usual salivary gland squash technique. Photomicrographs of prepared slides were taken under oil immersion (x100 objective) with the aid of a Wild M20 microscope with PS50 photoautomat and an MPS55 electronic control unit. The reference map constituted by Lefevre (1976) was employed to determine the chromosomal arms that carry the different inversions.

RESULTS

The chromosomal analyses of Tejuosho market and Bariga market populations of *Drosophila melanogaster* revealed seven different inversions. Inversions were found in chromosomes 2 and 3. No inversions were however observed in chromosomes 1 and 4. All inversions detected were single, paracentric and autosomal inversions. No complex inversions or pericentric inversions were observed. The inversions observed were distributed in the arms of the chromosomes as follows: two in the left arm of

chromosome 2 (2L), one in the right arm of chromosome 2- (2R), two in the left arm of chromosome 3- (3L) and two in the right arm of chromosome 3- (3R) (Table 1). The inversions found in this study have been arbitrarily named A, B, C, D, E, F and G. The descriptions of the inversions are as follows:

CHROMOSOME- 2, LEFT ARM (2L)

Inversion A (Plate 1a)

The inversion is a large paracentric inversion located in the left arm of chromosome 2 and has been arbitrarily named *In(2L)A. In(2L)A* was found in the Bariga market and Tejuosho market populations.

Inversion B (Plate 1b)

This inversion, *In(2L)B,* is a small paracentric inversion in the left arm of chromosome 2*. In(2L)B* was found in the Tejuosho market population only.

CHROMOSOME- 2, RIGHT ARM (2R)

Inversion C (Plate 1c)

In2R(C) is a small paracentric inversion in the right arm of chromosome 2 and is located around the middle of the chromosome arm. *In(2R)C* detected in this study was found in the Tejuosho market population only.

CHROMOSOME- 3, LEFT ARM (3L)

Inversion D (Plate 1d)

This inversion is a large paracentric inversion and it is located in the left arm of chromosome 3. *In(3L)D* was found in both Bariga market and Tejuosho market populations.

Inversion E (Plate 1b)

This is a relatively small paracentric inversion located on the left arm of chromosome 3. *In(3L)E* was found together with *In(2L)A* in the same larva. They were detected in the Tejuosho market population only.

CHROMOSOME- 3, RIGHT ARM (3R)

Inversion F (Plate 1e)

In(3R)F is a paracentric inversion located in the right arm of chromosome 3*. In(3R)F* was found in both the Tejuosho market and Bariga market populations.

Inversion G (Plate 1f)

In(3R)G is a relatively large paracentric inversion located at the subterminal portion of chromosome 3R. *In(3R)G* was found in the Bariga market population only.

DISCUSSION

The study of chromosome inversion polymorphism in the Bariga market and Tejuosho market populations of *D. melanogaster* yielded altogether seven inversions, all paracentric and autosomal. No pericentric inversion was recorded in this study. This observation is consistent with those from other surveys that pericentric inversions in *D. melanogaster* are very rare (Ashburner and Lemeunier, 1976; Stalker, 1976; Knibb *et al.,* 1981; Das and Singh, 1990). According to Aulard *et al.* (2002), pericentric inversions are very rare because of aneuploid eggs produced by recombination in female karyotypes. Paracentric inversions have probably resulted from the homologous recombination of repetitive elements such as transposons because transposable elements have been found at breakpoints in both *Drosophila* and mosquitoes (Hoffmann *et al.,* 2004).

No inversion was recorded in the X-chromosome and chromosome 4. The absence of inversion in the X-chromosome supports the rare occurrence of inversion involving the X- chromosome recorded by many researchers, such as Aulard *et al.* (2002) and Balanyà *et al.* (2004), although one case of inversion polymorphism in the X-chromosome was detected once in the Lagos population (Williams and Akpabio, 1993). According to Aulard *et al.* (2002), inversions involving the X-chromosomes are very rare because of possible deleterious effects in hemizygous males. And according to Das and Singh (1990) and Aulard *et al.* (2002), inversion polymorphism has not been recorded in chromosome 4. Absence of inversion polymorphism in chromosome 4 has been attributed to its very short length (Ashburner and Lemeunier, 1976).

