

Population genetics of *Drosophila nasuta nasuta*, *Drosophila nasuta albomicana* and their hybrids II. Coassociation of parental chromosomes in the hybrid populations

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Abstract. *D. n. nasuta* ($2n=8$) and *D. n. albomicana* ($2n=6$), the chromosomal races of the *nasuta* subgroup have mutual open genetic systems. Hybrid populations are completely fertile. By utilising fixed inversion differences in second and third chromosomes, the extent of coassociation of parental chromosomes in the gene pool of the hybrids have been estimated. There is a significant decline in the inversion polymorphism of the second chromosome, while in the third chromosome both the parental and the hybrid associations are equally frequent. The reduction in the frequency of heterokaryotypes in the second chromosome is due to the establishment of different coadapted systems in the parental chromosomes which has been favoured by selection. This does not occur in the third chromosome. This dichotomy of differential coadaptation within the elements of the same genotype is the first of its kind and the implications of these findings are discussed.

Keywords. Coadaptation; heterokaryo types; speciation.

1. Introduction

Drosophila nasuta nasuta and *D. n. albomicana* constitute two chromosomal races with $2n=8$ and $2n=6$ respectively. There exists a state of karyotypic mosaicism as evidenced by the presence of eleven classes of chromosomal combinations in F_2 , F_3 and F_{10} populations in variable frequencies ranging from 51% to 2% (Rajasekarasetty *et al* 1978 unpublished). Whether there is any preference either for the parental or the hybrid associations of homologous chromosomes in the hybrid populations was not studied earlier. Hence, experiments were designed to estimate the extent of coassociation of parental chromosomes of *D. n. nasuta* and *D. n. albomicana* and the findings form the germane of the present paper.

2. Materials and Methods

D. n. nasuta of Mysore, India and *D. n. albomicana* of Okinawa (University of Texas stock No. 3045.11) were employed for the present experiment. Reciprocal crosses were made using 15 virgin females and 15 males for each cross. In each generation 50 males and 50 females were collected and bred to obtain the next generation.

For salivary gland chromosome analysis, glands of well fed third instar larvae were dissected out in physiological saline and placed in 1N HCl for 2 min. Later they were transferred to 2% lacto-aceto-orcein stain and left for 15 min. The stained glands were squashed in 45% acetic acid with the addition of 2 drops of lacto-acetic acid (equal parts of lactic acid and 60% acetic acid). Finally the slides were sealed with paraffin lanolin mixture. Salivary gland chromosome preparations were made for F_1 , F_5 and F_{10} generations. 100 slides were scored for each of these generations.

3. Observations

The salivary gland chromosome complement of *D. n. nasuta*, *D. n. albomicana* and their hybrids include four long arms (X, 2L, 2R and 3) and a short arm.

The strains of *D. n. nasuta* and *D. n. albomicana* which are employed in the present experiment do not possess any inversions. But the salivary gland chromosomes of the F_1 hybrids revealed two heterozygous inversions. One of them was found in the left arm of the second chromosome (figure 1) and the other was in the third chromosome (figure 2). Further, in F_2 due to segregation of chromosomes, there will be individuals with or without these inversions. Presence of these heterozygous inversions in the succeeding generations reflects the coassociation of the concerned chromosomes of the parents and the individuals without these heterozygous inversions represent the chromosome complement of either parents. Hence, these inversions have been used as markers to score the frequencies of parental and hybrid combinations in the hybrid populations of *D. n. nasuta* and *D. n. albomicana*.

Table 1 gives the frequencies of individuals without these inversions, with one of them and with both of them in F_1 , F_5 and F_{10} generations of the reciprocal crosses of *D. n. nasuta* and *D. n. albomicana*. The total number of second and third chromosomes with or without inversions are compiled in table 2. The incidence of the coassociation of the second chromosomes, as reflected by the frequency of the heterozygous inversion is found to be significantly lower than the total number of parental combinations both in F_5 and F_{10} generations. On the other hand, the heterozygous

Table 1. Frequencies of individuals without any inversion, with one of them or both of the hybrid inversions in F_1 , F_5 and F_{10} generations from the reciprocal crosses of *D. n. nasuta* and *D. n. albomicana*.

