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SPONTANEOUS CROSSING OVER IN MALES OF GENUS *Drosophila*

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ABSTRACT

Crossing over is a well documented genetic phenomenon reported to occur in sexually reproducing organisms.Through this process new combinations of genes are produced that form raw materials for evolution. The event of crossing over is programmed to happen in prophase-I of meiosis that is accomplished in the presence of dozens of proteins appearing in cascade manner. Any discrepancy in the execution of this event may be due to lack of certain protein/s indicating it to be completely under the genetic control. As a general concept, it is known that heterogametic sex shows less frequency of crossing over than homogametic sex. Genus *Drosophila*,a well esteemed model organism has been considered to study this event and it has been found that spontaneous male meiotic crossing over does not occur in this genus. A brief explanation is being provided through this article describing the species which show substantial amount of spontaneous male meiotic recombination.

KEYWORDS: Male crossing over, genus *Drosophila*

At the dawn of twentieth century, investigations in the field of genetics gained speedy leap to explore the mechanisms involved in the inheritance of parental traits to next generations. Mendelian pattern of inheritance was up to then verified not only in garden pea but in a number of plants and animals. Results not obeying the Mendelian ratio, 3:1 and 9:3:3:1 were being sought to understand the causes of deviation of such results. During the investigations, it was established that genes are located in a linear order on the chromosome and may be inherited to further generations as an intact structure or may get recombined by the genes of its homolog by the process of crossing over (Klug et al. 2006). This phenomenon was tested in plants and animals by considering mutant forms. By the time, *Drosophila* was being used as an efficient animal model organism by the then biologists, actively involved in the field of genetics.

Crossing over between genes present on homologous chromosomes during the meiotic division produces new combination of genes on the chromosome, which as a result produce enough genetic variability among the individuals of a population. This is a ubiquitous process that occurs all through the sexually reproducing diploid organisms (Nei, 1969;Vizir and Korol, 1990;Korol et al., 1994; Vazquez et al. 2002;Lenormand, 2003). Through the process of crossing over, new gene combinations are formed that form raw material for evolution to act. Therefore, the process of crossing over is of great evolutionary significance. However, if the rate of crossing over is very high between the genes, the formation of a stable combination of genes would be prevented and therefore, the overall amount of recombination must be adjusted to an optimum level for any genetic system (Darlington,1958).

A number of animal species were subjected to study this genetic phenomenon and the results showed that this event occurs in both the sexes, although the rate of recombination may not be equal in both. Based on experimental results, it was inferred that heterogametic sex shows lesser frequency of crossing over than homogametic sex. The results of many studies involving a number of species indicated lesser frequency of crossing over in individuals with heterogametic sex (Ved Brat, 1966;Vizir and Korol,1990;Burt et al., 1991;Lenormand and Dutheil, 2005). Haldane-Huxley rule states that when crossing over is absent from one sex, it tends to be the heterogametic sex (XY males or ZW females).They hypothesized that by shutting off recombination in the heterogametic sex, undesired crossover products between opposite sex chromosomes are avoided (Haldane, 1922; Huxley, 1928). The subject of recombination focusing on difference between the two sexes in different organisms was well taken by Lenormand (2003) and Lenormand and Dutheil (2005). The varying difference in the rate of recombination due to sex differences were discussed by Burt et al. (1991).Charlesworth and Barton (1996) described that genetic recombination may result lower fitness of progeny in *Drosophila*. They called this effect as recombination load and interpreted that this has to happen even if selection favors increased genetic recombination.

Morgan (1912, 1914) for the first time reported that crossing over does not occur in males of *Drosophila*

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melanogaster. Since then,this phenomenon was examined in several species of *Drosophila* and reports on spontaneous male recombination are available in *D. melanogaster* (Patterson and Suche, 1934), *D. ananassae* (Kikkawa, 1938; Moriwaki, 1940; Kale, 1969; Hinton, 1970; Singh and Singh, 1988), *D. simulans* (Woodruff and Bortolozzi, 1976), *D. virilis* (Kikkawa, 1935), *D. litoralis* (Coyne, 1988) and *D. willistoni* (Franca et al. 1968). However, the frequency of male crossing over is found to be very low in all these species in which this aspect has been tested except *D. ananassae* which exhibits substantial level of spontaneous male recombination.

