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REVIEW ARTICLE

Drosophila ananassae: a species characterized by spontaneous male recombination in appreciable frequency

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Abstract. Mutation and recombination are primarily responsible for generating the genetic variability in natural populations of microorganisms, plant and animal species including humans. Upon such genetic variations, elemental forces of evolution such as natural selection, random genetic drift and migration operate to bring about micro-evolutionary changes. Recombination or crossing-over produces new combinations of genes due to interchange of corresponding segments between nonsister chromatids of homologous chromosomes, thus, it is an important evolutionary factor. Since the time of T. H. Morgan, *Drosophila* has been subjected to extensive investigations on crossing over while employing a number of markers, which were used for gene mapping. Interestingly, recombination occurs in females of *D. melanogaster* but not in males. Later on, male crossing over was investigated in various species and its occurrence was reported in *D. melanogaster*, *D. ananassae*, *D. simulans*, *D. willistoni*, *D. littoralis* and *D. bipectinata*. Recombination occurs at very low rate in all these species except for *D. ananassae*, which shows spontaneous male crossing over in appreciable frequency, which is meiotic in origin. This unusual phenomenon in *D. ananassae* is influenced by various genetic factors as well as it shows strain variation as far as frequency of male recombination is concerned. Further, the presence of chiasmata during meiosis in males at a frequency capable of accounting for the observed recombination frequency extends evidence for meiotic origin of recombination in males of *D. ananassae*.

Keywords. spontaneous male recombination; genetic peculiarity; meiotic in origin; genetic factors; presence of chiasmata; *Drosophila ananassae.*

Introduction

Mutation and recombination are the primary source of genetic variability in populations of microorganism, plant and animal species including humans. Through mutation, new alleles are generated in populations which may occur spontaneously or induced by external agents. Recombination generates new combinations of genes already existing in populations. Crossing over occurs during meiosis due to interchange of corresponding segments between nonsister chromatids of homologous chromosomes. Normally recombination occurs in germinal cells during the formation of gametes. Thus, the mutation and recombination are primary source of genetic variations in populations on which evolutionary forces such as natural selection, random genetic drift, migration etc. operate to bring about micro–evolutionary changes. In view of this, these are considered as elemental forces of evolution. In a number of species of plants and animals, recombination has been studied and genes have been mapped on different chromosomes. Among different species of animals and plants, *Drosophila*, an important biological model is unique as it shows crossing over in females but not in males (Morgan 1912, 1914; Whittinghill 1937, 1947). T. H. Morgan who detected a number of point mutations first used *D. melanogaster* in 1909 in genetic studies. He also proposed the theory of linkage and constructed the genetic maps of different chromosomes in this species. Since the initial work of Morgan in *D. melanogaster*, male crossing over has been studied in different species of *Drosophila*. Crossing over is enhanced by X-rays and temperature in *Drosophila* females and hence crossing over in males was suggested based on artificial induction (Plough 1921; Mavor and Svenson 1924). The occurrence of crossing over in spermatocytes was suggested on the basis of observation of Patterson and Suche (1934), who found high frequency of crossing over when older larvae with numerous spermatocytes were irradiated than the younger larvae having predominantly spermatogonial cells

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were irradiated. Thus, it was concluded that recombination occurred in spermatocytes. Friesen (1934, 1937) suggested that X-rays cause a closer association of homologous chromosomes and bring about recombination during meiosis. Parker (1948) reported the appearance of higher crossover or cluster in his data on induced crossing over. Clustering of crossover was observed because the homologues which are partially synapsed at identical loci in a cyst of primary spermatocytes represent the targets to give exchanges at the same level when hit by ionizing particles (Parker 1948). It has also been reported that in *Drosophila* males, most of the exchanges are in a preferred region and complementary crossovers were very unequal in frequency (Friesen 1936). There was much variation in the frequency of crossing over from individual to individual. He suggested that this kind of data could demonstrate spermmatogonial recombination. Whittinghill (1937) presented evidence that temperature may induce crossing over in males, which is different from crossing over in females, and the results were explained by suggesting spermatogonial crossing over in *D. melanogaster* as it occurred in specific regions with complementary crossover classes in unequal frequency.

