Chromosomal basis of raciation in *Drosophila*: A study with *Drosophila nasuta* and *Drosophila albomicana*

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Abstract. *Drosophila nasuta nasuta* (2n = 8) and *Drosophila nasuta albomicana* (2n = 6), a pair of cross fertile races have conspicuous karyotypic divergence and symptoms of postmating isolating mechanisms. Hybridization of these races followed by hybrid maintenance and hybrid recombination has resulted in the evolution of two novel races with new combinations of parental chromosomes referred to as Cytoraces I and II and this has illustrated an interesting aspect of karyotypic differentiation under laboratory conditions.

Keywords. *Drosophila*; chromosomal races; hybridization; evolution.

1. Introduction

Drosophila nasuta and *D. albomicana* are sibling members of the *nasuta* subgroup of the *immigrans* species group of *Drosophila*. In this article an attempt has been made to review the chromosomal basis of their differentiation.

D. nasuta was described by Lamb (1914) and the type specimens were collected from Seychelles Islands. Duda (1923) described *D. albomicana* from Paroe, Formosa and it was morphologically similar to *D. nasuta*. Wilson *et al* (1969) have made extensive cytogenetic and hybridization studies of the members of the *nasuta* subgroup and they were able to solve the status of some members. But, *D. nasuta* (*sensu strictu*) was not available to Wilson *et al* (1969) and in the absence of this member they felt that 'in view of the great similarities between the species of this complex and the remarkable degree of speciation which has taken place in south-east Asia, it seems more reasonable to assume that the true *nasuta*, more than 3000 miles from the closest known *albomicans*, is still another species'.

Nirmala and Krishnamurthy (1971) reported a *D. nasuta* strain from Soundathi (south India) possessing 2n = 8. The karyotype of *D. nasuta* from Seychelles Islands, from where Lamb (1914) described it was analysed by Wakahama and Kitagawa (1972) and based on the similarities between Seychelles Islands and south Indian strains, they opined that Indian *D. nasuta* may be the same species or a closely related species of *D. nasuta sensu strictu*. This was followed by the findings of Ranganath *et al* (1974), wherein the hybridization experiments showed that Indian and the Seychelles Islands strains of *D. nasuta* are completely cross fertile and they are one and the same species.

Hybridization studies involving south Indian strains of *D. nasuta* with 2n = 8 and *D. albomicana* of Taiwan with 2n = 6 showed that these two so called species constitute open genetic systems (Nirmala and Krishnamurthy 1972). This was confirmed by the studies of Ranganath *et al* (1974) that both the Indian as well as the Seychelles Islands strains of *D. nasuta* and the Taiwan and the Okinawan strains of *D. albomicana* are cross fertile. In view of this open genetic systems and cross fertility

between *D. nasuta* and *D. albomicana* and taking into cognizance the differences in their karyotypes, they have been treated as chromosomal races and called *D. n. nasuta* (2n = 8) and *D. n. albomicana* (2n = 6) (Nirmala and Krishnamurthy 1972; Ranganath *et al* 1974).

With regard to geographic distribution, *D. nasuta* is wide spread. It has been reported from Mombusa, Kenya; Tananarive Madagascar; Mahe, Seychelles; Mauritius Island; Reunion Island; Kandy, Sri Lanka (Kitagawa *et al* 1982), Mysore and other localities of India (Ranganath and Krishnamurthy 1972; Reddy 1973; Siddaveere Gowda *et al* 1977; Prakash 1980; Muniappa 1982; Gai 1985); and west coast of Africa (David and Tsacas 1980). *D. albomicans* is reported from several Japanese Islands and Malaysia (Kitagawa *et al* 1982); Thailand (cf. Wilson *et al* 1969); Taiwan (Lin *et al* 1977); and Shillong (Singh 1977). All these reports indicate that *D. nasuta* and *D. albomicana* are allopatric.