Inversions were observed in the four arms of chromosomes 2 and 3, two in the left arm of chromosome 2; one in the right arm of chromosome 2; two in the left arm of chromosome 3; and two in the right arm of chromosome 3. A number of studies on chromosome polymorphism in *D. melanogaster* have found the right arm of chromosome 3 to have the greatest variety of paracentric inversions (Mourad and Mallah, 1960; Stalker, 1976; Knibb *et al.,* 1981). The greater variety of inversions in 3R has been attributed to its length (Ashburner and Lemeunier, 1976). The right arm of chromosome 3 is the longest chromosome arm in *D. melanogaster* (Lefevre, 1976). Two inversion types only were detected in chromosome 3R in this study. This is probably due to the small sample size of larvae used.

Observations of the salivary gland chromosome preparations revealed that majority of the larvae sampled were inversion heterozygotes. This supports the fact that inversion heterozygotes have a selective advantage compared to standard (Hoffmann *et al*., 2004). Inversion heterozygotes exhibit heterosis with respect to certain components of fitness, such as: viability, development time, longevity, mating success, resistance to thermal extremes, fecundity, body size and bristle numbers (Das and Singh, 1990; Hoffmann *et al.*, 2004).

Some of the inversions detected in this study had been recorded by earlier researchers. For instance, *In2R(C)* is similar to *In2R(G)* detected by Akpabio (2000) in the Ikot-Ekpene (south-eastern Nigeria) and Lagos (south-western Nigeria) populations of *D. melanogaster*. *In(3L)D* is also similar to *In(3L)C* detected by Akpabio (1985) in the Satellite town (Lagos) and University of Lagos Campus populations of *D. melanogaster.* The occurrence of similar inversions in Satellite town, University of Lagos campus and Ikot-Ekpene is probable evidence that the inversions are not recent. This similarity in inversions also suggests that there is or had been migration from one place to the other or the inversions originated somewhere else and had been transported to other places.

The differences in frequencies of inversions may be due to both ecological and climatic factors. The differences may be ecological since inversion occurrence is an adaptive phenomenon, in which the population adapts to the environment where it may be found. The differences in inversion frequencies may also be climatic, showing the effect of time and season of the year apart from the geographical location (mountain, lowland, island, e.t.c.) of a sample site which determines the local climate (Hoffmann *et al.,* 2004; Aulard *et* al., 2002). Certain inversions may be adaptively more favoured in some climatic regions than in others. Consequently, such inversion frequencies may be high in those populations when sampled. This study however did not include the frequencies of the different inversions present in these populations. It also did not include the collection of samples during different seasons. More importantly, however, the two collection sites are just about 12km away from each other and are located at almost the same altitude (about 0-25m above sea level). Although little or no climatic variation is expected, conclusions however cannot be drawn until large samples from both populations are examined. The fact that Tejuosho market and Bariga market are in the same geographical or climatic zone may cause them to have identical ecological factors. In spite of these, there may be little or no mixing between the two populations, so they may indeed be separate populations but with occasional input from other areas as a result of fruit sales.

Differences in inversion frequencies within the same geographical zone may be determined by many factors, such as: distance between sites, human traffic between sites, natural boundaries, level of urbanization, population size, industrialization e.t.c (Akpabio, 2000; Aulard *et al.,* 2002; Iriarte *et al*., 2003). More studies will be needed to give insights into types of inversions in these populations of *D. melanogaster*, seasonal variations of the inversions and variations with respect to the earlier mentioned factors.