Spontaneous recombination in males have been found to occur in *D. melanogaster*, *D. simulans*, *D. ananassae*, *D. willistoni*, *D. littoralis* and *D. bipectinata* (Singh and Banerjee 1996), but in *D. ananassae* it occurs at a higher rate than others. In *D. ananassae*, it occurs at appreciable level. *D. ananassae* is also characterized by several unusual cytogenetic and genetic features such as spontaneous male recombination which is meiotic in origin, high mutability, spontaneous genetic mosaic, lack of genetic coadaptation, presence of parthenogenesis, Y-4 linkage of nucleolus organizer, extrachromosomal inheritance, and presence of chiasmata during meiosis in males (Singh 1985, 2000, 2010, 2018). Japanese workers (Moriwaki 1937; Kikkawa 1938) reported spontaneous male recombination in *D. ananassae* for the first time. Later on, it was investigated in detail by numerous researchers at global level (for references see review by Singh and Yadav 2015). Various factors are known to influence male crossing over in *D. ananassae*: mutations, strains, suppressors, enhancers, inversions, polygenes, age, cytoplasm etc. (Singh and Singh 1990a; Singh and Yadav 2015). The present review briefly summarizes the work done on spontaneous male recombination in *D. ananassae*, which is one of the most important unusual genetic features of this species, shown to be meiotic in origin based on genetic as well as cytogenetic studies.

Original discovery of spontaneous male recombination

For the first time, the spontaneous male recombination in *D. ananassae* was reported by Moriwaki (1937) who suggested that a dominant gene MIIb enhanced recombination in females and induced crossing over in males. He also suggested that the enhancing power could not be due to MIIb itself but another dominant gene EnII was also responsible (Moriwaki 1940). Kikkawa (1938) suggested that a similar enhancer exists for male crossing over located in the third chromosome. Interestingly, the rate of crossing over observed by Kikkawa was much higher than that observed by Moriwaki. There was much individual variation in recombination values observed by Kikkawa even when brothers were tested. Both of them did not suggest that male crossing over in *D. ananassae* was spermatogonial in its origin. Great individual variation in crossing over values were observed by Kikkawa (1938) and Mukherjee (1961). However, Moriwaki (1937, 1940) did not test recombination in different males. Thus, the individual variation was not accompanied by other characterstics of gonial crossing over such as clustering of exchanges and inequality of complementary crossovers (Ray-Chaudhuri and Kale 1966). Thus, at that time the mechanism of male recombination was not clearly understood in this species.

Strain variations in the frequency of male crossing over

A number of studies on male recombination in *D. ananassae* have been carried out while employing wild-type strains of different geographic origins and marker stocks of different chromosomes (Ray-Chaudhuri and Kale 1966; Kale 1969; Moriwaki and Tobari 1973, 1975; Moriwaki *et al.* 1979; Matsuda *et al.* 1993; Sato *et al.* 2000; Goni *et al.* 2012). Ray-Chaudhuri and Kale (1966) studied male crossing over while using a wild-type stock raised from flies collected from Kolkata and a second chromosome recessive stock. Their results show that spontaneous male recombination values do not appear to be correlated with map distance as observed from female data. There was equality of complementary crossovers and random distribution of exchanges throughout the tested region. Further, spermatogonial crossing over does not occur in males. There was decrease in the frequency of crossing over with increase of age of males. This supports the suggestion that crossing over occurs in spermatocytes and there was much individual variation in crossover values. Kale (1969) suggested meiotic origin of spontaneous male crossing over and in his experiments he used triple recessive marker stock and four wild-type strains (Calcutta, Port Blair, Bombay and Nagpur). The four strains differed significantly in crossing over values and there was a clear indication of meiotic origin of spontaneous male crossing over. Significant differences in recombination frequencies between reciprocal heterozygous males was found which led to suggest the role of Y-chromosome on male recombination (Moriwaki *et al.* 1979). The same authors reported a considerable variation in recombination frequencies in males in different wild-type strains, which indicated the role of polygenes and divergence in chromosomes as far as the occurrence of male crossing over is concerned.