2. Direction of evolution

The direction of evolution between the two races, viz *D. n. nasuta* and *D. n. albomicana* was discussed by taking into consideration their karyotypes and mating preference. Wilson *et al* (1969), Wakahama *et al* (1971), Nirmala and Krishnamurthy (1972) and Ranganath *et al* (1974) have argued and showed that the karyotype of *D. n. albomicana* (2n = 6) is derived from that of *D. n. nasuta* (2n = 8). The evolutionary event that is responsible for this change was the centric fusion between chromosome 3 and the sex chromosomes of *D. n. nasuta* to produce a metacentric chromosome of *D. n. albomicana* (X3; Y3) and this has reduced the diploid number from 2n = 8 to 2n = 6. Recently, Ranganath and Hagele (1981), while discussing the karyotypic evolution in the *nasuta* subgroup have demonstrated that the karyotype of *D. n. albomicana* is the recent product in the group and also illustrated it as a product of karyotypic ortho-selection involving successive centric fusions. In view of this karyotypic phylogeny, *D. n. nasuta* is ancestral to *D. n. albomicana*.

The direction of evolutionary lineage can also be discussed by studying the mating preference between closely related forms. Ramachandra and Ranganath (1987) have analysed the mating preference between *D. n. nasuta* and *D. n. albomicana*. In no choice experiments, when there was no choice in the cross involving males of one race with the females of the other, all the crosses were successful. In multiple choice experiments both the females and males of each race were placed together. Here, all the possible matings like homogamic, heterogamic and one male mating with both the females were recorded. However, homogamic and matings of males of *D. n. nasuta* with the females of both the races were more frequent compared to other matings. 'Female choice' experiments showed that both *nasuta* (ancestral) and *albomicana* (derived) females have chosen the males of *nasuta* (ancestral) to the males of the derived race, viz *D. n. albomicana*. Further, even in the male choice experiments, wherein males of one race were given the choice to select between the females of both the races, the males of these two races have preferred the females of *D. n. nasuta* more than that of *D. n. albomicana*. These observations fit into the hypothesis of Kaneshiro (1976) which states that females of ancestral species strongly discriminate against males of the derived species, while females of the derived species readily accept the males of the ancestral species.

Thus there is good correlation between the findings of the mating preference experiments and the karyotypic phylogeny mentioned earlier. In view of these, it can be safely mentioned that the direction of evolution was from *D. n. nasuta* to *D. n. albomicana*.

3. Karyotypic organization

The diploid chromosome complement of *D. n. nasuta* is $2n = 8$ (figure 1A, B) (Nirmala and Krishnamurthy 1971; Wakahama and Kitagawa 1972; Ranganath 1978; Ranganath *et al* 1974; Lakhotia and Kumar 1979). It includes one pair of metacentric chromosomes (chromosome 2), two pairs of acrocentrics (chromosome X and 3) and a pair of small basic dots (chromosome 4). In males one of the X chromosome is replaced by a submetacentric Y chromosome. The metaphase chromosome complement of *D. n. albomicana* ($2n = 6$; figure 1C, D) consists of two pairs of metacentric chromosomes (chromosome 2 and X3, X3 or X3, Y3) and a pair of long dots (Wilson *et al* 1969; Nirmala and Krishnamurthy 1972; Ranganath 1978).