Induced crossing-over

Various physical factors and chemical agents are known to induce crossing over in *Drosophila*. Ionizing radiation, temperature, a number of chemicals, physiological ageing, larval nutrition and presence of inversions have been experimentally tested factors that accelerate crossing over in F_1 males of *Drosophila* (Singh and Singh, 1990). These external agents induce the frequency of crossing over in males, even in those species where it is not reported to occur. In fact, the rate of crossing over can be induced in females by exposing or subjecting to external agents and this idea stimulated geneticists to see their effects in males too (Singh and Singh, 1990).

Spontaneous crossing over

Species which have been known to show spontaneous meiotic recombination are *D ananassae*,*D. bibectinata* and *D. melanogaster*. The following description states the reports on this phenomenon in them.

Drosophila ananassae

D. ananassae is one of the noticeable species in genus *Drosophila* owing to its several extraordinary characteristics (Singh, 2010). The most important one is the presence of spontaneous male meiotic crossing over occurring at an appreciable level (Kale, 1968;1969; Singh and Singh, 1986; 1987a, b; 1988a, b; 1989,1990;Mohanty and Singh, 1992). Exchange of chromosome segments between homologous chromosomes may occur even in somatic cells but the products of such events do not influence the next generation. However, mitotic recombination occurring in germ cells is a very rare phenomenon and is reported to occur in *Drosophila*. *D. ananassae* became the matter of curiosity because it revealed that crossing over in this species is meiotic in origin (Kale, 1969) and is controlled by various genetic factors such as enhancers, suppressors, polygenes and heterozygous inversions (Singh and Singh, 1987a, b; 1988a,b; 1990). Hinton (1970) reported that in certain strains of *D. ananassae*, the frequency of crossing over in males approaches to the frequency observed in females. Japanese biologists working in this field observed at cytological level and demonstrated that in F_1 males of *D. ananassae*, there is presence of substantial number of chiasmata capable of accounting normal recombination process (Matsuda et al. 1983).

D. ananassae shows spontaneous male meiotic crossing over at a considerable frequency (Kikkawa, 1938; Moriwaki, 1940; Kale, 1969; Singh and Singh, 1988a; b; c; Singh and Mohanty, 1990; 1991). It was the hard endeavour of Kale (1969) who performed extensive experiments to test whether the crossing over in *D ananassae* is mitotic or meiotic. Since he (Kale 1969) observed almost equal number of complementary crossovers, he was able to state that it is meiotic in origin. Two well recognized geneticists, Hinton (1970) and Moriwaki (Moriwaki et. al. 1970) working on the same issue at the same time also affirmed Kale's findings.To confirm that the recombinant types found due to crosses between F1 males and mutant females are the result of meiotic crossing over in *D. ananassae*, Matsuda et al. (1983) performed certain experiments to observe the presence of chiasmata and they were able to confirm its presence. This observation also confirmed meiotic origin of male crossing over in *D. ananassae*. The effects of heterozygous inversions on spontaneous male crossing over also authenticated it to be meiotic in *D. ananassae* (Singh and Singh, 1988a,b). The involvement of a single gene or polygenic control of male meiotic crossing over was also studied by Indian geneticists (Mukherjee, 1961; Kale, 1968; Mohanty and Singh, 1992) who repoted the occurrence of positive response to selection for high and low spontaneous male recombination in *D. ananassae* extending evidence for polygenic control of this genetical process.