Moriwaki *et al.* (1970) also found balanced complementary crossovers and random distribution of crossovers suggesting the meiotic origin of male crossing over. Interestingly, Moriwaki *et al.* (1970) found a correlation between map distance and recombination values in males. Moriwaki and Tobari (1973) studied crossing over in males in strains collected from six geographic localities in Southeast Asia and found that it was of common occurrence caused due to some genetic elements. Their results also indicated meiotic origin of male crossing over. Hinton (1970) also found high frequency of recombination values which was correlated with female data but the distribution of recombination within the marked region differed between the sexes. Moriwaki *et al.* (1979) studied male crossing over while using strains in second and third chromosomes with constructed genomes of autosome and Y-chromosome. Depending on the genome of males tested, crossing over frequency was highly variable. In the third chromosome, it was found to be 42.8% which is close to the value of females. The presence of major genetic factors in the autosomes with some factors in the Y-chromosome were identified. Matsuda and Tobari (1982) also studied male crossing over in different wild-type strains and found high level of male recombination comparable with female data. In one strain, they found variation in recombination frequency with respect to regional recombination behaviour. A site specific increase in recombination frequency was reported in a wild-type stock (Sato *et al.* 2000). The enhancement of recombination was found in a specific region in left arm of the second chromosome. Several wild-type laboratory stocks established from the flies collected from the natural populations were used in male recombination studies (Goni *et al.* 2012), which demonstrated spontaneous male crossing over from natural populations coming from Japan, Brazil and Indonesia. The presence of chiasmata was also demonstrated in diplotene cells. Their work demonstrated male crossing over at variable frequency among males from natural populations (Goni *et al.* 2012). Matsuda (1986) showed that increase in temperature enhanced male recombination while using certain wild-type and marker strains.

Genetic factors affecting male recombination

It is well established that spontaneous male recombination in *D. ananassae* is influenced by different genetic factors. Hinton (1970) suggested that spontaneous male recombination is controlled by a dominant enhancer (E) which is mapped in the right arm of chromosome three and a dominant suppressor (S) located in the right arm of second chromosome. The presence of E, S or both was detected in a majority of marker strains as well as strains coming from natural populations. He also suggested presence of additional modifiers of male recombination. In one case, Hinton (1970) reported that the total recombination frequency of 31% in males was found to approach that of 34% in comparable females but the distribution of recombination within the marked region differed between males and females. Hinton (1974) found that F_1 males produced by reciprocal crosses between two strains showed recombination value of 5% or 0.3% studied in the third chromosome and this discrepancy was due to an extrachromosomal suppressor which is maternally transmitted depending upon a specific third chromosome for its maintenance. Tobari and Moriwaki (1983) presented evidence for correlation between minute mutation and male crossing over frequency. Minute mutation and crossing over frequency vary considerably among different strains and probably inducer and suppressor are responsible for both the traits (Tobari and Moriwaki 1983). It is interesting to note that a high recombination frequency in males is associated with high mutation frequency which extends evidence that both the traits are controlled by a series of inducers and suppressors which are preserved in natural populations of this species. Hinton (1983) tested the correlation between the factors affecting male crossing over and also involved in mutation process. He used a large number of stocks and found that in one combination of a dominant male crossover enhancer with a dominant mutator showed synergistic enhancement in both crossing over and minute mutation frequency which indicated the possibility that a single extrachromosomally transmitted element suppress both mutability and recombination.

Polygenic control of male recombination

A few researchers conducted artificial selection experiments to see the effects of directional selection on male crossing over, which might extend evidence for polygenic control of this phenomenon. Mukherjee (1961) conducted experiments to test the effects of directional selection on male recombination in this species while using third chromosome markers and he was successful in selecting a low line which was due to the effect of inversion. Kale (1968) also tested the effect of selection on male recombination value. He found significant difference in the frequency of male recombination values between high and low lines. The progressive increase was not significant but the effect of selection was genetic. Further, Kale did not know the karyotypic constitution of stocks used in the experiments. Mohanty and Singh (1992) also conducted selection experiments in both the directions (high and low) by using second chromosome marker strain and a wild-type strain which was constructed by crossing different karyotypically homozygous lines. Selection was continued for nine generations and separate lines were maintained: high, low and control. The mean recombination frequencies for nine generations was: 2.22, 0.70 and 1.20 for high, low and control lines, respectively. The values of realized heritability and regression coefficient also showed the effect of selection was positive on male recombination frequency. But the response of selection was more

pronounced in high line when compared to low line. The results reported by Mohanty and Singh (1992) clearly indicated that male crossing over in this species is under polygenic control.