Heterochromatin distribution and differentiation in metaphase chromosomes of these two races, *D. n. nasuta* and *D. n. albomicana* were studied by Ranganath and
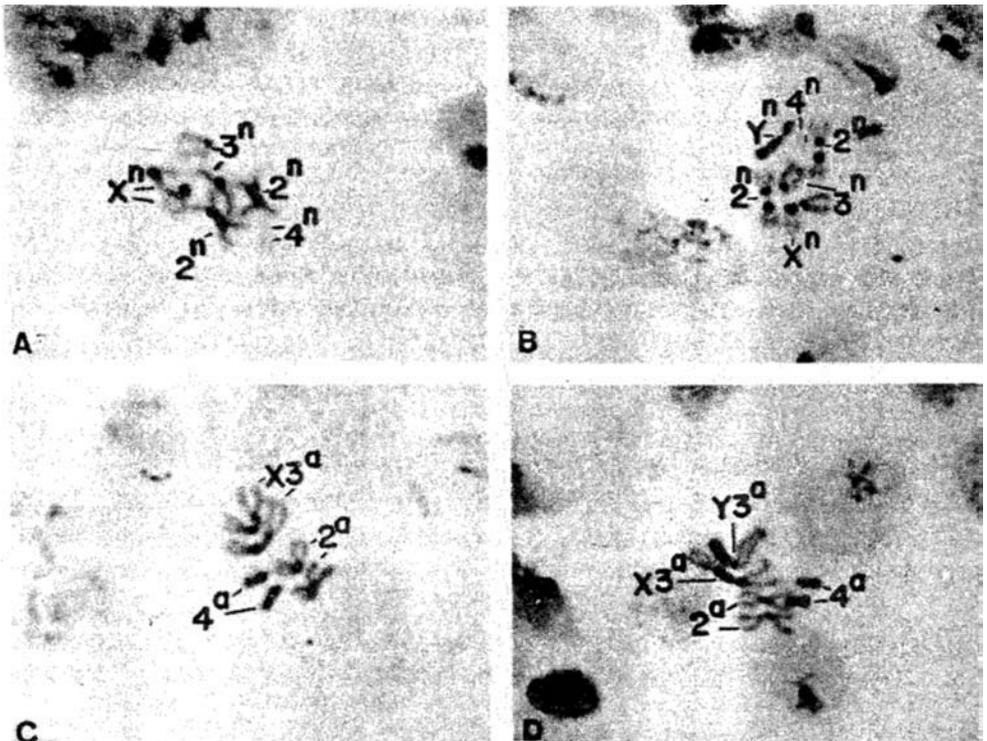

Figure 1. C-banded metaphase chromosomes of *D. n. nasuta* ($2n = 8$) female (**A**) and male (**B**); and of *D. n. albomicana* ($2n = 6$) female (**C**) and male (**D**). Chromosomes are designated with superscripts n for the chromosomes of *D. n. nasuta* and a for the chromosomes of *D. n. albomicana*.

Hagele (1982) and Ranganath *et al* (1982) by way of C-, N- and Q-banding methods. It has been demonstrated that between the homologous metaphase chromosomes of these races there exist length differences and this is mainly due to differences in the size of heterochromatin blocks. Significant differences are seen in chromosome 2 and 4 of these races. The N-banding studies of Ranganath and Hagele (1982) have revealed that the Y chromosomes of both races and the chromosome 4 of *D. n. albomicana* possess heterochromatin sections which behaves differently from those of other centric and pericentric heterochromatin regions. The AT-richness of heterochromatin in these *Drosophila* races was shown by its bright quinacrine fluorescence (Ranganath *et al* 1982). In the metaphase chromosomes of *D. n. nasuta* and *D. n. albomicana*, the regions of bright fluorescence coincide with C-banded regions.

Ranganath *et al* (1982) have shown that the DNA of *D. n. nasuta* has only one major AT-rich satellite fraction with a density of 1.664 g/cm^3 and it amounts to about 7 to 8% of the total DNA. On the other hand, *D. n. albomicana* had atleast 3 different AT-rich satellites with densities of 1.674 g/cm^3, 1.665 g/cm^3 and 1.661 g/cm^3 and these comprise 28–30% of its total DNA. *In situ* hybridizations to metaphase and polytene chromosomes have shown that cross hybridizations were successful and hence Ranganath *et al* (1982) have felt that there are homologous satellite DNA sequences in the heterochromatin areas of the chromosomes of *D. n. nasuta* and *D. n. albomicana* and the satellite DNAs of these races differ quantitatively rather than in quality.

Attempts have been made by Hagele and Ranganath (1983) to localize NORs by way of combined acid treatments and Ag-AS techniques. These studies suggest that the NORs in these races are present on heterochromatic Y-chromosomes and on chromosome 4 and this appears to be a rare combination in *Drosophila*.