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Table 1: The Different Inversions in *Drosophila melanogaster* found in this Study and their Localities of Collection

Inversions	Chromosome Arm Involved	Locality
A	2L	Bariga market and Tejuosho market
B	2L	Tejuosho market
C	2R	Tejuosho market
D	3L	Bariga market and Tejuosho market
E	3L	Tejuosho market
F	3R	Bariga market and Tejuosho market
G	3R	Bariga market

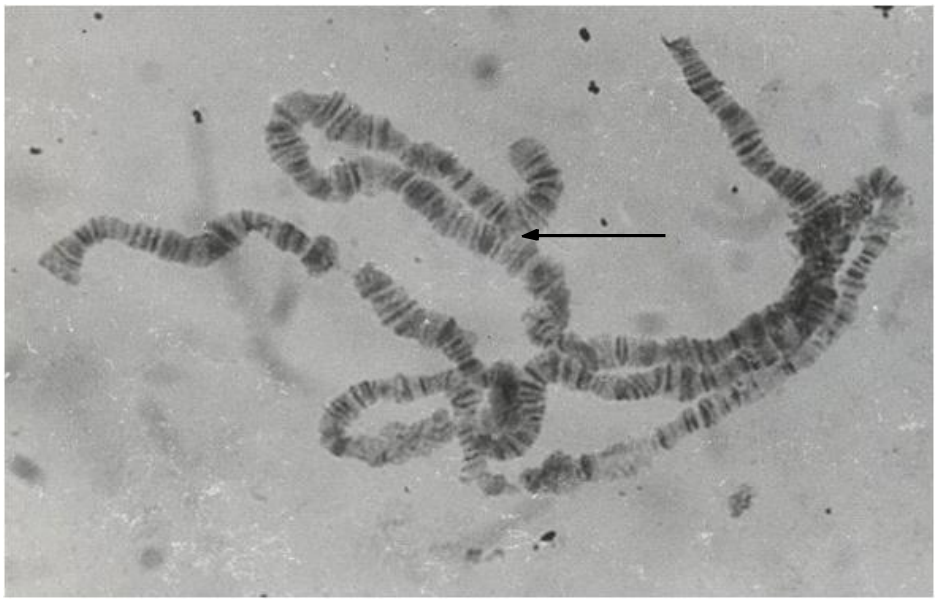

Plate 1a: *In(2L)A*
In(2L)A is a large paracentric inversion. Arrow points to the inversion junction, i.e. the point of divergence between the standard and inversion chromosome.

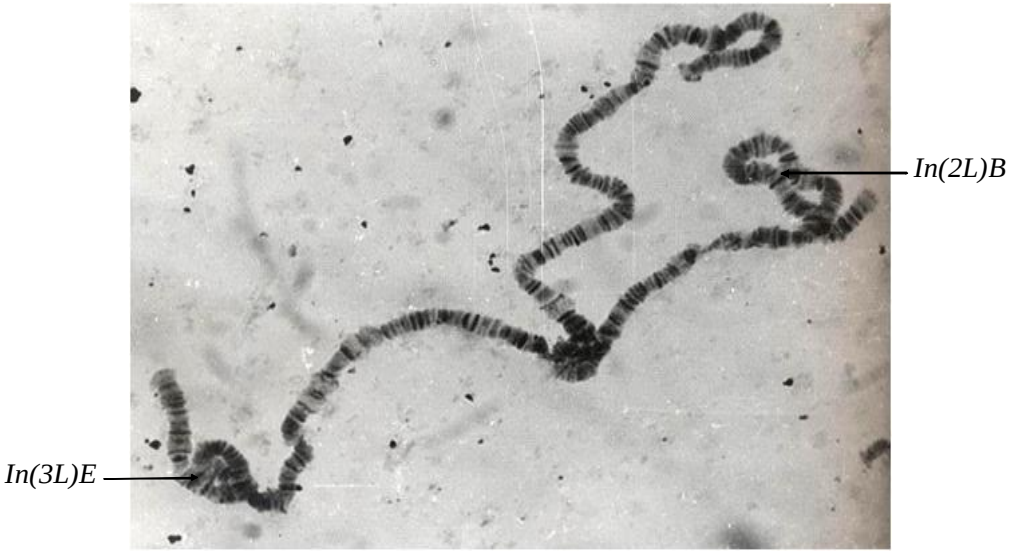

Plate 1b: *In(2L)B* and *In*(3L)*E*
In(2L)B is a small paracentric inversion and *In(3L)E* is a relatively small paracentric inversion. *In(2L)B* and *In(3L)E* are found together in the inversion heterozygote. The arrows point to the inversion junctions.