	Without any inversion	With 2L chromosome inversion	With 3rd chromosome inversion	With both 2L and 3rd chromosome inversions
<i>D. nasuta nasuta</i> ♂♂ × <i>D. nasuta albomicana</i> ♀♀				
F_1	—	—	—	100
F_5	28	17	37	18
F_{10}	36	15	32	17
<i>D. nasuta nasuta</i> ♀♀ × <i>D. nasuta albomicana</i> ♂♂				
F_1	—	—	—	100
F_5	32	12	35	21
F_{10}	29	12	41	18



Figures 1 and 2. 1. Heterozygous inversion found in the left arm of the second chromosome of the hybrid. 2. Heterozygous inversion found in the chromosome 3 of the hybrid.

Table 2. Total number of individuals having the hybrid inversions in 2L and 3 chromosomes from the reciprocal crosses of *D. nasuta nasuta* and *D. nasuta albomicana*.

	2L Chromosome inversion		3rd Chromosome inversion	
	Present	Absent	Present	Absent
<i>D. nasuta</i> ♂♂ × <i>D. nasuta albomicana</i> ♀♀				
<i>F</i> ₁	100	—	100	—
<i>F</i> ₅	35	65*	55	45
<i>F</i> ₁₀	32	68*	49	51
<i>D. nasuta nasuta</i> ♀♀ × <i>D. nasuta albomicana</i> ♂♂				
<i>F</i> ₁	100	—	100	—
<i>F</i> ₅	33	67*	56	44
<i>F</i> ₁₀	40	60*	59	41

*The differences between the frequencies of homo- and heterokaryotypes are significant:

$$X^2 = 4, \quad Df = 1, \quad P < 0.05$$

inversion in the third chromosome is as frequent as that of the homokaryotypes. That is, parental and the hybrid combinations for the third chromosomes exist in almost 1 : 1 frequency. Figure 3 presents the comparative picture of the frequencies of homo- and heterokaryotypes in *F*₁, *F*₅ and *F*₁₀ generations. Both the *F*₅ and *F*₁₀ generations present the same picture with regard to the frequencies of heterokaryotypes in the second and third chromosomes. Further, there is no significant difference in the frequencies of inversions in the reciprocal crosses under study.

4. Discussion

The gene pool, that is the totality of all genes in a mendelian population adjusts itself which Dobzhansky (1949) termed it as 'coadaptation'. Each chromosome carries a constellation of genes. Mather (1943) and Lerner (1958) have recognised two different types of balances between the genes in a pair of homologous chromosomes, (a) internal balance is between genes in a chromosome, and (b) relational balance is between genes in a pair of homologous chromosomes. Further, relational balance is responsible for the high adaptive values of inversion heterokaryotypes and for the establishment of inversion polymorphism (Dobzhansky 1955). The superior fitness of heterokaryotypes can result only from the chromosomes derived from the same population. On the other hand interpopulational hybridization upsets the relational balance maintained in the parental populations as evidenced by the findings of Dobzhansky (1957), and Dobzhansky and Pavlovsky (1958). They have reported that there was a loss of chromosomal polymorphism in inter-racial hybridization experiments involving *D. willistoni* and *D. paulistorum*. In such types of crosses the same gene arrangements but of the different geographic origin were brought together and these gene complexes break down by crossing over. Concordant results were reported for *D. pavani* (Brncic 1961). By observing the degree of breakdown of heterokaryotypes in inter-racial crosses he was able to prove the divergence of polygenes maintained by inversions in the natural populations of *D. pavani*. Contrary to the above reports the experiments involving *D. ananassae* have revealed