Segregation distortion

The phenomenon of segregation distortion or meiotic drive has been studied in detail for *D. melanogaster* (Sandler and Novitski 1957: Sandler *et al.* 1959). It is caused due to SD mutant gene and occurs only in males. It leads to unequal segregation of two alleles in a heterozygote due to certain unusual mechanism during meiosis. However, segregation distortion reported in *D. ananassae* by Mukherjee and Das (1971) differs from *D. melanogaster* in certain important aspects. In *D. ananassae*, it was reported in a laboratory stock (px pc), and occurred in both sexes. Further, it affected the recovery of recombinant classes only without any effect on parental combinations. This unusual phenomenon in *D. ananassae* could not be explained on the basis of its occurrence in *D. melanogaster*. The *px* and *pc* marker strain was used in recombination experiments by Singh and Mohanty (1989) but their results did not confirm the findings of Mukherjee and Das (1971) although it was found that *pc* gene showed incomplete penetrance which affected segregation ratio for both recombinant and nonrecombinant classes. However, Mukherjee and Das (1971) suggested that it opens a new line of thought concerning high frequency of spontaneous male crossing over and its relation to segregation distortion.

Meiotic origin of recombination

Kale (1969) studied spontaneous crossing over in males of *D. ananassae* using four different wild-type strains from different localities of India. Interestingly, his results clearly demonstrated that it is meiotic in origin. It is the first demonstration of meiotic origin of spontaneous recombination in males of *D. ananassae* based on recombination data. Kale's results showed that positive males produced either equal numbers of crossovers in two marked regions or preferred either one region depending upon the strains used in the experiments. These results clearly indicated spermatocytic (meiotic) origin of recombinants in the experiments conducted by Kale (1969). Significant age effect depending on the strains was found in males with older age. Further, variation in the frequency of crossing over in different strains suggests that it is under genetic control. Crossing over was also induced in males by X-rays and the results suggested that recombinants originated in treated spermatocytes as there was equality in complementary crossovers from the individual males (Kale 1967a). Meiotic origin of crossing over was also shown when pupae were irradiated by X-rays (Kale 1967b).

Demonstration of presence of chiasmata during meiosis in males

Based on the genetic data, it was clearly demonstrated that spontaneous male recombination is meiotic in origin (Kale 1969). Attempts were made to study the presence of synaptonemal complex during meiosis in males of *D. ananassae*. Meyer (1960) reported that the synaptonemal complex was present in females but not in males. Similarly, Swift (1969) also could not observe synaptonemal complex in males. Grell *et al.* (1972) tried to identify synaptonemal complex in testes of male by electron microscopy (EM) but no synaptonemal complex was observed in any case. Similarly, Moriwaki and Tsujita (1974) also tried to study synaptonemal complex in prospermatocytes by EM. They observed the presence of axial filaments in the centre of each chromosome in leptotene and early zygotene cells but could not see the synaptonemal complex with typical tripartite structure similar to that found in pro-oocytes. They also reported that in zygotene cells homologous chromosomes form incomplete synapses with the aid of imperfectly developed synaptonemal complexes and considered that crossing over takes place between these imperfectly synapsed homologues. Hinton and Downs (1975) observed chiasmata in meiotic prophase of spermatocytes although they were not able to detect any relationship between meiotic chromosome behaviour and specific genes that regulates crossing over in males. For the first time, Matsuda *et al.* (1983) demonstrated the presence of chiasmata at a frequency capable of accounting observed recombination frequency while using wild-type strains as well as chromosomes 2 and 3 markers strains. They also found a unique series of iso-site aberrations in F_1 males and suggested that crossing over in males is meiotic in origin because of a parallelism between distribution pattern of chiasmata and iso-site aberrations. Matsuda *et al.* (1983) also suggested that male recombination, chiasma formation and chromosomal aberrations may be traits of hybrid dysgenesis syndrome which is extensively studied in *D. melanogaster* (Hinton 1981).