In polytene cells, in both the races there are 4 long arms (X, 2L, 2R and 3) and a short arm (4) (Ranganath and Krishnamurthy 1973–74; Wilson *et al* 1969). In the F_1 hybrids of *D. n. nasuta* and *D. n. albomicana* fixed inversion differences were seen in 2L and 3 chromosome arms, while 2R and X were devoid of such differences (Ranganath 1978; Rajasekarasetty *et al* 1978, 1980). In addition to these, significant differences between the short chromosome arm 4 of these races have been demonstrated by Hagele and Ranganath (1982). The metaphase chromosome 4 of *D. n. albomicana* is nearly 5 times larger than that of *D. n. nasuta*. But in polytene cells, it is much shorter than that of *D. n. nasuta*. In the F_1 polytene cells, these homologous chromosomes do not pair and they appear as twins in contrast to other arms. Hagele and Ranganath (1982) have illustrated that this is due to a duplication, an inversion and a massive amount of heterochromatin in the chromosome 4 of *D. n. albomicana* and this makes it different from that of its homologue in *D. n. nasuta* which lacks these features.

4. Interracial hybridization

The F_1 hybrids of the cross between *D. n. nasuta* (2n = 8) and *D. n. albomicana* (2n = 6) had 2n = 7. Inspite of the above narrated differences between these races in their karyotypic organization, the F_1 and the succeeding hybrid progeny were fertile. It was of interest to know the dynamics of chromosome segregation during gametogenesis in the F_1 hybrids and its impact on the fertility of the next generation.

Ranganath and Krishnamurthy (1981) have probed this facet of hybrids and their findings indicate that F_1 males produce 6 different types of sperms. Of these 39% had the normal haploid chromosome complement while the remaining 61% were aneuploids for chromosomes X or 3. On the other hand, the F_1 female produced only two types of eggs with haploid quantum of chromosomes and the aneuploid eggs were not seen. Fertility test on F_2 and backcross progeny have shown that males are more often sterile than females. Tested males of 177 out of 400 were sterile and 14 out of 400 females analysed were sterile. Thus, the F_1s produce both fertile and sterile F_2 individuals. The birth of the succeeding generations is taken care of by the fertile individuals and hence it is possible to maintain the hybrid populations of *D. n. nasuta* and *D. n. albomicana* for any number of generations.

The chromosomal basis of coadaptation analysed by Ranganath (1978) showed that the F_1 hybrids of *D. n. nasuta* and *D. n. albomicana* were heterotic for certain parameters of fitness and there was a hybrid breakdown in F_2. This was taken as an evidence to demonstrate the divergence in the genetic constitution of these races.

The analysis of the karyotypes of the F_2 progeny and of the succeeding generations of the cross between *D. n. nasuta* and *D. n. albomicana* showed that the hybrid populations, karyotype-wise are extremely heterogeneous with different types of karyotypes. Ranganath (1978) and Rajasekarasetty *et al* (1979) have termed this as 'karyotypic mosaicism', wherein one can see different chromosome combinations other than the parental and of the F_1 hybrids.

Recently, Ramachandra and Ranganath (1986) have made a systematic assessment of fate of different parental chromosomes of *D. n. nasuta* and *D. n. albomicana* in their hybrid populations. They have recorded that the karyotypic mosaicism present in the hybrid populations declines over generations and during this process there was selective elimination of some parental chromosomes, while some other chromosomes were retained. Finally by F_{20} the karyotypic variability disappears and karyotypically a stable hybrid population evolves. Such an event has led to the emergence of two new strains of hybrid populations, which differ from their parents as to the karyotypic composition and hence these newly derived lines have been called Cytoraces (Ramachandra and Ranganath 1986). The salient features of this interesting experiment are as follows:

The hybridization between males of *D. n. nasuta* and females of *D. n. albomicana* has resulted in the evolution of a hybrid population with new karyotypic combination and this has been called Cytorace I (figure 2A, B). The males of Cytorace I had $2n = 7$ (2^a2^n; Y^nX3^a; 3^n; 4^n4^n) and females had $2n = 6$ (2^a2^n; $X3^aX3^a$; 4^n4^n). Of the 13 chromosomes of Cytorace I, 8 were of *nasuta* parent and 5 were of *albomicana* parent. The superscripts in the figures denote the parent from which that particular chromosome was inherited—n = *D. n. nasuta*; a = *D. n. albomicana*. Inspite of the difference in the diploid number of chromosomes in males and females, Cytorace I breeds true. The chromosomal mechanism underlying this true breeding nature of Cytorace I has been illustrated by Ramachandra and Ranganath (1986). Thus, this karyotypic duality between males and females of a strain with its true breeding character is a unique report and first of its kind in *Drosophila*.

The hybrid population of the cross between males of *D. n. albomicana* and females of *D. n. nasuta*, after passing through an ephimeral phase of karyotypic mosaicism has attained karyotypically a stable state with males and females having $2n = 6$. This hybrid population was called Cytorace II (figure 2C, D) (Ramachandra and
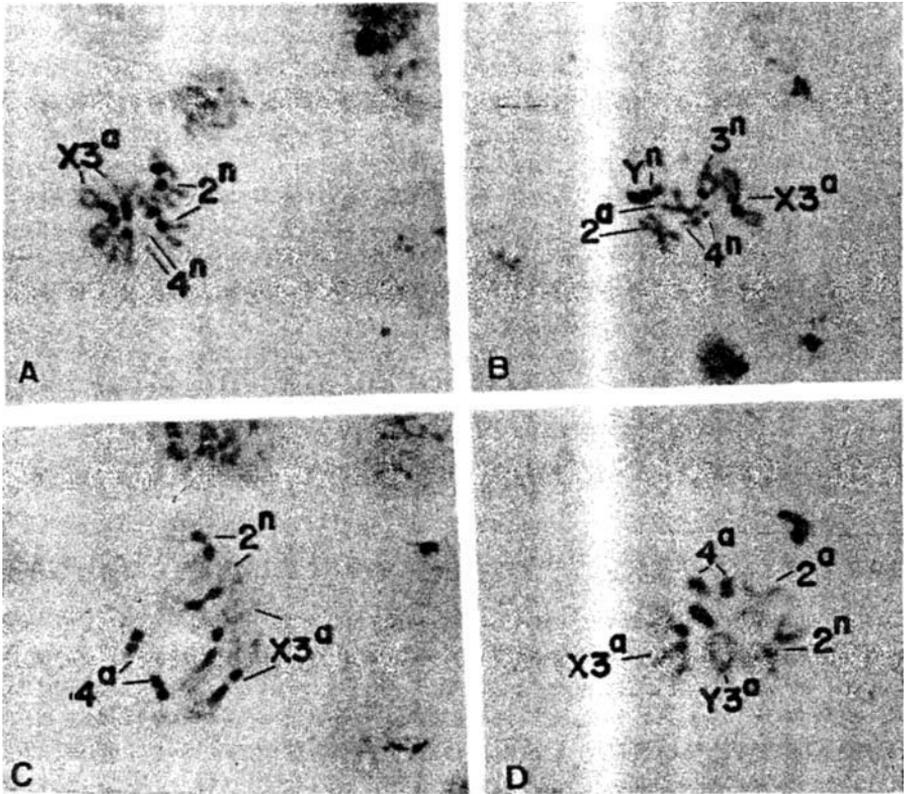
Figure 2. C-banded metaphase chromosomes of Cytorace I: female $2n = 6$ (A) and male $2n = 7$ (B); and of Cytorace II: female $2n = 6$ (C) and male $2n = 6$ (D). Chromosomes are designated with superscripts n for the chromosomes of *D. n. nasuta* and a for the chromosomes of *D. n. albomicana.*

Ranganath 1986). The chromosomes that constituted the male karyotype were 2^n2^a, $X3^aY3^a$, 4^a4^a and similarly, of the female it was 2^n2^a; $X3^aX3^a$; 4^a4^a. Of these 12 chromosomes, 10 were of *albomicana* parent, while only two came from *nasuta* parent.