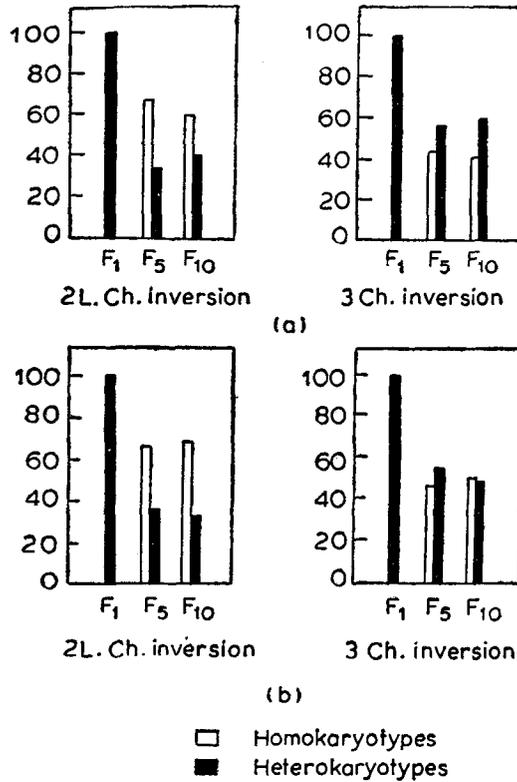


Figure 3. Frequencies in percent of the homo- and heterokaryotypes in the second and third chromosomes in the hybrid populations of *D. n. nasuta* and *D. n. albomicana* in F₁, F₅ and F₁₀ generations.

that the inter-racial hybridization has not led to the breakdown of heterosis and all the hybrid populations remained polymorphic even after ten generations (Singh 1972).

The present experiments with *D. n. nasuta* and *D. n. albomicana* present yet another level of genetic coadaptation that can occur during evolutionary divergence. Through inter-racial hybridization of the races under discussion, one inversion to the second and another to the third chromosome have been introduced into the hybrid populations. All the F₁ hybrids possess these inversions and they are absent in the parental races under study. However in succeeding generations the gene pool of the hybrids carry individuals with or without these inversions. The frequencies of these heterozygous inversions reflect the association of the chromosomes from the two races which can either increase or decrease depending on the extent of their coadaptation. If the present hybrid populations have more of heterokaryotypes, it can be taken as an indication of the superiority due to the association of the chromosomes of the two races. Further, it suggests the lack of genetic differences in the respective chromosomes. On the other hand, if there is the preponderance of homokaryotypes, it points out that the chromosomes of the parents have undergone sufficient genetic divergence and possess different coadapted systems. The incidence of the hybrid association of the second chromosomes is significantly

below the frequency of parental combination. Both in F_5 and F_{10} generations of the reciprocal crosses of *D. n. nasuta* and *D. n. albomicana* the frequencies of heterozygous inversions in the second chromosomes are drastically lower than the second chromosomes without inversion. Contrary to this, the third chromosome has given altogether a different picture. The degree of heterozygous inversions in the third chromosomes does not differ significantly from that of homokaryotypes. Both the parental and the hybrid combinations exist in almost 1 : 1 ratio. Thus the present observations on the second chromosomes are in agreement with those results reported by Dobzhansky and Pavlovsky (1958) in *D. paulistorum* and *D. willistoni* and Brncic (1961) in *D. pavani*, while the data on the third chromosomes is same as that of Singh's observations (1972) in *D. ananassae*.

In view of the present findings it is the considered opinion of the authors that the second chromosomes of the races under discussion have established different coadaptive systems and hence the selection has favoured the parental combination than the hybrid association. On the other hand, for the third chromosomes, due to the lack of differences in their coadaptive organization, selection has not discriminated between the parental and the hybrid combinations. This duality in the behaviour of the chromosomes within the same karyotype is a unique case and the first report of its kind in *Drosophila*. A plausible explanation for this is that the elements of the karyotype have reacted differently to the facets of natural selection during their evolutionary sojourn. Thus the present report on the dichotomy within the chromosomes of a karyotype in the attainment of genetic integration would constitute a valuable addition to our knowledge and has exposed yet another avenue on genetics of speciation.

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