Genetic mosaic and mitotic recombination

In this species, while scoring the progeny of testcross between heterozygous males and homozygous females for the second chromosome recessive markers, Singh and Mohanty (1992) detected a spontaneous bilateral genetic mosaic which is first report of genetic mosaic for autosomal genes of the genus *Drosophila* (figure 1). The mosaic fly was a male but sterile. In the left side of the fly, all the three receive markers (*cu e se*) were expressed and in the right side, all the normal characters were expressed. Sex chromosome mosaics are known in *Drosophila* but in this case autosomal genes were involved. Mosaics may occur due to loss of chromosomes, mitotic recombination,

Figure 1. Spontaneous genetic mosaic in *D. ananassae* (reproduced from Singh B. N. and Mohanty S. 1992 A spontaneous genetic mosaic in *Drosophila ananassae*. *Curr. Sci.* **62**, 372–374)

chromosome inactivation etc. But for autosomes, loss of chromosomes may not be the cause because resulting cells will be inviable. The most probable cause of this mosaic as suggested by Singh and Mohanty (1992) is double mitotic recombination, occurring on both sides of centromere during first division of zygote and segregation of chromosomes was X-type (one parental and one recombinant on each side of pole).

Effects of heterozygous inversions on crossing over

Chromosomal polymorphism due to paracentric inversions is very common in *Drosophila* and is subject to natural selection (Singh 1994, 1998, 2001, 2008, 2010, 2013, 2018, 2019). Although, the population dynamics of inversion polymorphism has been studied in detail for a number of species that show intraspecies and interspecies variations in the degree and pattern of inversion polymorphism, the effects of inversions on crossing over have also been tested, which provides evidence for intrachromosomal and interchromosomal effects of inversions on crossing over in different species of *Drosophila* (for references see Singh and Singh 1987a, b, 1988a, b, 1990a, b; Singh 2008). In fact, inversions were detected for the first time by their suppressive effects on crossing over in *D. melanogaster* (Sturtevant 1926). Heterozygous inversions may suppress crossing over in the same chromosome but it may enhance the recombination rate in the other chromosomes (Singh and Singh 1987a, b; Singh and Mohanty 1991). Effects of inversions on crossing over has also been studied cytologically between linked inversions of the same chromosome (Singh 1973, 1974; Singh and Singh 1988b; Singh and Mohanty 1990). It has been found that recombination is strongly suppressed by the heterozygous inversions. Inversions influence crossing over in males of *D. ananassae* also which shows that spontaneous male recombination is meiotic in origin (Singh and Singh 1988a). Linked inversions may show linkage disequilibrium due to suppression of crossing over and founder effect (Singh and Singh 1990b).

Conclusion

The genus *Drosophila* is characterized by the absence of crossing over in males and gene mapping in different species has been done on the basis of female recombination data. However, crossing over has been reported in males of certain species of *Drosophila* but occurs at very low rate. Interestingly, *D. ananassae* is characterized by an appreciable level of spontaneous male recombination which is meiotic in origin. In this way, it is a unique species in the entire *Drosophila* genus (Singh 2018). Further, it is affected by different factors such as genetic factors, strain variation, age effect, cytoplasmic factors, heterozygous inversions, polygenenic control etc. It is clearly demonstrated that the spontaneous male recombination is meiotic in origin and occurs in spermatocytes. This conclusion is based on both genetic data (Kale 1969) and presence of synaptonemal complex during meiosis in males (Matsuda *et al.* 1983). Heterozygous inversions also affect male crossing over which lends support to the suggestion that it is meiotic in origin (Singh and Singh 1988a). In certain strains of different geographic origins, crossing over occurs at high rate and seems to approach the frequency found in females. Thus, *D. ananassae* is genetically unique species and more work is needed to understand the mechanism of this unique feature of *D. ananassae* (Matsuda *et al.* 1993).

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