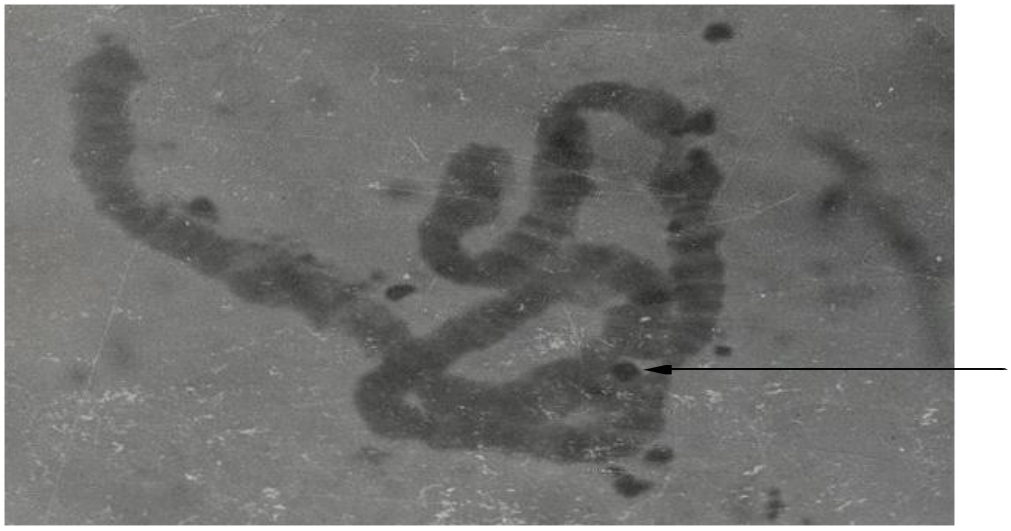

Plate 1c: *In(2R)C*
In(2R)C is a small paracentric inversion located around the middle region of chromosome 2R. Arrow points to the inversion junction.

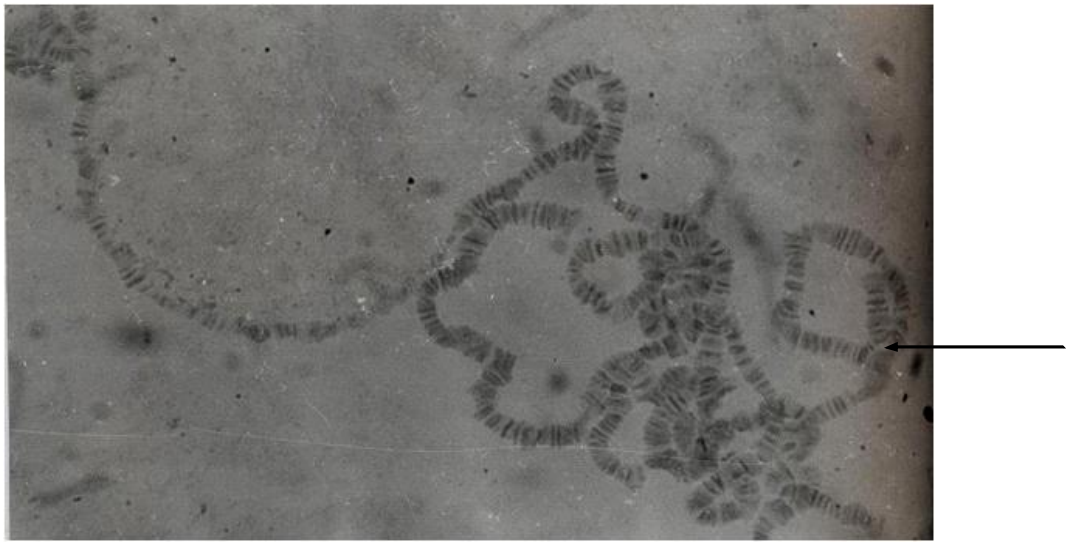

Plate 1d: *In(3L)D*
In(3L)D is a large paracentric inversion. Arrow points to the inversion junction