Drosophila bipectinata

D. bipectinata is a well known species inhabiting Indian subcontinent. It is a member of the *bipectinata* species complex of the *ananassae* subgroup of the *melanogaster* species group (Bock and Wheeler 1972).Indian cytogeneticists selected this species for its population genetics studies (Gupta and Panigrahy, 1990; Singh and Singh, 2001).Singh and Banerjee (1997) tested spontaneous male recombination in *D. bipectinata*by employing its double recessive mutant stock and a number of wild type stocks coming from different geographic origins.

Spontaneous recombination in males of *D.bipectinata* was tested in five wild type laboratory stocks of different geographic origins by using sepia eye and black body colour double recessive mutant stock by Singh and Banerjee, (1997). Their results indicated that *D.bipectinata* exhibits spontaneous male recombination. Their study also indicated inters-train variation with respect to the rate of male crossing-over.

Drosophila melanogaster

In fact ,*D. melanogaster* is one of the popular species of this genus that has credit to be utilized maximally for genetical research. Any text book of genetics describing gene mapping devotes a complete page depicting the arrangement of mutant genes on the haploid set of its chromosomes. This has been possible by the perseverant efforts of a number of researchers who made crosses between normal and mutant flies and tried to decipher the position of mutant genes. Due to polytene chromosomes in this species, deletion mapping has also been of immense help to map the genes on the chromosomes. By employing conventional methods of making crosses, a number of linked genes were scrutinized for the frequency of crossing over among them to map their position on the chromosomes in *D. melanogaster*. F_1 females obtained from the cross between wild and mutant flies were only showing crossing over where as F1 males of such crosses did not produce recombinant. Similar experiments conducted in some more species also provided similar results. This made the then geneticist to conclude that crossing over does not occur in males of *Drosophila*. However, in later experiments some recombinants did appear in *D. melanogaster*, but the rate of recombination was very low. Based on the clustered appearance of recombinant types, it was suggested that male crossing over in *D. melanogaster* is mitotic in origin (Whittinghill, 1947). Ramel (1962) tested the effect of inversions on crossing over and reported that mitotic crossing over is not influenced by heterozygous inversions. Sinclair and Grigliatti (1985) also explained pre-meiotic origin of recombination in *D. melanogaster* males associated with hybrid dysgenesis. Gethmann (1988) described that different species of insects coming under order Diptera show a low frequency of mitotic recombination in heterogametic sex. Grishaeva and Bogdanov (2000) discussed genetic control of meiosis in *Drosophila melanogaster*. They explained the role of more than 80 genes controlling meiosis and meiotic recombination in this species. In *Drosophila* males, the lateral alignment of chromosomes during synapsis does not occur and their chromosomes segregate in meiosis I following the "touch-and-go" principle (Grishaeva and Bogdanov, 2000). The role of various proteins and the molecular mechanism operating this event are published time to time (Bickel et al. 1996; Manheim and 2003; McKee, 2004;Nasmyth andHaering, 2009; Tsai et al. 2011).

CONCLUSIONS

Whenever there is a discussion on the aspect of crossing over, a well familiar science phrase “crossing over does not occur in *Drosophila* male” is most often cited by biologists. In fact, male crossing over occurs exceptionally in very few species of this genus. The essential component of proteins (structural and enzymes) needed to accomplish this process lack in all those species in which crossing over is not recorded. Whereas, all those species which show appreciable amount of crossing over are known to express such proteins in the F_1 males that are essential for this process. Advances in the field of molecular cell biology have enabled the biologists to understand the molecular events occurring at the time of eukaryotic recombination and the various proteins or factors which appear at different stages of Prophase-1 of meiotic cell division. The proteins appearing particularly during zygotene and pachytene between the non-sister chromatids of homologous chromosomes are of special significance. Their presence in F1 male of different *Drosophila* species would indicate the role of genes involved in the molecular mechanism of crossing over in *Drosophila*.

Even those species which show appreciable frequency of crossing over in males may be showing lesser frequency of recombination compared to their respective heterozygous females. Species like *D. ananassae* is exceptionally different from other species because it’s some of the strains show the rate of crossing over equal to females.

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