The comparative evaluation of the karyotypes of the parents and of the Cytoraces reveal that the Cytorace I is devoid of the X chromosome of *D. n. nasuta* and chromosome 4 of *D. n. albomicana*. Similarly, the Cytorace II is without the representation of chromosomes X, 3 and 4 of *D. n. nasuta*. These chromosomes which are not seen in the stabilized karyotypes of Cytoraces were found in their respective F_1 karyotypes and these have been eliminated in the succeeding hybrid generations. On the whole, the behaviour of dot chromosomes (chromosome 4) is very interesting. In each cross, there is a good correlation between the male parent of the cross and the dot chromosome that has been retained in the stabilized population. Male parents of Cytoraces I and II were *nasuta* and *albomicana* respectively. Correspondingly, the Cytorace I had the dot chromosomes of *nasuta* only, while the Cytorace II had the dot chromosomes of *albomicana* only. This type of affinity between the dot and Y chromosomes of these races may be underlined by the presence of NORs in these two chromosomes of these races. It is also evident in the karyotypes of these cyto-

races, that there is selective preference for the parental combinations of the dot chromosomes over the hybrid association. This may be due to 'incompatability' between these parental chromosomes in view of significant structural changes involved in the evolution of the dot chromosomes of *D. n. albomicana* as discussed earlier.

The karyotypes of Cytoraces I and II are the products of elements derived from two different races, viz *D. n. nasuta* and *D. n. albomicana*. The restructuring of the karyotypes has resulted in significant differences in the quantum of heterochromatin between the parental races and the newly evolved Cytoraces (Ramachandra and Ranganath 1986). Of these 4 races, the individuals of Cytorace I had the lowest amount of heterochromatin, while those of Cytorace II had the highest quantum of C-band DNA. Hence, these have been referred to as heterochromatin 'poor' and 'rich' strains respectively.

The extent of divergence between the parental races and the newly evolved Cytoraces has been shown by way of demonstrating the differences in their fitness phenotypes (Ramachandra N B and Ranganath H A, unpublished results). In brief, the sequence for 4 different parameters of fitness is as follows: for fecundity: Cytorace I = *D. n. nasuta* = Cytorace II > *D. n. albomicana*; for rate of development: Cytorace I > Cytorace II > *D. n. albomicana* > *D. n. nasuta*; for viability: *D. n. nasuta* = Cytorace II > Cytorace I = *D. n. albomicana*; and for adaptedness: *D. n. albomicana* > *D. n. nasuta* > Cytorace II > Cytorace I. These differences do suggest the underlying genetic differences between these races.

5. Conclusion

Interracial hybridization between two coadapted gene pools, viz *D. n. nasuta* and *D. n. albomicana* has resulted in the evolution of two new races. In a way, in this instance, hybridization has acted as an 'evolutionary catalyst' in terms of Dobzhansky *et al* (1976). The karyotypes of these cytoraces are new in composition and each one of them have inherited chromosomes from both the parents.

Recently, Templeton (1981) has argued that hybridization followed by the production of unstable hybrids, inbreeding and hybrid breakdown may result in a form of natural selection favouring those F_2 and later individuals that have better viability and fertility. This may result in the formation of a new rare recombinant class of genotype. Templeton (1981) has called this as 'transilience mode of speciation'. The karyotypes of the parental races, viz *D. n. nasuta* and *D. n. albomicana* as well as those of newly evolved races followed by hybridization, viz Cytoraces I and II, represent two distinct phases of karyotypic stability. These two phases were separated by a transient phase of karyotypic instability due to karyotypic mosaicism in the hybrid populations. Thus, this is an interesting facet of evolutionary process, viz 'karyotypic differentiation' followed by hybridization under laboratory conditions and these sequence of events as reported by Ramachandra and Ranganath (1986) fits into the 'transilience mode of speciation' proposed by Templeton (1981).

Acknowledgements

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