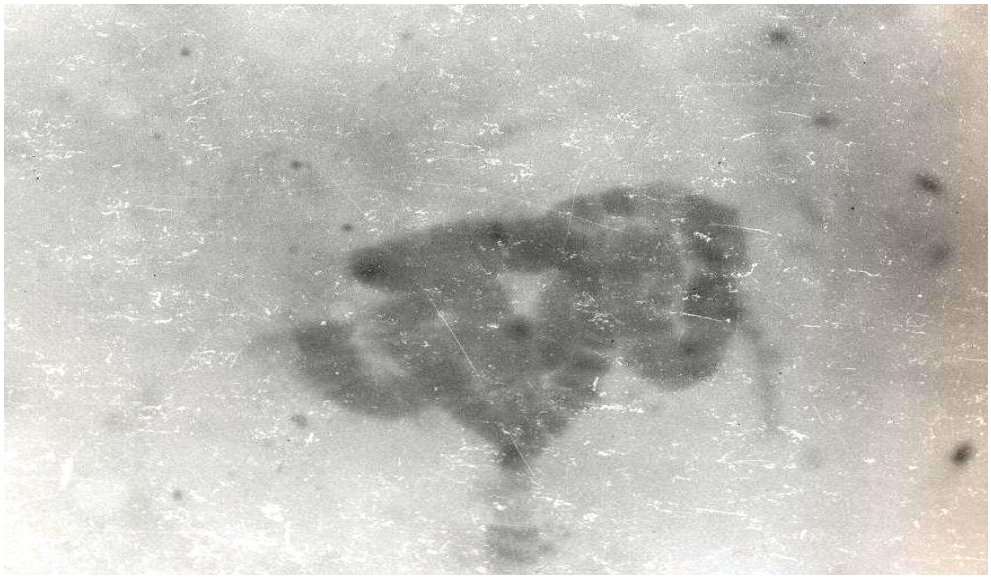

Plate 1e: *In(3R)F*
In(3R)F is a paracentric inversion.

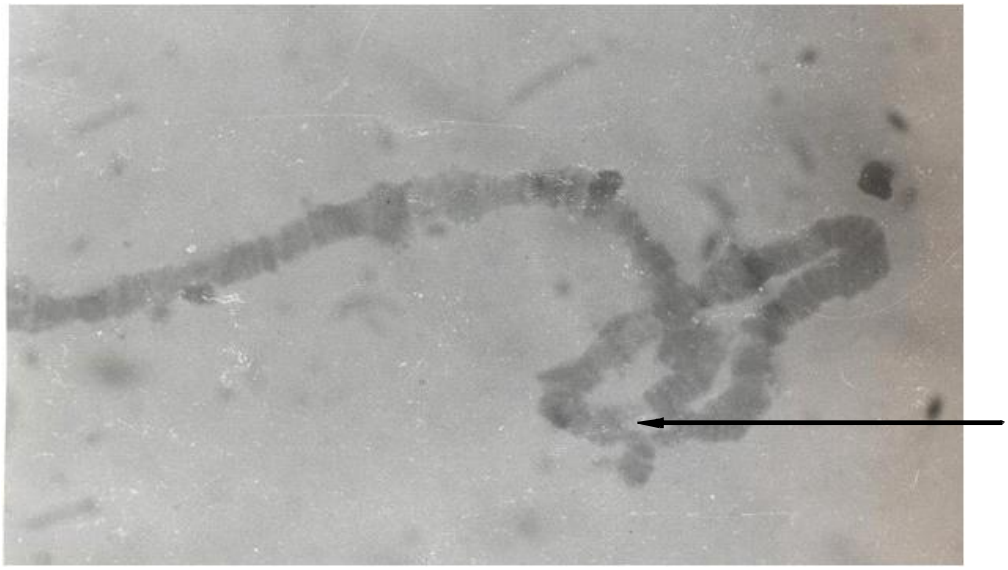

Plate 1f: *In(3R)G*
In(3R)G is a relatively large paracentric inversion. Arrow indicates inversion junction.